Nutrition of the Rabbit

2nd Edition

Edited by Carlos de Blas and Julian Wiseman
Nutrition of the Rabbit, 2nd Edition

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1 The Digestive System of the Rabbit

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1.1 Introduction

The digestive system of the rabbit is characterized by the relative importance of the caecum and colon when compared with other species (Portsmouth, 1977). As a consequence, the microbial activity of the caecum is of great importance for the processes of digestion and nutrient utilization, but also in the control of digestive pathologies. Furthermore, caecotrophy, the behaviour of ingestion of soft faeces of caecal origin, makes microbial digestion in the caecum more important for the overall utilization of nutrients by the rabbit. Additionally, the rabbit has developed a strategy of high feed intake (65–80 g kg⁻¹ body weight (BW)) and a rapid transit of feed through the digestive system to meet nutritional requirements.

To reach its full functional capacity, the digestive system of the growing rabbit must go through a period of adaptation from milk-base feeding to the sole dependence on solid feed. This adaptation process not only affects the digestion processes, but also microbiota colonization and the development of gut barrier mechanisms that protect the animal against digestive pathologies. This chapter: (i) gives a general and brief description of the morphological and functional characteristics of the digestive system of the rabbit that may be important for understanding the digestive processes explained in the following chapters; and (ii) explains how these characteristics change from the time of weaning until attainment of maturity.

1.2 The Digestive System of the Rabbit

The first important compartment of the digestive system of the rabbit is the stomach; this has a very weak muscular layer and is always partially filled. After caecotrophy the fundic region of the stomach acts as a storage cavity for caecotrophes. Thus, the stomach is continuously secreting and the pH is acid. The stomach pH ranges from 1 to 5, depending on site of determination (fundus versus cardiac-pyloric region) (Gutiérrez et al., 2002, 2003; Chamorro et al., 2007; Orengo and Gidenne, 2007; Gómez-Conde et al., 2009), the presence or absence of soft faeces (Griffiths and Davies, 1963), the time from feed intake (Alexander and Chowdhury, 1958) and the age of the rabbit (Grobner, 1982). The lowest figures (from 1 to 2.5) are determined in the cardiac region, in the absence of soft faeces, after 4 h of diet ingestion and in rabbits older than 3 weeks with low presence of milk (Orengo and Gidenne, 2007). The capacity of the stomach is about 0.34 of the total capacity of the digestive system (Portsmouth, 1977). The stomach is linked with a coiled caecum.
by a small intestine approximately 3 m long, where the secretion of bile, digestive enzymes and buffers occurs. The pH of the small intestine is close to 7 (Vernay and Raynaud, 1975; Nicodemus et al., 2002). The small intestine is the site where the greater part of digestion and absorption take place by passive or active transportation throughout the mucosa. Digestibility at the end of the ileum accounts for 0.8–1 of the total dietary amino acid and starch digestibility (Gutiérrez et al., 2002; García et al., 2005; Carabaño et al., 2009).

The caecum is characterized by a weak muscular layer and contents with a dry matter (DM) of 200 g kg⁻¹. The caecal contents are slightly acid (pH 5.4–6.8) (García et al., 2002). The capacity of the caecum is approximately 0.49 of the total capacity of the digestive tract (Portsmouth, 1977). The colon can be divided in two portions: the proximal colon (approximately 35 cm long) and the distal colon (80–100 cm long). The proximal colon can be further divided into three segments: the first segment possesses three taeniae with haustra between them; the second segment has a single taenia covering half of the circumference of the digestive tube; and the third segment or fusus coli has no taeniae or haustra, but is densely enervated. Thus, it acts as a pacemaker for the colon during the phase of hard faeces formation (Snipes et al., 1982).

Other tissues are also associated with the gut. Gut-associated lymphoid tissue (GALT) and specialized cells (goblet or Paneth cells, responsible for mucus and antimicrobial peptide secretion, respectively) regulate the interaction of the gut mucosa with the microbiota and develop the mechanisms of tolerance and protection against pathogens. The gut barrier function has been recently reviewed by Forthun-Lamothe and Boullier (2007) and Carabaño et al. (2008).

### 1.3 Age-related Changes in the Morphology and Function of the Digestive System

The different segments of the digestive system of the rabbit grow at different rates until reaching maturity. The development of the digestive tract begins in the fetal stage; at birth, the stomach and small intestine are the main components of digestive tract. According to Toofanian and Targowski (1982) and Sabatakou et al. (1999), the stomach glands are evident in late fetuses (26 days’ gestation) and true villi and intestinal glands (crypts of Lieberkühn) are observed at 29 days’ gestation. At birth, however, the intestine of the newborn does not possess all of the mucosal constituents that are present in the adult. These appear in the first week of age (Brunner’s glands in the duodenum) and the adult morphology is not completed until 20 days of age.

The developmental pattern follows a cranio-caudal gradient. The early development of these two segments is important to ensure the survival of the newborn (Fig. 1.1a). From birth to 18–20 days of age, kits drink large amounts of milk during a once-daily nursing, an amount that can reach 0.12 of their BW. This explains the importance of the relative weight of the stomach when its contents are also recorded (Fig. 1.1b). At around 18 days of age the suckling rabbit begins to eat solid food and decrease its milk intake (see Chapter 13 for more details) and the caecum and colon develop faster than the rest of the digestive tract (Fig. 1.1a). The fast growth of the caecum during this period is more evident if the caecal contents are included (Fig. 1.1b). From 3 to 7 weeks of age the caecum is filled by digesta and microbiota, and its contents reach a peak of about 0.06 to total BW at 7–9 weeks of age. The pH of the caecum is also affected by age and decreases from 6.8 at 15 days of age to 5.6 at 50 days of age (Padilha et al., 1995).

The study of the evolution of the functionality of the intestinal mucosa and pancreas is important to understand the ability of the animals (mainly around weaning) to digest substrates other than milk. There has been much effort in the last 10 years to clarify this subject, but some discrepant results remain (Tables 1.1 and 1.2). Differences in the management of animals before sampling (fast or free access to feed, type of diet), the interval of age studied, type of sample analysed (digesta, tissue or serum), place in the intestinal tract (duode-
num, jejunum or ileum), time of slaughter (morning or evening), enzymatic methodology (specificity of substrate, time, pH and temperature of the reaction) and unit used to express the activity (IU per mg of protein or mg of tissue or mg digestive content, etc.) may partially explain these discrepancies and make it difficult to give clear conclusions to formulate adequate post-weaning diets.

During the suckling period, the mucosal glands are able to produce enzymes to digest the main components of the milk, while the maturity and functionality of the pancreas are limited when compared with the adult. In this period, gastric lipase represents most of the lipolytic activity of the whole digestive tract, whereas this activity is not detectable in the 3-month-old rabbit (Marounek et al., 1995). Lactase activity is highest until 25 days of age, and sucrase and maltase rise until reaching the adult level at around 28–32 days (Gutiérrez et al., 2002; García Rebollar et al., 2004; Gallois et al., 2008b). The main proteolytic activity is also localized in the stomach of the young rabbit and its importance decreases with age as proteolytic activity in the caecum, colon and pancreas increases (Marounek et al., 1995). There is common agreement that the functionality of the digestive tract is limited from 21 to 42 days of age for amylase and lipase secreted by the pancreas and some enzymes of the gastric or intestinal mucosa; however,
protease activity is unclear. These findings are in line with the evolution of the pancreas, which greatly increases in weight when the animals begin to eat solid feed (Lebas et al., 1971), and the development of intestinal morphology (Gallois et al., 2008a). However, this limited enzymatic capacity allows young rabbits (35 days old) to digest 0.9–0.96 of starch by the end of the ileum (Gutierrez et al., 2002; Gómez-Conde et al., 2007).

Other enzyme activities that increase markedly with the age of the rabbit are those due to the presence of microorganisms that will determine the ability of the rabbit to utilize fibre sources. Cellulase, pectinase, xylanase and urease are some of the main enzymes provided by the intestinal microflora.

The major age-related changes in the morphologic and functional maturation of the digestive tract seem to be associated with the change from milk to solid food in the feeding pattern of the young rabbit. Furthermore, a higher solid-feed intake in this transition period leads to better growth performance and lower mortality in the growing period (Pascual, 2001). This has increased the interest in studying the effect of an improvement in solid-feed intake by different management techniques such as weaning or modulating the litter size. The

| Table 1.1. Evolution with the age of pancreatic enzymes, according to several authors. |
|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| Enzyme         | Sampling place | 7–21           | 21–45          | 45–90           | 90–180          |
| Amylase        | Pancreas       | ▲              | ▲              | ▲              | ▲              |
|                | Pancreas       | ▲              | ▲              | ▲              | ▲              |
|                | Pancreas       | ▲              | ▲              | ▲              | ▲              |
|                | Intestinal     | ▲              | ▲              | ▲              | ▲              |
|                | content        |                |                |                |                |
|                | Jejunum        | ▲              |                |                |                |
|                | Ileum          |                |                |                |                |
| Lipase         | Pancreas       | ▲              | ▲              | ▲              | ▲              |
|                | Pancreas       | ▲              | ▲              | ▲              | ▲              |
|                | Intestinal     | ▲              | ▲              | ▲              | ▲              |
|                | content        |                |                |                |                |
| Trypsin        | Pancreas       | ▲              | ▲              | ▲              | ▲              |
|                | Pancreas       | ▲              | ▲              | ▲              | ▲              |
|                | Intestinal     | ▲              | ▲              | ▲              | ▲              |
|                | content        |                |                |                |                |
| Chymotrypsin   | Pancreas       | ▲              | ▲              | ▲              | ▲              |
|                | Pancreas       | ▲              | ▲              | ▲              | ▲              |
| Proteases      | Intestinal     | ▲              | ▲              | ▲              | ▲              |

=, ▲, ▼, ▼: enzyme activity remains constant, increases or decreases, respectively, in each period.

1, Lebas et al. (1971); 2, Corring et al. (1972); 3, Blas (1986); 4, Marounek et al. (1995); 5, Dojanã et al. (1998); 6, Scapinello et al. (1999); 7, Gutierrez et al. (2002); 8, Debray et al. (2003); 9, Sabatakou et al. (2007); 10, Gallois et al. (2008b).
The Digestive System of the Rabbit

5

effect of age at weaning (from 21 to 35 days) seems to have little influence on the morphology and enzymatic activity in the upper tract (stomach and small intestine) (Corring et al., 1972; Scapinello et al., 1999; Gallois et al., 2005, 2008b). On the other hand, some authors (Gutierrez et al., 2002; Gómez-Conde et al., 2007) have observed villous atrophy accompanied by a reduction of brush border enzymes in 35-day-old rabbits weaned at 25 days compared with suckling rabbits of the same age. However, these problems seem to be dependent on the composition of the weaning diet. The inclusion of moderate levels of soluble fibre in the diet seems to be enough to avoid these problems (Gallois et al., 2005, 2008b; Alvarez et al., 2007; Gómez-Conde et al., 2007). The effects of weaning on the maturation of the caecum and colon seem to be positive. Early weaning increases the weight of the organs and their contents, encourages microbiota colonization (quantity and type of bacteria), promotes fermentative activity and accelerates the maturation of GALT (Piattoni and Maertens, 1999; Niza et al., 2001; Gutierrez et al., 2002; Xiccato et al., 2003; Gallois et al., 2005, 2008a; Carabaño et al., 2008; Kovács et al., 2008).

1.4 Development of the Immune Response: the Gut-associated Lymphoid Tissue

At birth, the rabbit immune system is immature. B-cell lymphogenesis begins in the fetal liver and omentum before switching to the bone marrow, where immunoglobulin (Ig) rearrangement has been described at around 12 days’ gestation (Mage et al., 2006). As maternal Ig levels decrease (at a few weeks after birth), B cells are transported from the liver and the bone marrow to the GALT, where somatic diversification and expansion of Ig genes takes place. In the rabbit, the GALT comprises an organized lymphoid tissue that consists of Peyer’s patches, the appendix and the sacculus rotundus, and a diffuse

### Table 1.2. Evolution with age of gastric and intestinal mucosa, according to several authors.

<table>
<thead>
<tr>
<th>Enzyme</th>
<th>Sampling place</th>
<th>Age (days)</th>
<th>Unit</th>
<th>Ref.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pepsin</td>
<td>Gastric mucosa</td>
<td>7–21</td>
<td>▲▲</td>
<td>IU g⁻¹ tissue</td>
</tr>
<tr>
<td></td>
<td></td>
<td>21–45</td>
<td>▲</td>
<td>IU g⁻¹ protein</td>
</tr>
<tr>
<td></td>
<td></td>
<td>45–90</td>
<td>▲</td>
<td>IU g⁻¹ tissue</td>
</tr>
<tr>
<td></td>
<td></td>
<td>90–180</td>
<td>▲</td>
<td>IU g⁻¹ protein</td>
</tr>
<tr>
<td>Lactase</td>
<td>Mucosa jejenum</td>
<td>▼</td>
<td>IU g⁻¹ protein</td>
<td>1</td>
</tr>
<tr>
<td>Mucosa jejenum</td>
<td>▼</td>
<td>IU g⁻¹ protein</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Maltase</td>
<td>Mucosa jejunum</td>
<td>▼</td>
<td>IU g⁻¹ protein</td>
<td>3</td>
</tr>
<tr>
<td>Mucosa jejunum</td>
<td>▼</td>
<td>IU g⁻¹ protein</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>Mucosa jejunum</td>
<td>▼</td>
<td>IU mg⁻¹ tissue</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>Jejunum</td>
<td>▼</td>
<td>IU g⁻¹ protein</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>Intestinal content</td>
<td>▼ ▼ ▼</td>
<td>IU g⁻¹ protein</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Sucrose</td>
<td>Mucosa jejenum</td>
<td>▼</td>
<td>IU g⁻¹ protein</td>
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<tr>
<td>Mucosa jejenum</td>
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<td>IU g⁻¹ protein</td>
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</tr>
<tr>
<td>Jejunum</td>
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</tr>
<tr>
<td>Duodenum</td>
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<td>IU g⁻¹ protein</td>
<td>7</td>
<td></td>
</tr>
<tr>
<td>Jejunum</td>
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<td>IU g⁻¹ protein</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td>Stomach content</td>
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<td>IU g⁻¹ tissue</td>
<td>9</td>
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<tr>
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</tr>
<tr>
<td>Mucosa jejenum</td>
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<td>IU mg⁻¹ tissue</td>
<td>12</td>
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<tr>
<td>Jejunum</td>
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<td>IU g⁻¹ protein</td>
<td>13</td>
<td></td>
</tr>
<tr>
<td>Intestinal content</td>
<td>▼ ▼ ▼</td>
<td>IU g⁻¹ protein</td>
<td>14</td>
<td></td>
</tr>
<tr>
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<tr>
<td>Mucosa jejenum</td>
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<td>IU g⁻¹ protein</td>
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<td></td>
</tr>
<tr>
<td>Jejunum</td>
<td>▼</td>
<td>IU g⁻¹ protein</td>
<td>17</td>
<td></td>
</tr>
<tr>
<td>Duodenum</td>
<td>▼</td>
<td>IU g⁻¹ protein</td>
<td>18</td>
<td></td>
</tr>
<tr>
<td>Jejunum</td>
<td>▼</td>
<td>IU g⁻¹ protein</td>
<td>19</td>
<td></td>
</tr>
</tbody>
</table>

=, ▲, ▼: enzyme activity remains constant, increases or decreases, respectively, in each period.

1, Marounek et al. (1995); 2, Dojanã et al. (1998); 3, Gutiérrez et al. (2002); 4, Debray et al. (2003); 5, García Rebollar et al. (2004); 6, Gallois et al. (2008b).
form represented by the lamina propria and intraepithelial lymphocytes (Carabaño et al., 2008). Therefore, the primary antibody repertoire is generated and developed between 4 and 8 weeks of age in the GALT (especially in the appendix) in response to the host interaction with the intestinal microbiota (Lanning et al., 2004; Mage et al., 2006). Intestinal bacteria are thus necessary for the rabbit immune system as they promote GALT development and the somatic diversification of Ig (Rhee et al., 2004). However, the bacterial species that trigger immune system development and the mechanisms they use remain to be elucidated. In this regard, research has identified Bacteroides fragilis and Bacillus subtilis (two members of the normal rabbit intestinal microflora) as inducers of GALT development and primary antibody repertoire diversification (Mage et al., 2006). Moreover, the mechanisms used by these bacterial species to drive GALT development and somatic diversification of Ig genes are not mediated by antigen interactions (Rhee et al., 2004). They seem to be induced by a B-cell superantigen through a direct interaction with the B-cell receptor or through stimulation of the innate immune system via Toll-like receptors (Rhee et al., 2004). In addition, the cytokine environment produced after the activation of macrophages and dendritic cells by bacterial products (e.g. lipopolysaccharide) may be another possible way of developing the immune repertoire (Rhee et al., 2004).

Bacterial translocation occurs spontaneously in the newborn rabbit, reaching a maximum at 6 days of age. By this time, the GALT begins to develop limited bacterial passage (Urao et al., 1996). The commensal flora starts to develop during the lactation stage, but the fermentative area only begins to grow after feed consumption. Dasso et al. (2000) reported that the follicular area in the appendix increases between 3 and 6 weeks after birth, and maintains the same relative importance until the adult stage. The proliferative area of the follicles also reached a maximum at 6 weeks and the proportion of total lymphocytes and the proportion of B cells in lamina propria increased in rabbits between 19 and 26 days of age (Campín et al., 2003; Carabaño et al., 2008). In this regard, weaning can accelerate the maturation of the immune system and its functionality, as a larger follicular area in the appendix and increased lymphocyte numbers in lamina propria have been recorded in rabbits weaned at 25 days (Carabaño et al., 2008). However, it is important to take into account that, at weaning, the immune system is not fully developed. An immature immune system together with the stress associated with weaning and the decrease in milk intake that confers protective Ig and bactericidal nutrients (peptides, short-chain fatty acids) might challenge rabbit’s health status (Gallois et al., 2007; Skrivanová et al., 2008; Romero et al., 2009).

Specific to the rabbit is suppression of B lymphopoiesis with age. This is reversibly arrested by 4 months (Kalis et al., 2007). Thus, the secondary antibody repertoire of the adult rabbit is developed by the expansion of specific B cells and somatic mutation of Ig genes in response to specific antigens at the secondary lymphoid organs (Lanning et al., 2000).

### 1.5 The Role of the Intestinal Flora in the Digestion and Absorption of Nutrients

The presence of the microbial population in the caecum, together with caecotrophy, permits the rabbit to obtain additional energy, amino acids and vitamins. The main genus of the microbial population in the caecum of the adult rabbit is Bacteroides (Gouet and Fonty, 1973), which comprises $10^9–10^{10}$ bacteria g$^{-1}$. Other genera such as Bifidobacterium, Clostridium, Streptococcus and Enterobacter complete this population to give a bacterial load of $10^{10}–10^{12}$ bacteria g$^{-1}$ (Bonnanfous and Raynaud, 1970; Gouet and Fonty, 1979; Forsythe and Parker, 1985; Penney et al., 1986; Cortez et al., 1992). However, more recent research, based on
molecular techniques, has shown that the complexity of the gut microbiota is greater than was previously described with classical approaches (Bennegadi et al., 2003; Badiola et al., 2004; Abecia et al., 2005). With these studies, it can be inferred that, as expected, the majority (0.66) of the components of the rabbit microbiota is unknown/uncultured and that bacteria only represent 0.40 of the total microbiota in young rabbits (18 days old), increasing their importance (0.80–0.90) when the animals begin to eat solid food. The use of molecular techniques has allowed an understanding of the importance of the transmission of the whole microbiota to the youngster through the mother and its evolution with age or the influence of nutrients in the development of digestive diseases (Carabaño et al., 2006; Gidenne et al., 2008). However, more information is needed to describe the bacterial community in the gastrointestinal tract of rabbits.

The role of the whole microflora community in the digestive processes can also be evaluated by its enzymatic activity or the end products of fermentation. The presence of cellulolytic bacteria in the caecum of the rabbit had been indicated by Hall (1952) and Davies (1965). Later, Emaldi et al. (1979) studied the enzymatic activities of the microflora and indicated that the main activities were, in decreasing order, ammonia use, ureolytic, proteolytic and cellulolytic. The great importance of other activities (i.e. xylanolytic, pectinolytic, mucolytic) has been indicated in studies conducted by Forsythe and Parker (1985), Marounek et al. (1995) and Sirotek et al. (2003). Forsythe and Parker (1985) estimated populations of $10^8$ and $10^9$ xylanolytic and pectinolytic bacteria g$^{-1}$, respectively.

The composition of the microflora does not remain constant throughout the life of the rabbit and is strongly influenced by the time of weaning (Padilha et al., 1995). During the first week of age, the digestive system of the rabbit is colonized by strict anaerobes, predominantly Bacteroides. At 15 days of age, the numbers of amylolytic bacteria seem to stabilize, whereas those of colibacilli decrease as the numbers of cellulolytic bacteria increase (Padilha et al., 1995). Milk intake may delay the colonization by cellulolytic flora, but does not seem to affect the evolution of the colibacilli population (Padilha et al., 1996). As a consequence of age-related changes in the microbial population, the production of volatile fatty acids (VFAs) increases with age (Bellier et al., 1995; Padilha et al., 1995). Moreover, as caecotrophy is initiated, the presence of bacteria of caecal origin can be detected. Smith (1965) and Gouet and Fonty (1979) were able to detect precaecal microbial flora after only 16 and 17 days of age, respectively. The presence of these precaecal microbes is dependent on caecotrophy, with high counts after caecotrophy and no viable cells after 5–6h (Jilge and Meyer, 1975). The composition of the microflora does not remain constant during the life of the rabbit.

As a result of the fermentative activity of the microflora, VFAs are produced in the proportion of 60–80 mol of acetate, 8–20 mol of butyrate and 3–10 mol of propionate 100 mol$^{-1}$ of VFAs (García et al., 2002). However, these proportions change with the time of the day, as described in the caecotrophy section of this chapter (see section 1.6), and with the developmental stage of the rabbit, with increases in the acetate concentration from 15 to 25 days of age and a reversal of the propionate to butyrate ratio from 15 to 29 days of age (Padilha et al., 1995). The potential of modification of VFA production by dietary changes will be described in the following chapters of this book. According to Marty and Vernay (1984), VFAs can be metabolized in the hindgut tissues, with butyrate being the preferred substance for the colonocytes. The liver is the main organ metabolizing absorbed propionate and butyrate. However, acetate is available for extrahepatic tissue metabolism. It is estimated that the rabbit obtains up to 0.40 of its maintenance energy requirements from VFAs produced by fermentation in the hindgut (Parker, 1976; Marty and Vernay, 1984).
1.6 Caecotrophy

1.6.1 Patterns of daily feed intake and soft faeces excretion

Soft faeces are excreted according to a circadian rhythm, which is the opposite to that of feed intake and hard faeces excretion. Caecotrophy occurs mainly during the light period, whereas feed intake and hard faeces excretion occur during darkness (Lebas and Laplace, 1974, 1975; Fioramonti and Ruckebush, 1976; Ruckebush and Hörnicke, 1977; Battaglini and Grandi, 1988; Merino, 1994; Bellier et al., 1995; Bellier and Gidenne, 1996; El-Adawy, 1996; Orengo and Gidenne, 2007). Figure 1.2 shows the pattern of soft faeces excretion and feed intake for adult rabbits under a schedule of 12 h light/12 h dark and ad libitum access to feed (Carabaño and Merino, 1996). Most of the rabbits showed monophasic patterns of soft faeces excretion from 08.00 to 17.00 h, with a maximum at 12.00 h. However, 0.25 of rabbits showed a diphasic pattern, with a second period of excretion during the night. The occurrence of diphasic patterns is more frequent when the length of the light period is reduced. Under continuous light conditions (24 h) caecotrophy runs freely and monophasically (Jilge, 1982). During the caecotrophy period, lasting from 7 to 9 h, there is an absence of hard faeces excretion and the feed intake is low.

Feed intake and hard faeces excretion occur along the complementary period, showing two phases. Feed intake increases from 15.00 to 18.00 h and then remains high until 24.00 h (Fig. 1.2). After this period, rabbits reduce feed intake until 02.00 h and then a new phase starts, with a maximum at 06.00 h. The second phase finishes at 08.00 h. Hard faeces excretion (from 18.00 to 08.00 h) shows a similar pattern, with two maxima at 24.00 and 06.00 h.

Age, physiological status and restricted access to feed can alter this pattern. Bellier et al. (1995) observed that weaned rabbits (6 weeks old) show a greater incidence of diphasic patterns and a longer caecotrophy period than adults (14 weeks old): from 04.00 to 12.00 h and from 22.00 to 24.00 h versus from 08.00 to 14.00 h, respectively. Lactating does show a different pattern of excretion from that described previously for non-lactating adult rabbits. During the lactation period, does exhibit an alternated rhythm of soft and hard faeces excretion. Caecotrophy occurs during two periods, from 02.00 to 09.00 h (0.40 of total excretion) and from 13.00 to 17.00 h (0.60 of total excretion), with a lack of excretion from 09.00 to 13.00 h (Lorente et al., 1988). This pattern could be mainly related to the maternal behaviour of does through the morning rather than to physiological status.

All of the experiments described above were carried out with ad libitum access to feed. When the feeding regime is changed from ad libitum to restricted access to feed, the rhythm of excretion is profoundly altered, whatever the length of the light period.

![Fig. 1.2. Soft faeces excretion and dry matter (DM) intake throughout the day (Carabaño and Merino, 1996).](image-url)
period. In this situation, the time of soft faeces excretion depends on the time of feed distribution (Fioramonti and Ruckebush, 1976). Disruption of the internal cycle may have important practical implications. Lebas and Laplace (1975) recommended distributing the feed once per day late in the afternoon. In other scenarios (e.g. one meal at 09.30 h or two meals at 09.30 and 16.30 h), changes in faecal excretion patterns and a lower growth rate should be expected.

1.6.2 Determination of soft faeces excretion and consumption

Several authors have tried to explain the physiological mechanisms that determine the differentiation and recognition of the two types of faeces in rabbits, according to the circadian patterns described above. The results obtained allow a partial understanding of the complex regulation of this behaviour.

Differentiation between soft and hard faeces begins during the transit of digesta through the caecum and proximal colon. From the results obtained by Björnhag (1972) and Pickard and Stevens (1972) it can be assumed that the formation of hard faeces is not by resorption of some components of caecal contents in the colon, but by mechanical separation of the different components of digesta. During hard faeces excretion, water-soluble substances and fine particles (<0.3 mm in diameter, including microorganisms) are brought back to the caecum by means of antiperistaltic movements and retrograde flow. Coarse particles (>0.3 mm in diameter) pass to the distal part of the colon. In contrast, the motility of both the caecal base and the proximal colon decreases during the formation of soft faeces (Ruckebush and Hörnicke, 1977). Endogenous prostaglandins (PGs) play an important role in the motor function involved in soft faeces formation. The infusion of both PGE\textsubscript{2} and PGF\textsubscript{2α} inhibits proximal colon movements, stimulates the distal colon and is followed by soft faeces production (Pairet et al., 1986). Changes in VFA concentrations and caecal pH occurring after a meal have been proposed as primary signals leading to a period of soft faeces excretion. Ruckebush and Hörnicke (1977) observed soft faeces excretion after an intracaecal infusion of VFAs in rabbits with restricted access to feed. However, postprandial VFA variations are not so evident in rabbits fed ad libitum, and therefore factors other than those mentioned above could also be implicated. Structures that are typically involved in feed intake regulation, such as the lateral hypothalamus and hypothalamic ventromedial nodes, do not seem to have the same roles as those described in other non-ruminant species. Damage to these structures does not imply changes in feed intake behaviour in rabbits (Gallouin, 1984).

During soft faeces excretion, the caecal contents are covered by a mucous envelope secreted at the proximal colon according to the described circadian rhythms. Therefore, the soft faeces consist of small pellets of 5 mm diameter that rabbits can recognize. Soft faeces are taken directly from the anus, swallowed without mastication and stored intact in the fundus of the stomach for 3–6 h (Gidenne and Poncet, 1985). The mechanisms of recognition are unclear. The special smell of soft faeces compared with that of hard faeces or the existence of mechano-receptors in the rectum have been proposed as factors involved in the reingestion of soft faeces. However, results obtained from rabbits deprived of olfactory bulbs and with an artificial anus that bypasses the rectum show that rabbits are still able to recognize and reingest soft faeces (Gallouin, 1984).

1.6.3 Nutritional implications

Caecotrophy in rabbits does not occur as a response to a nutritional imbalance, but represents a specialized digestive strategy. Caecotrophy begins at 3–4 weeks of age, when rabbits begin to consume solid food. In postweaned rabbits (4 weeks old), soft faeces production linearly increases with age, reaching a maximum at 63–77 days old (25 g DM day\textsuperscript{−1}). This period corresponds to the maximum growth requirements and to the greatest increment in feed intake. From 77 to 133
The marked circadian rhythms of caecotrophy and feed intake imply changes in both

1.7 Methodological Implications of Caecotrophy on Physiological Research Work

As a consequence of the mechanical separation of digesta at the caecum and proximal colon, the chemical composition of soft faeces is similar to that of the caecal contents but quite different from that of hard faeces (Table 1.3). Soft faeces contain greater proportions of protein, minerals and vitamins than hard faeces, while hard faeces are higher in fibrous components compared with soft faeces. As far as nutrient supply through soft faeces is concerned, protein represents from 0.15 to 0.22 of the total daily protein intake in growing rabbits and lactating does. The protein of soft faeces is high in essential amino acids such as lysine, sulphur amino acids and threonine (Proto, 1976; Spreadbury, 1978; Nicodemus et al., 1999; García et al., 2004), which represent from 0.10 to 0.23 of total intake. Belenguer et al. (2005) and Abecia et al. (2007) reported similar contributions of microbial lysine in body and milk proteins. This contribution came through the intake of soft faeces and a small direct intestinal absorption was observed. The importance of these amino acids depends on the efficiency of microbial protein synthesis. The proportion of microbial protein with respect to total protein of soft faeces varies with the diet from 0.30 to 0.68 (Spreadbury, 1978; García et al., 1995; García et al., 2005). Microbial activity is also responsible for the high content of K and B vitamins in soft faeces.

In conclusion, caecotrophy could overcome poor quality protein or low vitamin diets in traditional rearing conditions, but it is necessary to supply extra B vitamins, minerals and limiting amino acids in intensive rearing conditions.

Table 1.3. Average chemical composition of caecal contents and soft and hard faeces.

<table>
<thead>
<tr>
<th></th>
<th>Caecum</th>
<th>Soft faeces</th>
<th>Hard faeces</th>
<th>Ref.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dry matter (g kg⁻¹)</td>
<td>200</td>
<td>340</td>
<td>470</td>
<td>3, 4, 5, 6, 7</td>
</tr>
<tr>
<td>Crude protein (g kg⁻¹ DM)</td>
<td>280</td>
<td>300</td>
<td>170</td>
<td>3, 4, 5, 6, 7</td>
</tr>
<tr>
<td>Crude fibre (g kg⁻¹ DM)</td>
<td>170</td>
<td>180</td>
<td>300</td>
<td>3, 4, 5, 6, 7</td>
</tr>
<tr>
<td>MgO (g kg⁻¹ DM)</td>
<td>–</td>
<td>12.8</td>
<td>8.7</td>
<td>2</td>
</tr>
<tr>
<td>CaO (g kg⁻¹ DM)</td>
<td>–</td>
<td>13.5</td>
<td>18.0</td>
<td>2</td>
</tr>
<tr>
<td>Fe₂O₃ (g kg⁻¹ DM)</td>
<td>–</td>
<td>2.6</td>
<td>2.5</td>
<td>2</td>
</tr>
<tr>
<td>Inorganic phosphorous (g kg⁻¹ DM)</td>
<td>–</td>
<td>10.4</td>
<td>6.0</td>
<td>2</td>
</tr>
<tr>
<td>Organic phosphorous (g kg⁻¹ DM)</td>
<td>–</td>
<td>5.0</td>
<td>3.5</td>
<td>2</td>
</tr>
<tr>
<td>Cl⁻ (mmol kg⁻¹ DM)</td>
<td>–</td>
<td>55</td>
<td>33</td>
<td>2</td>
</tr>
<tr>
<td>Na⁺ (mmol kg⁻¹ DM)</td>
<td>–</td>
<td>105</td>
<td>38</td>
<td>2</td>
</tr>
<tr>
<td>K⁺ (mmol kg⁻¹ DM)</td>
<td>–</td>
<td>260</td>
<td>84</td>
<td>2</td>
</tr>
<tr>
<td>Bacteria (10⁹ g⁻¹ DM)</td>
<td>–</td>
<td>142</td>
<td>31</td>
<td>2</td>
</tr>
<tr>
<td>Nicotinic acid (mg kg⁻¹)</td>
<td>–</td>
<td>139</td>
<td>40</td>
<td>1</td>
</tr>
<tr>
<td>Riboflavin (mg kg⁻¹)</td>
<td>–</td>
<td>30</td>
<td>9</td>
<td>1</td>
</tr>
<tr>
<td>Panthotenic acid (mg kg⁻¹)</td>
<td>–</td>
<td>52</td>
<td>8</td>
<td>1</td>
</tr>
<tr>
<td>Cyanocobalamin (mg kg⁻¹)</td>
<td>–</td>
<td>3</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>

1, Kulwich et al. (1953); 2, adapted from Hörnicke and Björnhag (1980); 3, Carabaño et al. (1988); 4, Carabaño et al. (1989); 5, Fraga et al. (1991); 6, Motta-Ferreira et al. (1996); 7, Carabaño et al. (1997).
organ content weights and the chemical composition of their contents throughout the day. These circumstances make it necessary to take into account the sampling time in experimental procedures to obtain reliable digestibility data. The lack of homogeneity in the sampling procedures between different studies leads to difficulties in making comparisons and considerable misunderstanding. The diurnal variations of the main physiological parameters will now be summarized.

1.7.1 Weight and chemical composition of the organ contents

The weight of the stomach and caecal contents reflects the diurnal rhythm of intake and soft faeces production. Stomach contents show greater weights during the morning than during the night. The opposite is found for the weight of caecal contents. Diurnal differences in the weight of caecal and stomach contents of up to 20% and 30%, respectively, can be observed (Fraga et al., 1984; Gidenne and Lebas, 1987).

Differences in the stomach contents are explained by diurnal changes in the chemical composition of stomach, duodenum, jejunum and ileum contents. Intact soft faeces in the stomach have been detected from 09.00 to 18.00 h (Gidenne and Poncet, 1985; Carabaño et al., 1988), representing about a half of the total weight of the stomach contents. During the complementary period, the stomach only contains food. The protein content of precaecal digesta is the chemical parameter most affected by sampling time, showing greater values (from 0.50 to 1.00) during the soft faeces excretion period (Catala, 1976; Gidenne and Poncet, 1985; Merino, 1994). The same tendency has been observed for the chemical composition of colonic and rectal contents. However, the protein concentration of caecal contents remains stable throughout the day.

1.7.2 Ileal digestibility

The use of cannulated animals to determine ileal digestibility requires markers to estimate the ileal flow of DM and an ileal sample that is representative of that present throughout the day. Merino (1994) and Blas et al. (2003) observed, in cannulated animals, a diurnal variation in the crude protein (CP) content of ileal digesta, with greater values during the soft faeces excretion period than during the hard faeces excretion period (180 versus 120 g CP kg\(^{-1}\) DM). When caecotrophy was prevented, no variation was detected in the protein content of ileal digesta (average value 120 g kg\(^{-1}\) DM) (Merino and Carabaño, 2003). These results suggest that it is essential to take samples throughout the day to estimate the average composition of ileal digesta. Diurnal changes were detected in the marker concentration or fibre content of ileal digesta. However, sampling during the evening period (hard faeces excretion) does not produce significant differences when the ileal digestibility of the diet is determined by avoiding caecotrophy (Merino and Carabaño, 2003).

1.7.3 Fermentation patterns

The results obtained by Fioramonti and Ruckebush (1976) and Gidenne and Bellier (1992) in adult animals showed that the VFA concentration in caecal contents depends on the time of feeding, rising to a maximum 5 h after feeding. In weaned (4 weeks old) or growing (9 weeks old) rabbits fed ad libitum, diurnal differences in VFA concentrations and caecal pH of 50% and 10%, respectively, can be observed (Gidenne, 1986; Bellier et al., 1995; Bellier and Gidenne, 1996). Caecal VFA concentrations are greater during the hard faeces than during the soft faeces excretion period. According to Bellier et al. (1995), this increment could have two causes: (i) the greater flow of substrate to the caecum related to an increase in feed intake during this period; and (ii) enrichment of the microbial population as a consequence of antiperistaltic movements of the proximal colon. Caecal pH varies inversely to the increase in VFA concentration. Smaller values of caecal pH have been observed during hard faeces excretion. Consequently, it is
preferable to take the caecal samples during the hard faeces excretion period.

1.7.4 Transit time

Giving a marker as simple doses is the most frequent procedure used in transit time studies. This raises the question as to when the doses should be administered. According to Laplace and Lebas (1975), doses given before the caecotrophy period lead to a higher mean retention time (3–4 h) compared with doses given after caecotrophy. This effect can be explained by an increase in time before the first appearance of the marker in hard faeces. According to Jilge (1974), the time for the first appearance of the marker in faeces is the same (4 or 5 h) for doses given before or after the caecotrophy period. However, depending on the time of administration, the marker changes the site of its first appearance (soft or hard faeces) and, as a consequence, its detection will change.

According to these results, and taking into account the fact that feed intake starts just after the caecotrophy period, the hard faeces excretion period is recommended as the best time for marker administration.

1.8 Rate of Passage

The capacity of the rabbit to digest its feed depends not only on endogenous enzyme activities and digestion by the microbial population, but also on the rate of passage of the feed. The passage of feed through the stomach of the rabbit and caecum is relatively slow and varies between 3–6 and 4–9 h, respectively, as measured by the technique of comparative slaughter (Gidenne and Poncet, 1985). However, transit is very fast in the small intestine. Estimated retention times in the jejunum and ileum are 10–20 and 30–60 min, respectively (Lebas, 1979). Taking into account the entire digestive tract, the mean retention time varies from 9 to 30 h, with an average of 19 h (Laplace and Lebas, 1975, 1977; Udén et al., 1982; Fraga et al., 1984; Ledin, 1984). More recently, with rabbits cannulated at the ileum, the mean retention times for the ileo-rectal and oro-ileal segments, and for the stomach, have been calculated as 7–24, 4–9 and 1–3 h, respectively (Gidenne and Ruckebush, 1989; Gidenne et al., 1991; Gidenne and Pérez, 1993; Gidenne, 1994).

The wide variability in the results obtained might be related to factors such as the methodology used (e.g. type of marker, time and route of administration of the marker, mathematical calculations), characteristics of the animal (e.g. age, physiological status) and feeding variables (e.g. feed intake, particle size and fibre concentration of the diet, caecotrophy allowed or not). It has been reported that the marker ytterbium is retained for 3 h longer than chromium (Gidenne and Ruckebush, 1989) and that liquid-phase markers are retained for longer than solid-phase markers (Laplace and Lebas, 1975; Sakaguchi et al., 1992). Preventing caecotrophy reduces the mean retention time by 0–7 h, depending on the type of diet fed (Fraga et al., 1991; Sakaguchi et al., 1992), whereas restricting feed intake to 0.50 and 0.60 of ad libitum levels increases mean retention time by 7 and 13 h, respectively (Ledin, 1984). Increasing the dietary fibre content from 220 to 400 g kg⁻¹ decreases the total mean retention time by 12 h (an 11 h reduction in the ileo-rectal mean retention time) (Gidenne, 1994). Particle size can also modify the rate of passage, with longer times being obtained using diets with smaller particle size (Laplace and Lebas, 1977; Auvergne et al., 1987).

References


Davies, M.E. (1965) Cellulolysitic bacteria in some ruminants and herbivores as shown by fluorescent antibodies. *Journal of General Microbiology* 39, 139–141.


It is possible to classify the carbohydrate fractions of plants incorporated into animal feed into two groups: (i) those that are hydrolysable by the endogenous intestinal enzymes of the animal (these polysaccharides are located predominantly within the plant cell); and (ii) those that are hydrolysable only by enzymes produced by the microbiota (these are principally cell wall polysaccharides and are considered in more detail in Chapter 5). The former can be further separated into two main groups: first, the simple sugars and oligosaccharides, which are present at low levels (<50 g kg\(^{-1}\)) in rabbit feeds; and second, the polysaccharides represented mainly by the starches (contributing 100–250 g kg\(^{-1}\)). The structure and digestion of starch are described later in this chapter. First, the digestion of simple sugars and oligosaccharides is considered.

### 2.1 Simple Sugars and Oligosaccharides

These two types of carbohydrate are often classed simply under one general term, ‘the sugars’. Nevertheless, from a biochemical point of view, it is convenient to distinguish clearly between simple sugars and oligosaccharides because they are not digested by the same processes. For instance, the α-galactosides are only degraded by bacterial enzymes, whereas simple sugars are very rapidly hydrolysed by endogenous enzymes of the host and absorbed from the small intestine.

#### 2.1.1 Definition, structure and analysis

Sugars are generally found at low concentrations in animal feeds, although the level of sucrose can reach 500 g kg\(^{-1}\) in some raw materials such as molasses (Table 2.1). Among the sugars found in common raw materials, glucose and fructose are the two major types, found as monosaccharides or as sucrose (a disaccharide based on a combination of the two). Furthermore, compared with other mammals, lactose (glucose + galactose, α[1→4]) is at a very low level (50 g kg\(^{-1}\) dry matter (DM)) in the milk of the rabbit female (Maertens et al., 2006) and thus is not added to the pelleted feed for the young rabbit. Other disaccharides can also occur in the feed: maltose (two glucose units, α[1→4]), which mainly originates from starch hydrolysis, and melibiose (galactose + glucose, α[1→6]) which is found in some roots.

Oligosaccharides are defined as molecules with a low degree of polymerization (dp). Maltotriose corresponds to three units of glucose linked by α[1→4] bonds and
Table 2.1. Level of total sugars\(^a\) in some raw materials (INRA, 2004).

<table>
<thead>
<tr>
<th>Raw material</th>
<th>Sugars (g kg(^{-1}) air dry)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Beet molasses</td>
<td>466</td>
</tr>
<tr>
<td>Sugarbeet</td>
<td>160</td>
</tr>
<tr>
<td>Sugarbeet pulp</td>
<td>66</td>
</tr>
<tr>
<td>Citrus pulps</td>
<td>200</td>
</tr>
<tr>
<td>Apple pomace</td>
<td>140</td>
</tr>
<tr>
<td>Sweet lupin</td>
<td>64</td>
</tr>
<tr>
<td>Soybean meal</td>
<td>83</td>
</tr>
<tr>
<td>Sunflower meal</td>
<td>57</td>
</tr>
<tr>
<td>Brewer’s grain</td>
<td>9</td>
</tr>
<tr>
<td>Wheat bran</td>
<td>67</td>
</tr>
<tr>
<td>Barley</td>
<td>21</td>
</tr>
<tr>
<td>Winter pea</td>
<td>39</td>
</tr>
</tbody>
</table>

\(^a\)Analysed as total sugars soluble in ethanol (80%, v/v).

2.1.2 Digestion

Compared with starch, glucose and fructose are readily absorbed in the small intestine. However, fructose has been observed to be absorbed more slowly than glucose in pigs (Carré, 1992). In contrast with glucose, fructose is probably not absorbed through an energy-dependent mechanism. The level of sugars (soluble in 80% ethanol) in the ileal contents, including therefore ethanol-soluble \(\alpha\)-glucosides and glucose resulting from digestion of starch, may reach 25 g kg\(^{-1}\) DM for adult rabbits fed a standard commercial diet (Gidenne and Ruckebusch, 1989), indicating that the flow of sugars entering the caecum is not negligible. Further studies are necessary to evaluate the digestion of sugars, especially in the young animal.

Complete digestion of \(\alpha\)-galactosides has been observed in rats and pigs (Goodlad and Mathers, 1990, 1991). It is assumed that they are also totally digested by the caecal microbiota in rabbits, although this has not yet been measured.

2.2 Starch

2.2.1 Definition, structure and analysis

Starch (\(\alpha\)-glucan) is a major reserve polysaccharide of green plants and probably the second most abundant carbohydrate in nature next to cellulose. In some cases, the reserve polysaccharides of the plant are \(\alpha\)-fructans, such as inulin (linear \(\alpha\)-fructan, dp \(\approx\)30) in the Jerusalem artichoke (Helianthus tuberosus) or levan (branched \(\alpha\)-fructan, dp \(\approx\)100) in some grasses. Starch is found in nature as granules either in seeds, roots or tubers. The shape of the starch granule depends on the botanical source and many different sizes and forms are found – from tiny granules in oats or rice (5–6 µm) to larger granules in banana (38–50 µm). The interior of a granule is composed of alternating crystalline and amorphous regions. The disruption of this organization is the basis of gelatinization. The starch granule is modified by either chemical or physical treatment (e.g. heat,
A prerequisite for digestion is that the enzymes are adsorbed onto the starch granule. Hydrolysis may then proceed either through surface erosion or penetration via pinholes. The physicochemical and functional aspects of starch have been reviewed by Eliasson and Gudmundsson (1996).

From a biochemical point of view, starch is a polysaccharide composed simply of D-glucose units. Starch basically consists of a mixture of two types of chains: (i) amylose, a linear chain of glucose (α[1→4] links); and (ii) amylopectin, a branched chain (α[1→4] + α[1→6] links). However, the polymeric structure of starch is more complicated, and its primary structure is not yet fully understood. Starch is the subject of many investigations because of its multiple uses in chemistry, the food industry, fermentation processes and so on.

It is now recognized that some amylose molecules have several branches. In addition, the presence of materials intermediate between amylose and amylopectin has been suggested in amylomaize (maize rich in amylose) and wrinkled-pea starches (Hizukuri, 1996). The relative proportion of amylose and amylopectin may vary considerably according to the plant source, and this may significantly affect its digestion (Table 2.2). For instance, maize rich in amylose has a lower digestibility than standard maize. In addition, the starch granule is sometimes encapsulated in a protein matrix that reduces its accessibility to enzymes. Thus, starch degradation is dependent on the biochemical and physical structure of the granule.

Numerous processes currently used in animal feed manufacturing are able to modify the starch granule, either slightly by steaming in the pelleting process or strongly by using temperature combined with hydration and pressure in the extrusion process. The interaction between starch and water is well known: the starch structure is strongly hydrophilic and the ratio of starch to water is inversely correlated to the gelatinization temperature (Champ and Colonna, 1993). In general, with an excess of water and temperatures over 55°C, the granules swell and solubilize (disorganization/dispersion of the structure); this is the gelatinization step (in the case of pure starch, a viscous solution results). Following cooling, the chains of glucose can reassociate. This is termed retrogradation and can lead to forms of starch that are resistant to amylases. Complete gelatinization of the starch granule is essential for the correct determination of the starch using enzymatic procedures.

Starch is usually determined in animal feeds or raw materials through the Ewers EC (optical rotation determination) or enzymatic methods (hydrolysis followed by glucose determination). The two techniques provide, in general, very well correlated data, with slightly higher values for the Ewers EC method (+0.5–4%). The differences between the two methods are greater for legume than for cereal materials. The difference lies in the fact that the Ewers EC method may interfere with unextracted sugars or acid-labile polysaccharides. For example, the recommended starch method for beet pulp is the enzymatic one. Specific

<table>
<thead>
<tr>
<th>Source</th>
<th>Starch (g kg⁻¹ DM)</th>
<th>Amylose (proportion of starch)</th>
<th>Faecal digestibility of starch in the rat a</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soft wheat</td>
<td>650–700</td>
<td>0.25–0.30</td>
<td>0.98–1.00</td>
</tr>
<tr>
<td>Maize</td>
<td>650–800</td>
<td>0.20–0.24</td>
<td>0.98–1.00</td>
</tr>
<tr>
<td>Maize rich in amylose</td>
<td>500–650</td>
<td>0.60–0.65</td>
<td>0.66–0.77</td>
</tr>
<tr>
<td>Smooth pea</td>
<td>430–480</td>
<td>0.31–0.35</td>
<td>0.99</td>
</tr>
<tr>
<td>Fava bean</td>
<td>300–430</td>
<td>0.31–0.34</td>
<td>0.99</td>
</tr>
<tr>
<td>Banana (green)</td>
<td>150–250</td>
<td>0.15–0.18</td>
<td>0.49</td>
</tr>
<tr>
<td>Cassava roots</td>
<td>800–850</td>
<td>0.17</td>
<td>0.95–0.97</td>
</tr>
<tr>
<td>Potato (uncooked)</td>
<td>600–650</td>
<td>0.20</td>
<td>0.27–0.28</td>
</tr>
</tbody>
</table>


Table 2.2. Starch and amylose concentrations in some raw materials, and respective faecal digestibility for the rat.
procedures are also recommended for starch determination in digesta and faeces (Kozlowski, 1994). If no previous ethanol extraction of samples has been carried out when using enzymatic procedures, starch, ethanol-soluble α-glucosides and glucose are considered as a whole.

2.2.2 Digestion of starch in the different parts of the gastrointestinal tract

Starch is almost completely digested in the digestive tract of rabbits, as in other livestock species. For this reason, the faecal excretion of starch is generally minimal (less than 0.02 of intake), although in some cases it can reach 0.10 of intake, depending mainly on the age of the rabbit and the source of the starch, both of which will be discussed later.

It is acknowledged that starch digestion takes place mainly in the small intestine. However, starch may also be degraded to some extent in other parts of the digestive tract, such as the stomach and large intestine. It would be of particular interest to evaluate the degradation of starch (or of intermediate α-glucosides and glucose not absorbed in the small intestine) by the microbiota in the large intestine and to review the factors affecting the ileal flow of starch and the possible consequences on caeco-colic fermentative activity, as well as on the stability of the microbial ecosystem and digestive health. Therefore, the following section discusses various aspects of the process of starch digestion in the different parts of the gastrointestinal tract of rabbits.

Gastric digestion

There are no reliable measurements of the extent of starch hydrolysis in the stomach. It has been observed that the starch concentration in the gastric digesta is clearly less than in the diet (Fraga et al., 1984; Blas, 1986). Wolter et al. (1980) observed that, for restricted-fed rabbits slaughtered 4 h after feeding, 0.31 of the starch ingested had been hydrolysed in the stomach. However, this is probably an overestimate because of dilution of the diet with soft faeces recycled through caecotrophy; moreover, the intake of marker through soft faeces was not taken into account.

Amylase in the stomach originates essentially from the soft faeces and saliva, and remains at a constant level from week 4 of life independently of starch intake (Blas, 1986). The gastric pH is the main factor limiting its activity. Marounek et al. (1995) did not find amylase activity in the contents of the stomach of 4-week-old and 3-month-old rabbits, with enzyme-substrate incubations undertaken at pH 2.5. On the other hand, Sequeira et al. (2000) observed amylase activity in the gastric contents of 9-week-old rabbits with incubations carried out at pH 6.9.

In fact, the amylase activity of the stomach contents disappears completely if the pH is lower than 3.2 (Blas, 1986), and the gastric pH in the antrum is usually around 2 (see Chapter 1). However, the buffering capacity of the diet, soft faeces and saliva probably prevents immediate acidification. For instance, Blas (1986) found a pH of 4–4.5 in the stomach contents of growing rabbits 150 min after feeding following a 24-h fast; and Herrmann (1989) even reported a pH of >5 in certain areas of the stomach after high feed intake. However, rabbits that are fed ad libitum have 20–30 ‘voluntary meals’ a day, and the gastric pH is thus normally <2.5. Nevertheless, as a consequence of physiological hypochlorhydria in young rabbits, the gastric pH in 3-week-old rabbits and still >4 in 4-week-old rabbits, as reviewed by Gidenne and Fortun-Lamothe (2002). On the other hand, while soft faeces are being stored the pH of the fundus can rise to 4.0–5.1, whereas the pH of the antrum always remains very acidic (Griffiths and Davies, 1963).

Under these less acidic conditions, the amylase in the stomach contents, especially that of microbial origin from soft faeces, maintains appreciable activity (Alexander and Chowdhury, 1958; Griffiths and Davies, 1963; Hörnicke and Mackiewicz, 1976; Blas, 1986; Vernay, 1986). Table 2.3 illustrates this process of gastric fermentation (originating...
from starch, sugars and perhaps other carbohydrates), demonstrating that the concentration of lactate in both the gastric digesta (and not in that of the other parts of the digestive tract) and the blood falls significantly when caecotrophy is prevented.

**Intestinal digestion**

As stated above, it is acknowledged that starch digestion takes place mainly in the small intestine, and the most important enzyme involved is pancreatic amylase. Other enzymes of the epithelial cells of the intestinal mucosa are also necessary (maltase, amyloglucosidase), resulting finally in the release of glucose, which in principle is absorbed in situ.

Studies to assess the capacity of rabbits to digest starch in the small intestine vary widely in methodological aspects, such as: (i) target samples (pancreatic tissue or secretion, intestinal mucosa, intestinal contents); (ii) time of sampling (evening, morning, without or with a previous fasting period); (iii) conditions in assaying the enzyme activity (with or without considering optimal kinetic parameters, concerning substrate and enzyme concentrations, incubating period, temperature, pH); and (iv) units used to express enzyme activity (as relative to protein in pancreatic tissue or secretion, as relative to pancreatic tissue or secretion, as relative to intestinal mucosal protein or tissue, as relative to intestinal contents, as total in pancreatic tissue, intestinal mucosa or intestinal contents kg⁻¹ live weight). Logically, these methodological variations make it difficult to evaluate the age-dependent evolution of capacity to digest starch intestinally and, especially, the possible role of starch intake in modulating this capacity.

Despite these difficulties, the ontogenic development of such digestive capacity is well established. Amylase activity increases rapidly between weeks 2 and 7 of life (Corring et al., 1972; Blas, 1986; Scapinello et al., 1999; Gutiérrez et al., 2002a; Toral et al., 2002; Debray et al., 2003; Gidenne et al., 2007; Gallois et al., 2008a) and is still increasing in 3-month-old rabbits (Marounek et al., 1995; Dojanà et al., 1998); similarly, the amyloglucosidase activity of the jejunal mucosa generally increases between 37 and 60 days of age (Otutumi et al., 2005). However, the ontogenic development of intestinal maltase activity remains controversial. According to Toofanian (1984) and Gallois et al. (2008a), maltase activity increases very rapidly between weeks 2 and 4 of life, but not afterwards; others have reported increasing maltase between 32 and 42 days of life (Debray et al., 2003; Gidenne et al., 2007), and even between 1 and 3 months (Marounek et al., 1995). Still further studies have reported no changes in maltase activity between 25- and 35-day-old rabbits (Gutiérrez et al., 2002a) or between 32- and 42-day-old rabbits (Scapinello et al., 1999). Finally, Otutumi et al. (2005) found similar maltase activity in the jejunal mucosa of 37- and 60-day-old rabbits, while it was higher in jejunal contents for 60- than for 37-day-old rabbits, maltase activity being expressed per mg of, respectively, mucosa or contents.

Modulating the intestinal capacity for starch digestion according to diet is usually approached by varying starch intake. In many species, it is acknowledged that the digestive potential of the small intestine adapts to higher starch intake by increasing pancreatic amylase, intestinal maltase and amyloglucosidase secretion. Blas (1986) found higher amylase activity in the pancreatic secretions of both growing (28- and 42-day-old) and adult rabbits with a higher starch intake in samples

### Table 2.3. Effect of caecotrophy prevention on lactate concentration in the gastric contents and blood of rabbits (Vernay, 1986).

<table>
<thead>
<tr>
<th>Feed intake (g day⁻¹)</th>
<th>Control</th>
<th>Caecotrophy prevention for 4 days</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Gastric contents (mM)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fundus</td>
<td>4.7</td>
<td>1.9</td>
</tr>
<tr>
<td>Corpus</td>
<td>3.4</td>
<td>1.9</td>
</tr>
<tr>
<td>Antrum</td>
<td>2.4</td>
<td>1.6</td>
</tr>
<tr>
<td><strong>Blood (mM in plasma)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Venous</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gastric</td>
<td>3.4</td>
<td>1.9</td>
</tr>
<tr>
<td>Ileal</td>
<td>3.8</td>
<td>2.1</td>
</tr>
<tr>
<td>Caecal</td>
<td>2.8</td>
<td>1.9</td>
</tr>
<tr>
<td>Portal</td>
<td>3.6</td>
<td>2.5</td>
</tr>
<tr>
<td>Arterial (abdominal aorta)</td>
<td>3.0</td>
<td>1.8</td>
</tr>
</tbody>
</table>
obtained 150 min after feeding following a 24-h fast (no differences were found in basal samples taken following a 24-h fast). Similar results have been observed in adult rabbits in both pancreatic and intestinal tissue, and also in the intestinal contents (Abbas et al., 1991).

However, more recent studies that have investigated differences in the starch intake of young rabbits by modifying the dietary starch concentration (consequently changing other components, such as fibre) seem to disagree with the above-mentioned adaptability of the digestive potential. For instance, Debray et al. (2003) found no differences either in pancreatic amylase or in intestinal mucosal or intraluminal maltase in 42-day-old rabbits consuming twice the amount of starch than controls. Furthermore, Gidenne et al. (2007) reported higher amylase activity in the total intestinal contents in 42-day-old rabbits consuming one-third less starch than controls, while Gutiérrez et al. (2002a) reported no changes in pancreatic amylase in 35-day-old rabbits consuming twice the amount of starch (by replacing lactose) than controls and higher pancreatic amylase and jejunal mucosal maltase when consuming one-third less starch.

Finally, studies in young rabbits inducing differences in starch intake by stimulating feed intake through early weaning or milk restriction have reported contradictory results. Corring et al. (1972) found that pancreatic amylase activity in 30-day-old rabbits was higher in those weaned at 21 days than in those remaining suckling. Gutiérrez et al. (2002a) found even wider differences in 35-day-old rabbits depending on whether they were weaned at 25 days old or remained suckling, although jejunal mucosal maltase decreased in those that were early weaned as a consequence of impairing mucosal morphology. Conversely, higher feed and starch intake before weaning in milk-restricted rabbits had no effect on amylase and maltase activities in the intestinal contents at weaning or 10 days later (Scapinello et al., 1999). Gallois et al. (2008a) reported lower amylase activity in the intestinal contents but higher maltase activity in the intestinal mucosa of 28-day-old rabbits that were still suckling than in those early weaned at 21 days of age (without negative effects of early weaning on mucosal morphology).

Caecal fermentation

Starch undigested in the small intestine is in principle very quickly hydrolysed and fermented by the microbiota in the caecocolic segment to lactate and volatile fatty acids (VFAs), absorbed in situ. Different studies have demonstrated the presence of amylase activity in this part of the digestive tract (Yoshida et al., 1968; Blas, 1986; Makkar and Singh, 1987; Marounek et al., 1995). Some data suggest that amylase could be of microbial origin and also from the ileal digesta flow. For instance, amylase activity in the caecum and the colon is even greater in germ-free rabbits than in normal rabbits (Yoshida et al., 1968), and is more than twice as high in the rabbit caecum than in the rumen of steers (Makkar and Singh, 1987). Blas (1986) observed that amylase activity in the caecal contents hardly varied with age in 4- to 8-week-old rabbits, but was four times greater with a diet rich in starch than with a low-starch diet. On the other hand, Marounek et al. (1995) found amylase activity in caecal contents to be five times greater in 4-week-old rabbits than in 3-month-old rabbits.

Stable high counts of amylolytic bacteria in the caecal contents of 2- to 7-week-old rabbits have been reported (Padiha et al., 1995). Different strains of rabbit caecal bacteria (Actinomyces israelii, Dichelobacter nodosus, Mitsuokella multiacidus, Bacteroides spp., Eubacterium spp., Clostridium spp.) have been shown to produce extracellular or membrane-bound α-amylases (Sirotek et al., 2006). Paradoxically, a study on the in vitro fermentation of soluble potato starch used as a substrate for determining α-amylase, by inocula prepared from caecal contents of 36- or 78-day-old rabbits, indicated slow and poor fermentation (long lag phase, long time to reach maximum fermentation rate, low maximum fermentation rate), especially in the
younger rabbits (Laurenčič, 2007). This suggests that starch fermentation could be negligible if considering the usual mean retention time of digesta in this digestive segment (6–12 h); it could be hypothesized that a low availability of glucose exo-splitting enzymes (β-amylase, amyloglucosidase) is a limiting factor. Nevertheless, the differences between ileal and faecal digestibility of starch shown later seem to clearly indicate in vivo fermentation of starch passing the ileo-caecal junction.

### 2.2.3 Factors affecting starch digestibility

As stated above, starch digestion is primarily affected by the age of the rabbit and by the dietary level and origin of the starch. Other factors may also have some influence, such as the feed manufacturing process or the use of exogenous enzymes as dietary supplements.

<table>
<thead>
<tr>
<th>Source of starch</th>
<th>Dietary level of starch (g kg⁻¹ DM)</th>
<th>Digestibility of starch</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ileal</td>
<td>Faecal</td>
<td></td>
</tr>
<tr>
<td>Purified maize starch</td>
<td>158</td>
<td>0.945</td>
<td>Gidenne (1992)</td>
</tr>
<tr>
<td></td>
<td>353</td>
<td>0.947</td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.993</td>
<td>0.996</td>
<td></td>
</tr>
<tr>
<td>Barley</td>
<td>306</td>
<td>0.982</td>
<td>Merino and Carabaño (1992)</td>
</tr>
<tr>
<td></td>
<td>0.995</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Purified maize starch</td>
<td>256</td>
<td>–</td>
<td>Gidenne and Perez (1993b)</td>
</tr>
<tr>
<td></td>
<td>0.997</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maize</td>
<td>292</td>
<td>–</td>
<td>Gidenne and Perez (1993b)</td>
</tr>
<tr>
<td></td>
<td>0.990</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Barley</td>
<td>283</td>
<td>–</td>
<td>Gidenne and Perez (1993b)</td>
</tr>
<tr>
<td></td>
<td>0.998</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pea</td>
<td>280</td>
<td>–</td>
<td>Gidenne and Perez (1993b)</td>
</tr>
<tr>
<td></td>
<td>0.996</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Purified maize starch</td>
<td>280</td>
<td>0.992</td>
<td>Amber (1997)</td>
</tr>
<tr>
<td></td>
<td>353</td>
<td>0.991</td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.999</td>
<td>0.999</td>
<td></td>
</tr>
<tr>
<td>Maize</td>
<td>103</td>
<td>0.972</td>
<td>Amber (1997)</td>
</tr>
<tr>
<td></td>
<td>255</td>
<td>0.971</td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.989</td>
<td>0.990</td>
<td></td>
</tr>
<tr>
<td>Barley</td>
<td>102</td>
<td>0.970</td>
<td>Amber (1997)</td>
</tr>
<tr>
<td></td>
<td>251</td>
<td>0.984</td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.994</td>
<td>0.994</td>
<td></td>
</tr>
<tr>
<td>Wheat, wheat bran</td>
<td>116</td>
<td>0.987</td>
<td>Gidenne et al. (2000)</td>
</tr>
<tr>
<td></td>
<td>0.992</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wheat</td>
<td>329</td>
<td>0.930</td>
<td>Gidenne et al. (2000)</td>
</tr>
<tr>
<td></td>
<td>0.997</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wheat, wheat bran</td>
<td>220</td>
<td>0.983</td>
<td>Pinheiro (2002)</td>
</tr>
<tr>
<td></td>
<td>0.997</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Purified potato starch, wheat</td>
<td>223</td>
<td>0.967</td>
<td>Pinheiro (2002)</td>
</tr>
<tr>
<td></td>
<td>0.996</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
starch (0.983 versus 0.967), the latter being very resistant to in vitro digestion with thermostable amylase during 270 min at pH 4.5 and 37°C (Pinheiro and Gidenne, 2000). Consequently, the ileal flow of starch is low: 1.0–3.2 g day⁻¹ (Gidenne, 1992), 0.3–1.3 g day⁻¹ (Amber, 1997), 0.2–2.3 g day⁻¹ (Gidenne et al., 2000) and 0.5–1.1 g day⁻¹ (Pinheiro, 2002). The amount of starch fermented in the caeco-colic segment of adult rabbits is between 0.01 and 0.07 of the starch intake.

GROWING RABBITS. A review of 30 studies involving 65 different diets, from 1982 to 2009, reveals that faecal digestibility in growing rabbits (4–11 weeks old) is higher than 0.98 (averaging 0.99) in most cases, independent of the age of the rabbits, starch intake and starch source (barley, wheat, maize, oats, triticale, cassava, purified maize starch or purified potato starch). There are some exceptions that will be discussed later, essentially suggesting an interaction between the age of rabbit and some starch sources.

The effect of rabbit age is very limited for the majority of starch sources. In fact, faecal digestibility of starch during week 4 of life, in still-suckling young rabbits beginning to consume feed, is almost total (0.98–0.99) with starch from barley, wheat or pea, with minor but statistically significant reduction when including pea (Blas, 1986; Gidenne et al., 2007). However, as shown in Table 2.5 and Fig. 2.1, faecal losses of starch can increase in some cases, usually for maize and particularly for the youngest rabbits. The resistance of maize starch to digestion is also seen in pigs and ruminants, but not in poultry. The endosperm structure of maize seeds and their resistance to grinding are considered the main factors behind this lower degradation (Rooney and Pflugfelder, 1986). These disappear in the process of manufacturing purified maize starch. Nevertheless, some studies using maize as the only or main starch source have reported faecal digestibility of starch similar to that from other sources, from 0.98 to 1.00 (Toral et al., 2002; Xiccato et al., 2002; Furlan et al., 2003). It must be stated that the differences between varieties of a particular grain, with special reference to the amyllose-amylpectin ratio, may affect faecal losses of starch. This may also help to explain some values of <0.98 of faecal digestibility of starch from wheat, barley, oats and wheat bran (Parigi-Bini et al., 1990; Cossu et al., 2004; Volek and Marounek, 2008) (see Table 2.5).

In different studies with both growing and adult rabbits, comparing various dietary starch levels (Blas, 1986; Blas et al., 1990; Parigi-Bini et al., 1990; Gidenne, 1992; de Blas et al., 1995; Amber, 1997; Gidenne and Perez, 2000; de Arruda et al., 2002; Gutiérrez et al., 2002a), the faecal digestibility of starch has tended to decrease systematically in diets.

Table 2.5. Faecal digestibility of starch from several studies on growing rabbits showing values of <0.98.

<table>
<thead>
<tr>
<th>Source of starch</th>
<th>Age (weeks)</th>
<th>Faecal digestibility of starch</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Barley, wheat bran</td>
<td>8</td>
<td>0.967</td>
<td>Parigi-Bini et al. (1990)</td>
</tr>
<tr>
<td>Wheat bran, barley</td>
<td>8</td>
<td>0.945</td>
<td>Parigi-Bini et al. (1990)</td>
</tr>
<tr>
<td>Maize</td>
<td>7–9</td>
<td>0.945</td>
<td>de Arruda et al. (2002)</td>
</tr>
<tr>
<td>Wheat, wheat bran</td>
<td>8–11</td>
<td>0.950</td>
<td>Cossu et al. (2004)</td>
</tr>
<tr>
<td>Maize, wheat bran</td>
<td>7</td>
<td>0.961</td>
<td>de Faria et al. (2004)</td>
</tr>
<tr>
<td>Maize, purified maize starch</td>
<td>11</td>
<td>0.973</td>
<td>dos Santos et al. (2004)</td>
</tr>
<tr>
<td>Maize</td>
<td>6–9</td>
<td>0.970</td>
<td>Otutumi et al. (2005)</td>
</tr>
<tr>
<td>Sorghum</td>
<td>6–9</td>
<td>0.979</td>
<td>Otutumi et al. (2005)</td>
</tr>
<tr>
<td>Maize, wheat bran</td>
<td>8</td>
<td>0.971</td>
<td>Furlan et al. (2006)</td>
</tr>
<tr>
<td>Buckwheat, maize, wheat bran</td>
<td>8</td>
<td>0.979</td>
<td>Furlan et al. (2006)</td>
</tr>
<tr>
<td>Maize, wheat bran</td>
<td>9</td>
<td>0.957</td>
<td>Michelan et al. (2006)</td>
</tr>
<tr>
<td>Maize, cassava hulls, wheat bran</td>
<td>9</td>
<td>0.972</td>
<td>Michelan et al. (2006)</td>
</tr>
<tr>
<td>Oats, barley, wheat bran</td>
<td>8</td>
<td>0.966</td>
<td>Volek and Marounek (2008)</td>
</tr>
</tbody>
</table>
with lower starch content in comparison with those of higher starch content (even with the same source of starch). Although statistically significant, this decrease remains small and may often be considered irrelevant. There is no clear explanation for these results. In fact, a lower dietary starch level corresponds to a higher fibre level, and thus it can be hypothesized that a faster rate of passage leads to a lower efficiency in starch degradation. A presence of endogenous α-linked glucose polymers (e.g. dextrans in the microbial reserves) being proportionally more important in diets lower in starch can also be hypothesized.

Results on the ileal digestibility of starch in growing rabbits are summarized in Table 2.6, with values ranging between 0.88 and 0.98 and averaging 0.94. No clear evidence of effect of the dietary starch level or source on its ileal digestibility has been detected, although studies with sources of more resistant starch (e.g. maize) are not available. However, some other factors can be considered as affecting the efficiency of starch digestion in the small intestine. In this context, the ileal digestibility of starch in 35-day-old rabbits is significantly lower than in 42-day-old rabbits when the dietary starch level is increased enough (Soler et al., 2006). It is also decreased significantly when the dietary neutral detergent-soluble fibre is reduced in iso-starch diets by using different fibre sources (oat hulls, lucerne hay, beet-apple pulp), and this seems to be associated with an impaired intestinal mucosal morphology (Gómez-Conde et al., 2007). On the other hand, the ileal flow of starch in 35-day-old rabbits has been found to range between 0.6 and 2.3 g day\(^{-1}\) (Gutiérrez et al., 2002a), 0.8 g day\(^{-1}\) (Nicodemus et al., 2003), 0.1 and 1.5 g day\(^{-1}\) (Soler et al., 2006), 0.5 and 1.2 g day\(^{-1}\) (Gómez-Conde et al., 2007) or 0.1 and 0.4 g day\(^{-1}\) (Sánchez-Martínez, 2009). The amount of starch fermented in the caeco-colic segment of 4- to 6-week-old rabbits is between 0.03 (Gallois et al., 2008b) and 0.11 (Gutiérrez et al., 2002a) of the starch intake, without excluding possible higher proportions if...
sources of more resistant starch are used. As a reference, in the study of Gallois et al. (2008b), with a diet containing 113 and 147 g kg\(^{-1}\) DM of starch (wheat and wheat bran) and cellulose, respectively, the amount of starch fermented in the caeco-colic segment of 21-day-weaned rabbits at 28 days old was only 0.1 g day\(^{-1}\), while the amount of cellulose digested in the whole gastrointestinal tract was 0.9 g day\(^{-1}\) (using the mean value of faecal digestibility for cellulose (0.17) reported by Gidenne, 2003). In contrast, in the study of Gutiérrez et al. (2002a), with a diet containing 226 and 141 g kg\(^{-1}\) DM of starch (wheat) and cellulose, respectively, the amount of starch fermented in the caeco-colic segment of 25-day-weaned rabbits at 35 days old was about 20 times higher (2.2 g day\(^{-1}\)), while the amount of cellulose digested in the whole gastrointestinal tract was only about twice as high (2.1 g day\(^{-1}\), using the mean value of faecal digestibility for cellulose given above).

Other studies have indirectly approached the efficiency of the small intestine for starch digestion by measuring the starch concentration in the terminal ileum of growing rabbits, as summarized in Fig. 2.2. Within these studies, large variations in sampling times make it difficult to establish clear conclusions, because the composition of the ileal contents varies according to the feed-intake pattern of the animal, including caecotrophy. Nevertheless, these results suggest that the amount of starch reaching the caecum increases at earlier ages when the rabbit is fed with high-starch diets, and that an interaction with the starch source cannot be excluded. Thus, purified potato starch (uncooked), known to be resistant to intestinal digestion in the piglet, seems to be highly digested in the intestine of the young rabbit; the starch concentration in the ileum with a diet including a high proportion of this starch source was around 10 g kg\(^{-1}\) DM (Pinheiro, 2002), while it reached 110–130 g kg\(^{-1}\) DM with maize-rich diets (Blas et al., 1994; Gidenne et al., 2005a). Similarly, Gutiérrez et al. (2002b) found a higher starch concentration in the terminal ileum of early-weaned 35-day-old rabbits when using pea instead of wheat (60 and 36 g kg\(^{-1}\) DM, respectively). It has also been found that,

**Table 2.6. Ileal digestibility of starch in growing rabbits slaughtered between 19.00 and 22.00 h.**

<table>
<thead>
<tr>
<th>Source of starch</th>
<th>Dietary level of starch (g kg(^{-1}) DM)</th>
<th>Age (days)</th>
<th>Ileal digestibility of starch</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wheat, wheat bran</td>
<td>75</td>
<td>35</td>
<td>0.918</td>
<td>Gutiérrez et al. (2002a)</td>
</tr>
<tr>
<td>Wheat, wheat bran</td>
<td>103</td>
<td>35</td>
<td>0.916</td>
<td>Gutiérrez et al. (2002a)</td>
</tr>
<tr>
<td>Wheat</td>
<td>168</td>
<td>35</td>
<td>0.914</td>
<td>Gutiérrez et al. (2002a)</td>
</tr>
<tr>
<td>Wheat</td>
<td>226</td>
<td>35</td>
<td>0.884</td>
<td>Gutiérrez et al. (2002a)</td>
</tr>
<tr>
<td>Wheat</td>
<td>215</td>
<td>35</td>
<td>0.955</td>
<td>Nicodemus et al. (2003)</td>
</tr>
<tr>
<td>Wheat, wheat flour, wheat bran</td>
<td>279</td>
<td>39</td>
<td>0.968</td>
<td>Nicodemus et al. (2004)</td>
</tr>
<tr>
<td>Wheat</td>
<td>67</td>
<td>35</td>
<td>0.974</td>
<td>Soler et al. (2006)</td>
</tr>
<tr>
<td>Wheat</td>
<td>186</td>
<td>35</td>
<td>0.955</td>
<td>Soler et al. (2006)</td>
</tr>
<tr>
<td>Heat-treated wheat + oat hulls</td>
<td>211</td>
<td>35</td>
<td>0.932</td>
<td>Gómez-Conde et al. (2007)</td>
</tr>
<tr>
<td>Heat-treated wheat + lucerne hay</td>
<td>208</td>
<td>35</td>
<td>0.950</td>
<td>Gómez-Conde et al. (2007)</td>
</tr>
<tr>
<td>Heat-treated wheat + beet-apple pulp</td>
<td>205</td>
<td>35</td>
<td>0.968</td>
<td>Gómez-Conde et al. (2007)</td>
</tr>
<tr>
<td>Wheat, wheat bran</td>
<td>113</td>
<td>28</td>
<td>0.941</td>
<td>Gallois et al. (2008b)</td>
</tr>
<tr>
<td>No starchy ingredients</td>
<td>24</td>
<td>35</td>
<td>0.957</td>
<td>Sánchez-Martínez (2009)</td>
</tr>
<tr>
<td>Wheat</td>
<td>116</td>
<td>35</td>
<td>0.954</td>
<td>Sánchez-Martínez (2009)</td>
</tr>
</tbody>
</table>
compared with ileal digesta, caecal digesta with a maize-rich diet contains 50% less starch in 38-day-old rabbits and 32% less in 49-day-old rabbits, while these figures are 24% and 3%, respectively, with a diet containing less maize (Blas et al., 1994). Finally, as mentioned above, amylase activity in the caecal contents does not differ throughout the growing period, whereas pancreatic amylase secretion increases during this period. This may be interpreted as the result of an increment in the microbial contribution to the pool of amylase in the caecal contents of younger rabbits.

Feed manufacturing process

The oral administration of cooked purified maize starch in adult rabbits causes a clear post-prandial response of glycaemia in peripheral blood. This is similar to that produced by glucose, but somewhat later and more prolonged (Fig. 2.3). However, uncooked purified maize starch hardly affects basal glycaemia. This is due to slower digestion leading to a prolonged but much less pronounced increase in glycaemia in the portal blood, which has little impact on glycaemia in the peripheral blood. It is unlikely that slower digestion results in greater faecal losses of starch, but it could affect the amount of starch fermented in the large intestine.

In practice, it would be interesting to clarify whether, under normal feeding conditions, the feed manufacturing process (involving heating, moisture and pressure) affects starch digestion, especially in young rabbits. Unfortunately, there is little information available on this matter.

Fig. 2.2. Effect of age and dietary starch level or source on starch concentration in the terminal ileum of growing rabbits. 1, Sampling at 150 min after feeding following a 24-h fast (Blas, 1986); 2, sampling at 20.00 h, fed ad libitum (Blas et al., 1994); 3, sampling at 10.00 and 18.00 h (a) or at 13.00 h (b), fed ad libitum (Pinheiro, 2002); 4, sampling at 13.00 h, fed ad libitum (Gidenne et al., 2004a); 5, sampling at 13.00 h, fed ad libitum (Gidenne et al., 2005a). DM, dry matter.
hand, these losses increased with the extruded diet, and the authors suggested that starch may be retrograded after cooling. The alternative is the inclusion of previously extruded or cooked starch sources in pelleted diets. Otutumi et al. (2005) reported improved faecal digestibility of starch from both extruded maize and sorghum in 5- or 9-week-old rabbits. Obviously, no effect of extrusion or cooking on faecal digestibility of starch was found when it was already 0.99 when using raw maize, wheat, triticale, pea or cassava (Gutiérrez et al., 2002b; Furlan et al., 2003, 2004, 2005; Otutumi et al., 2005). On the other hand, these processes could reduce the amount of starch escaping from the small intestine. Significant decreases in the ileal starch concentration in 35-day-old rabbits have been reported by cooking pea or wheat (Gutiérrez et al., 2002b), and especially by extruding maize in 29- or 50-day-old rabbits (Gidenne et al., 2005a).

**Enzyme supplementation**

It is well established that the effectiveness of exogenous enzymes depends on their capacity to resist gastric pH and proteolytic attack by host digestive enzymes, as well as to survive the feed manufacturing process (Inborr, 1989; Bedford, 1995). Yu and Tsen (1993) observed that the incubation of thermostable amylase with rabbit intestinal contents at pH 7.5 did not greatly reduce its activity, while the activity fell to 0.2 in 10 min and reached negligible values in 30 min when the incubation was performed with the contents of the stomach at pH 2–3.2.

Mahagna et al. (1995) observed that the addition of amylase to a sorghum-based diet in meat-type chicks did not improve the faecal digestibility of starch and reduced the amount of amylase present in the intestinal contents, suggesting that the addition of an enzyme having activity similar to that of the pancreatic enzyme appears to have no benefit. Logically, enzyme supplements including α-amylase, even if thermostable, are ineffective in increasing the faecal digestibility of starch when it is already >0.99 in control diets (Fernández et al., 1996; Sequeira and Villamide, 1999; Gutiérrez et al., 2002b). However, a significant reduction of the ileal starch concentration in 35-day-old rabbits fed pea- or wheat-including diets has been reported (Gutiérrez et al., 2002b).
2.2.4 Consequences of starch digestion on fermentative activity in the caeco-colic segment

As discussed earlier, the ileal flow of starch is low. However, since it varies depending on the age of the rabbit and the intake or origin of starch, the activity of the caeco-colic microbiota can potentially be modified. As variations in the level of starch intake are classically linked to inverse variations in fibre intake, the possible effect of undigested starch on microbial activity can only be elucidated by comparing diets with negligible differences in the diverse fibrous constituents, as some diets formulated to compare different starch sources. Gidenne et al. (2005a) found that an increase in the starch content of digesta in the terminal ileum of 7-week-old rabbits (from 19 to 109 g kg\(^{-1}\) DM), as a consequence of replacing exclusively extruded maize with maize, was associated with a reduction of faecal digestibility of cellulose (from 0.24 to 0.15), no changes in the total VFA concentration in the caecal contents and slight changes in the fermentation pattern (increasing the butyrate proportion at the expense of propionate). In 10-week-old rabbits, the effect of dietary starch source (maize versus barley) on caecal fermentation was weak and limited to a higher proportion of isovalerate (Belenguer et al., 2000) or valerate (Xiccato et al., 2002), both minor VFAs being linked to amylo-lytic microbiota (Padilha et al., 1995). In 12-week-old rabbits, Belenguer et al. (2008) reported a lower caecal VFA concentration but a higher butyrate proportion at the expense of acetate and propionate, for rabbits fed a ‘maize’ diet in comparison with a ‘wheat’ diet, but only when the fibre source was lucerne and not sugar beet pulp. In vitro fermentation induced by the corresponding inocula produced a higher butyrate proportion at the expense of acetate, as well as higher gas production at any time, with inocula from rabbits fed a ‘maize’ diet in comparison with a ‘wheat’ diet, whatever the fibre source. According to Bird et al. (2007), a higher amount of resistant starch from maize reaching the hindgut may lead to butyrogenic fermentation in piglets. In adult rabbits, the starch concentration in the ileum ranged from 3 to 27 g kg\(^{-1}\) DM, depending on the source of starch (purified maize starch, barley, pea, maize), while the faecal digestibility of hemicelluloses ranged from 0.37 to 0.54, although changes in the nature of dietary fibre were appreciable because of the high level of inclusion of starch sources (Gidenne and Perez, 1993b). However, Amber (1997) found that both ileal flow and the amount of starch fermented in the caeco-colic segment were slightly greater with a maize-rich diet than with a barley-rich diet, and no relevant differences in the faecal digestibility of the fibres were observed.

In any case, fibre remains the main factor determining fermentative activity. The influence of starch is negligible, although relevant in young animals fed starch-rich diets, especially containing resistant starch.

2.2.5 Role of starch on digestive health

Suckling rabbits

Reviewing a total of 17 studies involving 40 different diets, from 1995 to 2006, it appears that dietary starch levels (also linked to fibre or fat changes) do not greatly affect the mortality rate of the young rabbits, from the time they begin to consume feed until weaning. In fact, the consumption of milk represents an important part of nutrient intake and contributes to health protection, thus explaining that the health status of the suckling rabbit is largely independent of the feed. The protective role of milk intake has been observed (Fortun-Lamothe and Boullier, 2007; Gallois et al., 2007). In the context of epizootic rabbit enteropathy (ERE), Martínez-Paredes et al. (2009) reported very high mortality during week 6 of age in rabbits weaned at 28 days old, but very low mortality in those that remained suckling until 42 days old, where the mortality rate clearly increased during week 8 of age.
Table 2.7. Mortality rates after weaning in growing rabbits fed on diets differing in starch and fibre levels.

<table>
<thead>
<tr>
<th>Dietary fibre</th>
<th>Ratios</th>
<th>Starch (g kg(^{-1}) DM)</th>
<th>Mortality (%)</th>
<th>Comments</th>
<th>No. of rabbits involved</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lignin (ADL)</td>
<td>Cellulose</td>
<td>Hemicelluloses (NDF-ADF)</td>
<td>Water-insoluble pectin(^a)</td>
<td>Lignin to cellulose</td>
<td>DF(^b) to ADF</td>
<td></td>
</tr>
<tr>
<td>51</td>
<td>146</td>
<td>131</td>
<td>44</td>
<td>0.35</td>
<td>0.89</td>
<td>264</td>
</tr>
<tr>
<td>46</td>
<td>167</td>
<td>181</td>
<td>82</td>
<td>0.28</td>
<td>1.23</td>
<td>136</td>
</tr>
<tr>
<td>56</td>
<td>162</td>
<td>134</td>
<td>70</td>
<td>0.35</td>
<td>0.94</td>
<td>127</td>
</tr>
<tr>
<td>56</td>
<td>162</td>
<td>154</td>
<td>87</td>
<td>0.35</td>
<td>1.11</td>
<td>67</td>
</tr>
<tr>
<td>79</td>
<td>150</td>
<td>148</td>
<td>62</td>
<td>0.53</td>
<td>0.92</td>
<td>142</td>
</tr>
<tr>
<td>71</td>
<td>191</td>
<td>151</td>
<td>86</td>
<td>0.37</td>
<td>0.90</td>
<td>47</td>
</tr>
<tr>
<td>34</td>
<td>148</td>
<td>140</td>
<td>63</td>
<td>0.23</td>
<td>1.12</td>
<td>211</td>
</tr>
<tr>
<td>39</td>
<td>168</td>
<td>152</td>
<td>75</td>
<td>0.23</td>
<td>1.10</td>
<td>151</td>
</tr>
<tr>
<td>56</td>
<td>173</td>
<td>204</td>
<td>69</td>
<td>0.33</td>
<td>1.19</td>
<td>87</td>
</tr>
<tr>
<td>96</td>
<td>195</td>
<td>211</td>
<td>63</td>
<td>0.49</td>
<td>0.94</td>
<td>30</td>
</tr>
<tr>
<td>45</td>
<td>170</td>
<td>153</td>
<td>54</td>
<td>0.26</td>
<td>0.96</td>
<td>211</td>
</tr>
<tr>
<td>43</td>
<td>188</td>
<td>177</td>
<td>96</td>
<td>0.23</td>
<td>1.18</td>
<td>108</td>
</tr>
</tbody>
</table>

ADF, acid detergent fibre; ADL, acid detergent lignin; DF, detergent fibre; DM, dry matter; ERE, epizootic rabbit enteropathy; NDF, neutral detergent fibre.

\(^a\)Calculated as uronic acids + galactose + arabinose + rhamnose in insoluble dietary fibre, from values reported by Brillouet et al. (1988), Bach Knudsen (1997) and Llobera and Cañellas (2007).

\(^b\)Digestible fibre as hemicellulose + water-insoluble pectins.

\(^c\)Nutrient content calculated according tables of FEDNA (2003), 6571 and 632 rabbits for the high- and low-starch diet, respectively.
Growing rabbits

It is well established that the susceptibility of rabbits to digestive disorders is greater after weaning, on account of the many physiological changes occurring around this time. A former hypothesis suggested that an overload of rapidly fermentable carbohydrates in the large intestine increases the likelihood of digestive disorders in weaned rabbits (Cheeke and Patton, 1980). The previous sections indicate the limited flow of starch at the ileum. Furthermore, two large-scale studies separating the effects of starch and fibre have revealed a low impact of starch intake on the incidence of digestive disorders in growing rabbits (Gidenne et al., 2004b, 2005a, b). Thus, the effects on digestive health are mainly linked to changes in fibre intake (see Chapters 5 and 10). Accordingly, Gidenne and García (2006) proposed that the restriction of the dietary starch level could be higher than the usual one of 150–155 g kg\(^{-1}\) DM, or even removed.

Table 2.7 summarizes the mortality rates in the post-weaning or full-growing periods in six different studies, with diets varying in starch and fibre content. In all cases, the high-starch diets were maintained above the fibre requirements with the exception of lignin and lignin to cellulose ratio, which are generally lower than the recommended values (≥61 g kg\(^{-1}\) DM and >0.40 respectively). A reduction in the starch to fibre ratio resulted in decreased mortality. In practice, this means that, with respect to digestive health and especially in the context of ERE, fibre requirements should be increased at the expense of starch content.

In the young rabbit (before 6 weeks old), however, the role of starch in digestive troubles may not be excluded, taking into account the already-mentioned variations in the ileal flow of starch (by two, four or 15 times) and its potential impact on caecal microbiota. Nevertheless, Remois et al. (1996) found the inclusion of thermostable amylase and/or amyloglucosidase in a rabbit diet to have no effect on mortality rate. Conversely, Gutiérrez et al. (2002b) reported lower mortality as a consequence of the inclusion of an enzymatic supplement containing α-amylase and reducing the starch concentration at the ileum.

Adult rabbits

The relationship of starch intake to the incidence of digestive disorders in adult rabbits seems to be very limited within the usual dietary starch levels. de Blas et al. (1995) have suggested a trend towards an increase in the replacement rate of rabbit does (associated with more diarrhoea and sudden death at parturition) as the starch content of the diet increases while the fibre content decreases. However, other studies with changes in the starch content, at the expense of those of fibre or fat, have not reported relevant differences in the replacement rate of does (Lebas and Fortun-Lamothe, 1996; Pascual et al., 1998, 1999; Quevedo et al., 2006).

References


Digestion of Sugars and Starch


3 Protein Digestion

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3.1 Some Characteristics of the Main Protein Sources Included in Rabbit Diets

Proteins are macromolecules made up of long chains of amino acid residues covalently linked by peptide bonds to form polypeptide chains. In each protein, these polypeptide chains are folded in three dimensions to form a characteristic tertiary structure. The properties of each amino acid depend on the structure of its chain (size and electric charge). Eight of them (isoleucine, leucine, lysine, methionine, phenylalanine, threonine, tryptophan and valine) are considered essential from a nutritional perspective because their carbon skeletons cannot be synthesized in higher animals.

The nutritive value of a protein is determined not only by its amino acid composition, but also by its digestibility or proportion of ingested protein that is digested in the gut and absorbed as free amino acids. The main factors involved in protein digestibility in rabbits, as in other non-ruminant species, are chemical structure and properties (the insoluble proteins are more resistant to digestion) and accessibility to enzyme activity.

Plant proteins are divided into two major classes: seed and leaf proteins. The main seed proteins are a part of the reserve material that is necessary for the development of the embryo of the future plant. Thus, the cereal endosperm contains approximately 0.7 of total cereal protein; the remainder is in the germ and in the outer bran. The proportions of the different types of proteins (Table 3.1) differ between cereals; the soluble albumins and globulins derive from the cytoplasm of the cells, and the insoluble prolamins and glutelins are storage proteins. The bran includes the aleurone layer of endosperm (inner bran) and, because of this, has higher proportions of both crude protein (CP) and cell walls than the whole grain. The storage proteins are richer in non-essential amino acids (especially glutamic acid and proline) and lower in lysine and threonine than cytoplasmic proteins (Table 3.2). As a consequence, the amino acid composition of cereals depends on the relative proportions of the different types of proteins. Protein from cereals represents about 0.13 of the total protein of rabbit diets (EGRAN databank), whereas for cereal by-products, mainly wheat bran, it is about 0.2.

In general, the grains of legumes and oil seeds contain higher proportions of albumins and globulins than cereal grains (Table 3.1). Thus the proteins of legumes are richer in essential amino acids (especially lysine) and should be more digestible than those of cereals. However, the value of these seeds, when

they are used unprocessed, is limited by the presence of various antinutritive factors (e.g. trypsin inhibitors, lectins or tannins). The protein concentrates used the most in rabbit diets in Europe are soybean and sunflower meals, with inclusion levels of 80–90 g kg\(^{-1}\), which thus comprise from 0.35 to 0.4 of total dietary protein.

The proteins of forage plants are concentrated in the leaves (Table 3.3). Leaf proteins, unlike storage proteins in grains, are concerned with the growth and biochemical functions of the cells. Because of their enzymatic nature, the amino acid composition of plant leaf proteins varies within narrow limits (Makoni et al., 1993). The major portion of leaf proteins are separated from the cell wall by a membrane, although a comparatively small fraction of insoluble protein remains tightly bound to the cellulose of the cell wall. The forage most extensively used in rabbit diets is lucerne hay (0.90 of diets; Villamide et al., 2009) with inclusion levels from 200 to 400 g kg\(^{-1}\). Therefore, lucerne protein represents at least 0.25 of the dietary protein. The protein content of lucerne hay is very variable, mainly depending on its maturation state and drying process. Thus, INRA (2002) tables classify dehydrated lucerne into four groups according to protein content (from <160 to 220–250 g kg\(^{-1}\)).

### 3.2 Protein and Amino Acid Balance

The capability of the different feedstuffs to meet the protein and amino acid require-

<table>
<thead>
<tr>
<th>Lucerne(^a)</th>
<th>Crude protein</th>
<th>Amino acid</th>
<th>Cytoplasmic protein(^b)</th>
<th>Chloroplast membrane(^b)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lucerne hay</td>
<td>191.9</td>
<td>Lysine</td>
<td>0.060</td>
<td>0.051</td>
</tr>
<tr>
<td>Leaves (0.82 hay)</td>
<td>277.5</td>
<td>Sulphur amino acids</td>
<td>0.016</td>
<td>0.013</td>
</tr>
<tr>
<td>Stems (0.18 hay)</td>
<td>125.0</td>
<td>Arginine</td>
<td>0.037</td>
<td>0.051</td>
</tr>
</tbody>
</table>

\(^a\)Alvir et al. (1987).
\(^b\)Makoni et al. (1993).

The ratio of cytoplasmic to chloroplast protein is 0.25:0.75 of total leaf protein.
ments of rabbits depends on the nitrogen unit used (Carabaño et al., 2000). Figure 3.1 shows the relative value of sunflower meal, wheat, wheat shorts and lucerne hay with reference to soybean meal using different units (total CP or methionine, apparent digestible faecal or ileal, and true digestible ileal contents of both protein and methionine). Thus, lucerne hay could represent 0.21 of the soybean meal value if it is evaluated as apparent digestible faecal CP, and 0.42 if it is compared as a crude methionine source (Fig. 3.1). Similarly, the corresponding values for sunflower meal are 0.71 and in 1.46. Therefore, a proper definition of the nitrogen unit both in rabbit requirements and in feedstuff evaluation will allow an increase in the accuracy of diet formulation, reducing the risks of intestinal pathologies such as epizootic rabbit enteropathy (Carabaño et al., 2008) and environmental pollution (Maertens et al., 2005).

### 3.2.1 Crude protein and total amino acids

CP and amino acid contents are the most common units used to express nitrogen requirements and the nutritive value of feedstuffs. The main advantage of this is the considerable amount of available information, because feedstuff evaluation can be directly determined in the laboratory and extrapolated between animal species. However, in experiments designed to determine the amino acid requirements for rabbits, a different apparent faecal digestibility of amino acids was observed depending on whether they came from conventional feeds (from 0.64 to 0.80, on average) or had a synthetic origin (from 0.93 to 1.0) (Taboada et al., 1994, 1996; de Blas et al., 1998). These results emphasize the importance of using digestible instead of total units to express both protein and amino acid requirements for rabbits.

![Fig. 3.1](https://example.com/fig31.png)

**Fig. 3.1.** Relative value of some protein sources in rabbit diets in relation to soybean meal (100) using different nitrogen units (total versus apparent (app.) faecal digestible versus app. ileal digestible versus true ileal digestible crude protein (CP) or methionine (met) contents). Adapted from data of Llorente et al. (2006, 2007a).
3.2.2 Faecal digestibility

Current nitrogen recommendations (see Chapter 6) are expressed in apparent faecal digestible protein (DP), being the DP: digestible energy (DE) ratio directly related to body nitrogen retention and excretion (Trocino et al., 2000). Its use brings a better relationship between dietary supply and rabbit requirements as it considers the high variation of protein digestibility among raw materials (see Chapter 8, Table 8.5). The main features of protein digestibility are difficult to assess through the chemical analyses commonly used in feed evaluation. Only 0.5 and 0.16 of apparent faecal CP digestibility (CPd) variation of complete diets and ingredients, respectively, is explained by the chemical composition. In an inter-laboratory study in which 164 experimental diets were evaluated, Villamide et al. (2009) found a negative correlation between CPd and acid detergent lignin \( (r = -0.7) \). When dietary CP is included in the equation with a positive sign, the validation error of the prediction decreases slightly (from 0.045 to 0.043). Protein digestibility seems to vary more according to type of feed ingredient than to the chemical composition (de Blas et al., 1979, 1984). In the above-mentioned data, a negative relationship of lucerne hay content \( (r = -0.22) \) or of the proportion of dietary protein from lucerne hay \( (r = -0.27) \) with CPd was observed, whereas this relationship was positive for sunflower meal content \( (r = 0.22) \).

Villamide and Fraga (1998) proposed some equations to predict the DP of different groups of feed ingredients (Table 3.4). The best single predictor for all groups is the CP content, although with a different correlation for each group (from 0.904 to 0.967 for fibrous by-products and protein concentrates, respectively). An increase in the CP content of a feedstuff increases its CPd because the proportional contribution of endogenous nitrogen to faecal nitrogen decreases. In the same way, the structure of proteins of feedstuffs with a high CP content (e.g. legume feeds, lucerne leaves) is generally less resistant to digestion. The determination of the proportion of nitrogen bound to acid detergent fibre, which includes heat-damaged protein and nitrogen associated with lignin, permits the estimation of that portion of the nitrogen content of feeds that is indigestible. In fact, a high negative correlation between CPd and nitrogen linked to acid detergent fibre has been observed in both diets \( (r = -0.87, n = 8; \text{Martinez and Fernández, 1980}) \) and feedstuffs \( (r = -0.95, n = 11; \text{Villamide and Fraga, 1998}) \). However, as this analysis is not frequently undertaken in rabbit assays, it is still not possible to obtain more homogeneous and representative data that allow an accurate CPd prediction of the main ingredients included in rabbit diets.

Information regarding the digestibility of amino acids is even more limited. García et al. (1995b) observed that the type of lucerne hay affects both the content and the digestibility of most amino acids. A positive correlation between protein and amino acid digestibility is evident, but there is a difference of 0.07 between extreme CPd values, whereas a variation of 0.14 is obtained for lysine. However, when attempting to predict

<table>
<thead>
<tr>
<th></th>
<th>n</th>
<th>Equation</th>
<th>( R^2 )</th>
<th>RSD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dry forages</td>
<td>26</td>
<td>( \text{DP} = -38.4 + 0.831 \text{CP} )</td>
<td>0.892</td>
<td>3.44</td>
</tr>
<tr>
<td>Fibrous by-products</td>
<td>11</td>
<td>( \text{DP} = 8.73 + 0.716 ) ( -0.184 \text{ADL} )</td>
<td>0.964</td>
<td>3.16</td>
</tr>
<tr>
<td>Cereals and their co-products</td>
<td>27</td>
<td>( \text{DP} = -2.34 + 0.751 \text{CP} )</td>
<td>0.911</td>
<td>3.90</td>
</tr>
<tr>
<td>Protein concentrates</td>
<td>18</td>
<td>( \text{DP} = -55.3 + 0.941 \text{CP} )</td>
<td>0.936</td>
<td>7.14</td>
</tr>
</tbody>
</table>

ADL, acid detergent lignin; CP, crude protein; RSD, residual standard deviation.
the amino acid digestibility of feeds, another problem arises. Not all of the amino acids that disappear from the large intestine are used for protein synthesis, unless they have been reused through soft faeces.

### 3.2.3 Ileal digestibility

The ileum is the last segment of the digestive tract where the amino acids can be absorbed. Therefore, ileal digestibility is considered to give a more precise estimate of the real availability of amino acids for animal protein synthesis both in rabbits (Carabaño et al., 2000) and in other non-ruminant species.

Ileal and faecal digesta contain important amounts of protein of endogenous origin (3.8 and 2.5 g 100 g⁻¹ dry matter DM intake at the ileal and faecal level, respectively; García et al., 2004; Llorente et al., 2005) originating from digestive secretions, epithelial cells and mucins or microorganisms. This endogenous protein represents about 0.64 of the total nitrogen flow at both the ileal and the faecal levels. The relative importance of endogenous protein varies with the DM intake, but also varies with the type of diet and protein origin. Thus, in diets with the same intake and similar chemical composition based on peas or soybean hulls, the endogenous protein at the ileal level represents 0.65 and 0.55, respectively, of the total ileal flux.

The amino acid composition of endogenous protein at the ileal and faecal level is shown in Table 3.5. The endogenous protein at the ileal level contains higher concentrations of some non-essential (glutamic acid, glycine and serine) amino acids than faecal ones. These differences can be explained by the different composition of endogenous secretions when compared to those of microbial origin. Therefore, for a more reliable definition of digestible protein and amino acids of feedstuffs, a correction for endogenous losses must be performed. When this correction is done, a new unit arises and is referred to as ‘true’ (TID) instead of ‘apparent’ (AID) ileal digestibility.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ileum</td>
<td>Ileum</td>
<td></td>
</tr>
<tr>
<td>Cystine</td>
<td>3.1</td>
<td>2.7</td>
<td>3.3</td>
</tr>
<tr>
<td>Histidine</td>
<td>1.6</td>
<td>1.3</td>
<td>1.2</td>
</tr>
<tr>
<td>Isoleucine</td>
<td>3.7</td>
<td>3.8</td>
<td>3.2</td>
</tr>
<tr>
<td>Leucine</td>
<td>4.5</td>
<td>4.3</td>
<td>4.7</td>
</tr>
<tr>
<td>Lysine</td>
<td>3.2</td>
<td>3.6</td>
<td>3.3</td>
</tr>
<tr>
<td>Methionine</td>
<td>0.9</td>
<td>0.8</td>
<td>1.1</td>
</tr>
<tr>
<td>Phenylalanine</td>
<td>1.7</td>
<td>4.1</td>
<td>4.1</td>
</tr>
<tr>
<td>Threonine</td>
<td>4.9</td>
<td>5.6</td>
<td>5.3</td>
</tr>
<tr>
<td>Tyrosine</td>
<td>1.7</td>
<td>3.5</td>
<td>3.4</td>
</tr>
<tr>
<td>Valine</td>
<td>5.3</td>
<td>5.1</td>
<td>4.7</td>
</tr>
<tr>
<td>Total</td>
<td>30.6</td>
<td>34.8</td>
<td>33.2</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Alanine</td>
<td>3.1</td>
<td>3.4</td>
<td>3.7</td>
</tr>
<tr>
<td>Arginine</td>
<td>4.1</td>
<td>3.6</td>
<td>4.3</td>
</tr>
<tr>
<td>Aspartic acid</td>
<td>7.0</td>
<td>7.2</td>
<td>7.0</td>
</tr>
<tr>
<td>Glutamic acid</td>
<td>12.6</td>
<td>12.5</td>
<td>9.1</td>
</tr>
<tr>
<td>Glycine</td>
<td>6.1</td>
<td>8.0</td>
<td>4.1</td>
</tr>
<tr>
<td>Proline</td>
<td>4.8</td>
<td>4.7</td>
<td>3.3</td>
</tr>
<tr>
<td>Serine</td>
<td>6.6</td>
<td>5.8</td>
<td>4.4</td>
</tr>
<tr>
<td>Total</td>
<td>44.3</td>
<td>45.2</td>
<td>35.9</td>
</tr>
</tbody>
</table>
The variation in each amino acid digestibility with respect to the CP ileal digestibility (AID or TID) for soybean meal is shown in Fig. 3.2. Some amino acids (e.g. glycine, threonine) are considerably less digestible than protein (0.14 and 0.06 respectively for AID and TID), whereas others (e.g. methionine, isoleucine) are more digestible (0.06 for AID and 0.05 for TID). Therefore, using the same digestibility value for all amino acids leads to major errors, mainly when apparent values are used, because the endogenous correction further leads to a decrease in the variation of amino acid digestibility with respect to protein digestibility.

Studies using cannulated does have aimed to evaluate the main protein sources of rabbit diets (García et al., 2005; Llorente et al., 2005, 2006, 2007a). Total and ileal (apparent and true) and faecal (apparent) digestible contents of CP and of most limiting amino acids of these raw materials are shown in Table 3.6. Total CP averages 205 g kg\(^{-1}\) DM, because feedstuffs with very low CP content have not been evaluated due to a low effect on dietary nitrogen and the considerable errors associated with its evaluation. Lysine, methionine and threonine represent 0.05, 0.015 and 0.036 on average of the total CP of these feed ingredients. TID of CP is relatively high (average 0.81), while the apparent ileal values (average 0.66) are 0.15 lower due to the great importance of endogenous losses at the ileal level. This effect is especially important for threonine and lysine digestibilities in the evaluation of cereals (0.38 and 0.22 as average higher TID than AID of threonine and lysine, respectively). Apparent faecal digestibility of CP shows intermediate values (average 0.76), indicating an important disappearance of protein in the large intestine (about 0.1), although at a different rate for each amino acid. Threonine seems to disappear to a larger extent (0.12 as average) than lysine (0.01) and methionine, which is apparently more digestible at the ileal than faecal level for 11 out of 15 feedstuffs. AID values are necessary to estimate the total ileal flux arriving in the caecum (indigestible plus endogenous nitrogen), which should be used for microbial growth. This micro-

![Fig. 3.2. Apparent (a) and true (b) ileal amino acid digestibility of soybean meal with respect to its crude protein digestibility (Llorente et al., 2006).]
Table 3.6. Total and digestible protein and amino acid content (g kg\(^{-1}\) dry matter) using different units for the most important sources of protein in rabbit diets (García et al., 2005; Llorente et al., 2005, 2006, 2007a).

<table>
<thead>
<tr>
<th>Source</th>
<th>Total</th>
<th>Apparent faecal digestible</th>
<th>Apparent ileal digestible</th>
<th>True ileal digestible</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>CP</td>
<td>Lys</td>
<td>Met</td>
<td>Thr</td>
</tr>
<tr>
<td>Sunflower meal 1</td>
<td>306</td>
<td>12.8</td>
<td>7.7</td>
<td>12.3</td>
</tr>
<tr>
<td>Sunflower meal 2</td>
<td>393</td>
<td>14.2</td>
<td>8.6</td>
<td>14.3</td>
</tr>
<tr>
<td>Sunflower meal 3</td>
<td>417</td>
<td>15.6</td>
<td>9.7</td>
<td>15.9</td>
</tr>
<tr>
<td>Soybean meal</td>
<td>540</td>
<td>31.9</td>
<td>6.6</td>
<td>20.1</td>
</tr>
<tr>
<td>Full-fat soybean</td>
<td>442</td>
<td>26.5</td>
<td>5.6</td>
<td>17.0</td>
</tr>
<tr>
<td>Peas</td>
<td>283</td>
<td>17.4</td>
<td>2.9</td>
<td>9.4</td>
</tr>
<tr>
<td>Barley</td>
<td>121</td>
<td>4.2</td>
<td>2.0</td>
<td>4.1</td>
</tr>
<tr>
<td>Maize</td>
<td>119</td>
<td>4.2</td>
<td>2.3</td>
<td>4.1</td>
</tr>
<tr>
<td>Wheat</td>
<td>156</td>
<td>6.2</td>
<td>2.6</td>
<td>4.7</td>
</tr>
<tr>
<td>Wheat shorts</td>
<td>186</td>
<td>7.9</td>
<td>2.8</td>
<td>5.7</td>
</tr>
<tr>
<td>Wheat bran</td>
<td>160</td>
<td>6.9</td>
<td>3.2</td>
<td>5.9</td>
</tr>
<tr>
<td>Gluten feed</td>
<td>237</td>
<td>11.7</td>
<td>3.9</td>
<td>8.7</td>
</tr>
<tr>
<td>Soybean hulls</td>
<td>163</td>
<td>11.6</td>
<td>2.4</td>
<td>6.7</td>
</tr>
<tr>
<td>Lucerne hay 1</td>
<td>183</td>
<td>8.9</td>
<td>2.8</td>
<td>7.4</td>
</tr>
<tr>
<td>Lucerne hay 2</td>
<td>202</td>
<td>8.5</td>
<td>2.8</td>
<td>8.3</td>
</tr>
</tbody>
</table>

CP, crude protein.
bial activity in the caecum produces considerable changes in the amino acid composition of digesta and, consequently, the faecal amino acid balance leads to a problematic interpretation (García et al., 2005). Nevertheless, values for CP faecal digestibility of feed ingredients measured in cannulated does fit with average dietary values determined in growing rabbits (0.73, \( n = 164 \); Villamide et al., 2009).

There are important differences among feedstuffs both in protein and in amino acid digestibility (from 0.4 to 0.9), being mainly related to the CP content (\( r = 0.91, 0.81 \) and 0.61 for CPd, AID and TID, respectively) and the type of protein (concentrates versus forages or fibrous by-products). The AIDs of CP and threonine for the different feedstuffs are lower in rabbits than in pigs (INRA, 2002), whereas lysine and methionine AID values are similar. However, both CP and limiting amino acid TID values are higher for almost all feedstuffs than the standard ileal digestibility as determined in pigs, due to the greater importance of endogenous protein in rabbits.

TID determination is time-consuming and expensive because of the use of semipurified diets supplied to cannulated animals, endogenous determinations and amino acid analysis. Therefore, an attempt has been made to predict TIDs from easier and less costly methods. Encouraging results have been obtained using an in vitro method (Llorente et al., 2007b) developed for pigs and adapted to rabbits (Ramos et al., 1992). Although the in vitro CP digestibility is higher than the corresponding in vivo values (0.225, 0.119 and 0.58 on average for AID, CPd and TID, respectively), the precision of their estimation is high. In fact, the coefficients of variation for amino acid TID estimation are <0.057, even when the in vitro CP digestibility is used as predictor. The same process has been undertaken using in vivo CPd as predictor, in order to estimate ileal digestibility of different feed ingredients from the faecal figure. Figure 3.3 shows the estimated relationships for the three main amino acids. These equations have been used to estimate the values shown in Table 8.5 (Chapter 8).

The effect of using ileal digestible units in practical formulation is not exactly known, because rabbit requirements have not yet been determined. However, in a formulation study using ileal digestible threonine instead of total threonine, the cost of the diet decreased (by 3.3% and 2.8% for AID and TID, respectively) and the inclusion of concentrates and cereal by-products instead of forages was favoured (Carabaño et al., 2009). The presence of many fibrous sources in small amounts in rabbit diets has a limited influence on protein formulation irrespective of the unit used because of the very low protein and amino acid content.
3.3 Nitrogen Metabolism in the Caecum

Residues of intestinal digestion and the urea recycled through the blood are potential substrates that allow caecal bacteria to obtain energy and nitrogen for growth. At the end of the ileum, fibre is the main component of the digesta (about 0.70 of total DM), while nitrogen is second in importance (about 0.15 of total DM). However, these figures may be poor indicators of the contribution of each component to microbial growth. Taking into account the low fermentability of the fibre (0.30 for neutral detergent fibre digestibility) and the high content of endogenous substances in nitrogen residues (about 0.64), both components may contribute equally to maintain the resident intestinal microbiota. There is very little information about the quantitative utilization of nitrogen by caecal microbiota. However, early qualitative studies suggest that the caecal microbiota is able to utilize the nitrogen that enters the caecum and transform it into other nitrogen-containing components such as microbial protein and ammonia. Several studies (Yoshida et al., 1968, 1971, 1972; Rerat, 1978), where germ-free animals have been compared with conventional ones, have observed that the caecal content of germ-free rabbits is enriched in different nitrogenous compounds such as urea, free amino acids, peptides and other nitrogen sources of endogenous origin (mucoproteins, pancreatic enzymes or desquamated cells). On the other hand, in conventional animals the caecum contains more ammonia and true protein (enriched in essential amino acids) and lower quantities (up to ten fold) of endogenous components. Further studies focusing on the characterization of the caecal microbiota (Emaldi et al., 1979; Forsythe and Parker, 1985a) have confirmed that the enzymatic capacity of bacteria might be able to hydrolyse digesta that reaches the caeca. These bacteria are in decreasing order of importance, ammonia-users, ureolytic species, proteolytic species, pectinolytic species, xylanolytic species, and cellulytic species. Similar to in the rumen, 0.57 of viable counts are ammonia-users, being Bacillus species, Staphylococcus species and Bacteroides vulgates, with Clostridium clostridioforme the main ureolytic bacteria. Furthermore, some of the most frequent isolated caecal bacteria, Bacteroides species, are the most active genera in mucin digestion (Hill, 1986; Sirotek et al., 2003), one of the non-protein components of the endogenous nitrogen that enters the caecum.

Figure 3.4 shows a tentative scheme of caecal nitrogen metabolism. The proteolytic activity of caecal bacteria results in volatile

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**Fig. 3.4.** Caecal nitrogen metabolism in the rabbit.
fatty acids (VFAs) as energy-yielding compounds and ammonia production for growth. Hoover and Heitmann (1975) observed that 0.95–0.98 of labelled C14-alanine infused into the caecum was located in VFAs, with a small proportion in other amino acids. These labelled VFAs appear rapidly in the blood, showing a maximum at 0.5 h post-infusion. However, the activity of labelled amino acids was negligible or undetected in the blood, suggesting that amino acids are only minimally absorbed, if at all, in the last segments of the intestinal tract. A similar conclusion has been obtained by using labelled lysine in animals that have been prevented from caecotrophy (Belenguer et al., 2005).

Ammonia produced from protein and urea hydrolysis is partially used by caecal bacteria as the main substrate for protein synthesis (Hoover and Heitmann, 1975; Forsythe and Parker, 1985a,b) and another portion is absorbed in the caecal wall, contributing to urea production (0.27 of total urea; Forsythe and Parker, 1985c). The extent of these processes has not yet been totally quantified; however, the characteristics of the diet affect total ammonia caecal concentration and the incorporation of ammonia nitrogen into microbial protein.

An increment in caecal ammonia concentration has been related by different authors (Carabaño et al., 1988, 1989, 1997; Fraga et al., 1991; Motta-Ferreira et al., 1996; García et al., 1995a, 2000, 2002; Nicodemus et al., 2002) to the dietary DE:DP ratio (Fig. 3.5). When the protein intake exceeds nutritional requirements, urea recycling from the blood to the caecum may be increased, leading to an elevation in the caecal ammonia concentration. According to Forsythe and Parker (1985c) the contribution of urea-nitrogen to the caecal ammonia pool is around 0.25 of caecal ammonia turnover.

Other dietary factors can affect the caecal ammonia concentration. The presence of condensed tannins or other phenolic components may decrease the proteolytic capacity of caecal microorganisms, as occurs in the rumen (Waghorn et al., 1987). This may in part explain the low caecal ammonia values obtained in diets that contain grape pomace or olive leaves (Motta-Ferreira et al., 1996; García et al., 2000).

The efficacy of synthesis of microbial protein from ammonia seems to be more related to the characteristics of dietary carbohydrates than to nitrogenous composition. The caecal ammonia concentration in the rabbit fed a balanced diet is in the range of 4.5–6 mmol l⁻¹ ammonia, which seems adequate for appropriate protein microbial synthesis when compared with the ammonia concentration of the rumen. However, the availability of energy in the caecum could be

![Fig. 3.5.](image)

Effect of the dietary energy (E) to protein (P) ratio on caecal ammonia concentration. DCP, digestible crude protein.
the limiting factor for bacterial growth. Inclusion in the diet of increasing levels of fibre or sources of fibre with high lignification decreases VFA production and the protein concentration in the caecum (strongly related to microbial protein; Carabaño et al., 1988; Fraga et al., 1991). On the other hand, the inclusion of more fermentable fibre (linked to pectins or hemicelluloses) or fibre with a high proportion of fine particles (<0.3 mm in diameter) improves both total and microbial nitrogen in the soft faeces (García et al., 2000).

The final result of bacterial activity in the caecum is a substantial change in the amino acid composition of the protein that enters the caecum from the ileum. According to García et al. (2005) the bacterial activity leads to an enrichment in lysine (0.072 g day\(^{-1}\); 0.63 of the ileal flow), methionine (0.026 g day\(^{-1}\); 0.95 of the ileal flow) and threonine (0.059 g day\(^{-1}\); 0.40 of the ileal flow) when comparing total excretion in hard and soft faeces with apparent ileal flow. Furthermore, the enrichment of these essential amino acids was higher in diets where the faeces contained a higher proportion of microbial protein.

### 3.4 Protein Digestion in Young Rabbits

The study of protein digestion in young rabbits has acquired more relevance in the last 10 years due to its influence on intestinal health (Carabaño et al., 2009). Although information has increased with respect to the previous decade, important gaps in knowledge in some aspects make it difficult to interpret results. Methodological aspects related to markers, sample collection and analysis (Gallois et al., 2008), diet design or endogenous losses may explain some conflicting results. The enzymatic capacity to digest protein at the ileal level seems to be higher than that for some nutrients, but, around weaning, the enzymatic capacity for protein digestion may be limited (see Chapter 1). However, the AID of CP in young rabbits (from 21 to 35 days) shows similar or even higher figures compared to that of older animals (42–45 days) (Table 3.7) (García-Ruiz et al., 2006; Gallois et al., 2008). The lack of stability in intake (feed and caecotrophy) and caecal contents or a lower importance of endogenous losses could explain these discrepancies. In fact, when the average values of AID are compared to faecal ones, only 0.71 of the total digested protein is digested at the ileum in young rabbits. This figure is lower than those reported in adult animals, which vary from 0.82 to 0.90 for forages or concentrates, respectively (Table 3.7).

Protein digestion in young rabbits is not only limited for forages. Gutiérrez et al. (2003) also found differences in ileal digestibility among protein sources with the same faecal digestibility. The low protein digestion at the ileum and a greater limitation of

<table>
<thead>
<tr>
<th>Age (days)</th>
<th>Apparent ileal CP digestibility (AID)</th>
<th>Apparent faecal CP digestibility (CPd)</th>
<th>Apparent caecal CP digestibility</th>
<th>Ratio AID:CPd</th>
</tr>
</thead>
<tbody>
<tr>
<td>28(^a)</td>
<td>0.691</td>
<td>0.791</td>
<td>0.100</td>
<td>0.872</td>
</tr>
<tr>
<td>42(^a)</td>
<td>0.681</td>
<td>0.782</td>
<td>0.101</td>
<td>0.871</td>
</tr>
<tr>
<td>35(^a)</td>
<td>0.701</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>45(^a)</td>
<td>0.678</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>35(^c)</td>
<td>0.643</td>
<td>0.789</td>
<td>0.146</td>
<td>0.712</td>
</tr>
<tr>
<td>Adult does(^d)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Concentrates</td>
<td>0.732</td>
<td>0.813</td>
<td>0.081</td>
<td>0.900</td>
</tr>
<tr>
<td>Forages</td>
<td>0.548</td>
<td>0.671</td>
<td>0.122</td>
<td>0.817</td>
</tr>
</tbody>
</table>

\(^a\)Gallois et al. (2008).

\(^b\)Garcia-Ruiz et al. (2006), age effect \(P = 0.003\).

\(^c\)Average data from diets with a 0.6:0.4 ratio of concentrate to forage \((n = 9)\) (Gutiérrez et al., 2003; Chamorro et al., 2007; Gómez-Conde et al., 2007).

\(^d\)Average data from feed ingredients. Concentrates: oilseed and meals and cereals; forages: cereal by-products, lucerne and soybean hulls (Carabaño et al., 2009).
energy in the caecum (lower proportion of VFAs) agrees with a higher caecal ammonia concentration observed in the youngest when compared with adult rabbits (García et al., 2002; Gidenne and Fortun-Lamothe, 2002; Nicodemus et al., 2002).

### 3.5 Soft Faeces and Protein Digestibility

The main effect of soft faeces ingestion is protein reutilization. There are many data on the chemical composition of soft faeces, suggesting that the composition is similar to that of the caecal contents. When comparing the protein concentration of soft faeces with that of the caecal contents of rabbits, employing the same methodology, the following equation was obtained (Fig. 3.6):

\[
y = 100.88 + 0.689 (\pm 0.8) \times, \quad R^2 = 0.712, \quad P < 0.001, \quad n = 31,
\]

where \(y\) = CP (g kg\(^{-1}\) DM) of soft faeces, and \(x\) = CP (g kg\(^{-1}\) DM) of caecal contents.

The CP concentration of caecal contents in these studies ranged from 190 to 340 g kg\(^{-1}\) and the corresponding CP concentration in soft faeces from 230 to 335 g kg\(^{-1}\). This suggests that the nitrogen content of the mucosal envelope, which covers the caecal contents in the last sections of the large intestine to produce the final soft faeces, may be near to 55 g kg\(^{-1}\). The amount of endogenous nitrogen secreted daily as the mucosal envelope is near to 0.05 g day\(^{-1}\) (assuming an average soft faeces production of 20 g DM day\(^{-1}\), with 280 g CP kg\(^{-1}\) DM). In the same way, the relationship between the crude fibre content of the soft faeces and caecal contents is high (\(r = 0.90\)), although the crude fibre of soft faeces is 8% lower than that of the caecal contents (Carabaño et al., 1988).

The amount of soft faeces excretion varies with age, physiological status, diet and faeces collection method. Using data from 36 diets supplied to rabbits weighing 2.0 kg live weight, in which a wooden collar was worn at 08.00 h and removed 24 h later, and with diets in which the neutral detergent fibre content varied from 230 to 550 g kg\(^{-1}\) (Carabaño et al., 1988, 1989, 1997; García et al., 1995a, 2000; Motta-Ferreira et al., 1996; Nicodemus, 2000; Nicodemus et al., 2006), the excretion of soft faeces ranged from 15 to 32 g DM day\(^{-1}\), with a

![Fig. 3.6. Effect of the crude protein (CP) concentration of the caecal contents on the CP of soft faeces (Carabaño et al., 1988, 1989, 1997; Fraga et al., 1991; García et al., 1995a; Motta-Ferreira et al., 1996). DM, dry matter.](image)
mean value of 21.3 g DM day\(^{-1}\) (i.e. around 10 g DM kg\(^{-1}\) live weight). On the other hand, Gidenne and Lebas (1987) reported a constant and positive relationship \((r = 0.64)\) between the amount of hard and soft faeces excreted from 28 to 133 days of age.

The contribution of soft faeces to the total CP intake varies, according to the chemical composition of the diet and the composition of the feed ingredients within diets, from 0.104 to 0.286 (using the studies previously mentioned). The highest values are associated with low-digestible diets that increase the flow of indigestible protein to the caecum (Motta-Ferreira et al., 1996), whereas the lowest values are related to diets that supply small amounts of protein to the caecum (García et al., 2000). In practical diets, the protein supply from the soft faeces is, on average, 0.18 of the total CP intake.

The values for soft faeces production obtained in lactating does fed conventional diets are higher (around 35 g DM day\(^{-1}\)) than in growing rabbits (Lorente et al., 1988; Nicodemus et al., 1999), but the contribution of soft faeces to the total CP intake (around 0.16) is maintained in the same range because of the higher feed intake of the does. In this sense, the microbial lysine contribution to tissue lysine in lactating does estimated by using milk and liver lysine enrichments is 0.23 and 0.19, respectively (Abecia et al., 2007). These values are similar to those obtained in growing rabbits using liver enrichment (0.23; Belenguer et al., 2005).

As a result, the ingestion of soft faeces improves the diet’s apparent faecal digestibility, especially protein digestibility. When coprophagy is prevented, DM digestibility decreases slightly by around 0–0.17, but CP digestibility decreases by 0.04 to 0.72. This decrease is higher when the dietary protein comes from forage than from mixed or non-forage diets (Fraga and de Blas, 1977; Fraga et al., 1984; Raharjo et al., 1990; Sakaguchi et al., 1992; Merino, 1994). However, in these studies the CPd of rabbits not practising caecotrophy has been calculated including the sum of nitrogen of hard and soft faeces, as nitrogen excreted. As a consequence of the higher proportion of nitrogen excreted, the apparent protein digestibility was lower in animals not practising caecotrophy than in those practising it. When the soft faeces’ nitrogen was removed from the balance, this difference disappeared (Merino, 1994) and coprophagy had no effect on either the ileal digestibility of DM (0.537 versus 0.572) or the ileal digestibility of CP (0.723 versus 0.721) in cannulated adult females (Merino and Carabaño, 2003).

On the other hand, the ingestion of soft faeces increases the ileal flow of DM (by 0.31), nitrogen (by 0.18) and the endogenous proportion of the most important limiting essential amino acids (arginine, lysine, phenylalanine and threonine) (García et al., 2004). This increment in the endogenous ileal nitrogen flow is due to the increase in the DM intake, as both variables are closely related (García et al., 2004).

As a consequence, the ingestion of soft faeces enables rabbits to use part of the amino acids that will not be absorbed beyond the ileum for microbial protein synthesis. In fact, caecotrophy contributes to recycling 0.36 of the total protein excreted (soft plus hard faeces), which is mainly of bacterial origin (around 0.67; García et al., 2005). Moreover, this protein is a good source of the most frequently limiting amino acids (methionine, lysine and threonine), as has been reported by several authors (Proto, 1976; Nicodemus et al., 1999; García et al., 2004, 2005). However, the amino acid composition of soft faeces is influenced by its microbial content, differences in the digestibility of dietary amino acids and the contribution of nitrogen of endogenous sources (especially that of the mucosal envelope). The enrichment in these essential amino acids of soft faeces is higher when animals are fed on diets that increase the synthesis of microbial nitrogen (García et al., 2005).

In lactating does fed on diets that meet all of the essential nutrient requirements, Nicodemus et al. (1999) observed that the contributions of some of the essential amino acids (methionine, lysine, threonine, isoleucine and valine) are higher than the CP contribution of soft faeces to nutrient intake (0.15; see Fig. 3.7). However, the difference
was only significant in the case of threonine, which has been identified as the third most limiting amino acid in rabbits. The main results of digestive processes, which determine the amino acid composition of soft faeces with respect to diet composition, are the increase in the methionine to cystine ratio as a consequence of the relatively high value of this ratio in bacterial protein and the decrease in arginine, histidine and phenylalanine. Therefore, the amino acid supply from soft faeces from conventional diets does not seem to be enough to alter the dietary amino acid pattern in order to meet the essential amino acid requirements of rabbits.

Many advances have been achieved in understanding nitrogen digestion of rabbits, which has allowed the adaptation of rabbit nutrition to meet commercial changes, environmental laws and so on. However, many opportunities exist to further expand the knowledge of amino acid metabolism to meet specific requirements, mainly in young animals, for improving the health and welfare of rabbits.

References


Fat Digestion

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4.1 Chemical Structure and Physical Properties of Fats

The word ‘fat’ is commonly misused to indicate all lipids, a complex group of organic substances composed of carbon, hydrogen and oxygen, and characterized by solubility in organic apolar solvents. Lipids can be divided into simple lipids, which do not contain fatty acids (FAs), and complex lipids, which are esterified with FAs (Fig. 4.1).

Triglycerides can be considered ‘true’ fats because they represent the most typical form of energy accumulation in animal and vegetable organisms. Therefore, only these lipids have real nutritional importance. Triglycerides are the highest energy-yielding component of feeds, yielding an average of 2.25 times more energy than other components (i.e. protein and starch). Triglycerides are formed by one glycerol molecule, a trihydric alcohol, to which three FAs are esterified (Fig. 4.2). The physical, chemical and nutritive properties of triglycerides depend on the characteristics of their FAs (Fig. 4.3) – in other words, the number of carbon atoms and the number and position of unsaturated bonds (double bonds).

The number of carbon atoms in triglyceride FAs is usually even due to the addition or subtraction of a pair of carbon atoms during FA synthesis or oxidation in higher animals and plants. In comparison, microorganisms are capable of producing FAs with odd numbers of carbon atoms. Short-chain FAs are formed of two (C2) to eight (C8) carbon atoms, medium-chain FAs have 10–16 carbon atoms and long-chain FAs have ≥18 carbon atoms (up to 22–24).

The number of double bonds is the second distinctive property of FAs: saturated FAs (SFAs) contain only single (saturated) bonds between carbon atoms, while unsaturated FAs (UFAs) present one or more double (unsaturated) bonds. UFAs can be divided into monounsaturated FAs with only one double bond (e.g. oleic acid, C18:1) and polyunsaturated FAs (PUFAs) with two (e.g. linoleic acid, C18:2) or more (up to six) double bonds. The position of the double bonds in the carbon chain determines the ability of PUFAs to act as precursors of other essential compounds, such as hormones. Mammals and other higher animals are able to elongate the carbon chain (e.g. from C18 to C22), but are unable to insert double bonds between the carbon atoms in position 1 (n-1 or ω-1) of the chain (starting from the terminal methyl group, CH₃-), and the carbon in position 9 (n-9 or ω-9). For this reason, animals need an adequate quantity of
essential FAs (EFAs) in their diet, namely n-3 FAs (with their first double bond in position 3) and n-6 FAs (with their first double bond in position 6). Dietary EFAs are primarily represented by linoleic acid (C18:2, n-6) and linolenic acid (C18:3, n-3). The former is essential for the synthesis of arachidonic acid (C20:4, n-6), the precursor of several compounds essential for heart, retina and brain functions, and the immune system (Enser, 1984; Sanders, 1988). A low n-6 to n-3 FA ratio in foods is beneficial in reducing the incidence of cardiovascular and thrombotic diseases in humans.

The melting point of fats and oils is influenced by FA chemical structure and falls with a decrease in the number of carbon atoms and an increase in the number of unsaturated bonds (Table 4.1). For this
reason, triglycerides of vegetable origin are liquid at room temperature (oils) being richer in unsaturated bonds, while triglycerides of animal origin are solid (fats).

The degree of unsaturation also affects fat stability because double bonds are easily oxidized, thereby forming hydroperoxides that are rapidly broken down into short-chain compounds, which give fat and feed their typically rancid odour. The rate of oxidation rises as the number of unsaturated bonds increases. As an example, linolenic acid (C18:3) is oxidized ten times more rapidly than linoleic acid (C18:2), which is oxidized ten times more rapidly than oleic acid (C18:1) (Enser, 1984).

A chemical index of the degree of unsaturation is the iodine number: the weight (in g) of iodine capable of reacting with 100 g of triglyceride. In fact, two iodine atoms can react with each double bond. In animal and vegetable lipids, the iodine number represents the average degree of unsaturation of the entire pool of FAs composing the triglycerides (Table 4.1).

### 4.2 Fats in Rabbit Feeds

The triglycerides usually present in rabbit feed and pure vegetable and animal fats contain primarily medium- or long-chain FAs (C14–C20), with C16 and C18 FAs being most common (Table 4.1). Rabbits have no specific fat requirements apart from a small amount of EFAs (INRA, 1989). This need is easily met by the lipids contained in the conventional raw materials used in the formulation of compound feeds. Traditionally, rabbit feeding is based on low- or moderate-energy diets. Pure fats or oils are therefore not added and the dietary crude fat content does not exceed 30–35 g kg⁻¹, on average. Only a part of this chemical constituent is composed of triglycerides, given that the larger part is composed of other compounds such as glycolipids, phospholipids, waxes, carotenoids and saponins (Fig. 4.1) (Van Soest, 1982; Cheeke, 1987). All of these substances are soluble in ethyl ether or petroleum ether, the solvents utilized to determine the crude fat or ether extract (EE) content using the Weende feed analysis method. These lipids possess rather low digestibility and metabolic utilization and are therefore considered scarcely relevant from a nutritional point of view.

Currently, the addition of limited amounts of fats (10–30 g kg⁻¹) to rabbit diets is rather common under intensive rearing systems (Maertens, 1998). In breeding does, this increases dietary energy concentrations and stimulates energy intake by the female, who experiences a severe energy deficit during lactation (Xiccato, 1996; Pascual et al., 2003, 2006). In weaning rabbits, the dietary addition of fat may improve

<table>
<thead>
<tr>
<th>Type of fat</th>
<th>Iodine number</th>
<th>Melting point (°C)</th>
<th>Fatty acids (g 100 g⁻¹ of total oil)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vegetable oils</td>
<td></td>
<td></td>
<td>16:0</td>
</tr>
<tr>
<td>Coconut oil</td>
<td>8–10</td>
<td>20–35</td>
<td>8.0</td>
</tr>
<tr>
<td>Maize oil</td>
<td>115–127</td>
<td>&lt;20</td>
<td>12.0</td>
</tr>
<tr>
<td>Olive oil</td>
<td>79–90</td>
<td>20</td>
<td>14.0</td>
</tr>
<tr>
<td>Safflower oil</td>
<td>145</td>
<td>&lt;20</td>
<td>12.3</td>
</tr>
<tr>
<td>Soybean oil</td>
<td>130–138</td>
<td>&lt;20</td>
<td>11.5</td>
</tr>
<tr>
<td>Animal fats</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Butter</td>
<td>26–38</td>
<td>28–36</td>
<td>27.0</td>
</tr>
<tr>
<td>Beef tallow</td>
<td>35–45</td>
<td>36–45</td>
<td>26.2</td>
</tr>
<tr>
<td>Lard</td>
<td>50–65</td>
<td>35–45</td>
<td>25.7</td>
</tr>
<tr>
<td>Poultry fat</td>
<td>80</td>
<td>&lt;30</td>
<td>21.4</td>
</tr>
</tbody>
</table>
body condition, stimulate development of the immune system and improve health (Xiccato et al., 2003; Maertens et al., 2005). In growing and fattening rabbits, fat supplementation may favourably change the FA profile and the nutritional value of rabbit meat (Hernández, 2008).

### 4.3 Triglyceride Digestion and Utilization

Triglycerides ingested by rabbits in the diet are submitted to rather complex processes of digestion and absorption but, on the whole, these processes are similar to those observed in other non-ruminants (Brindley, 1984; Freeman, 1984; Cheeke, 1987). Triglycerides are emulsified and then hydrolysed by lipolytic enzymes before being finally absorbed in the small intestine.

As observed in different species (human, pig, rat, cattle), the digestive process in suckling animals begins in the stomach, where pre-duodenal lipases (oral and sometimes gastric) hydrolyse the naturally emulsified fat in milk. In suckling rabbits, gastric lipases account for most of the lipolytic activity (Marounek et al., 1995; Zita et al., 2008).

After weaning, triglycerides from solid feed require emulsification, and therefore fat digestion occurs only in the small intestine (schematically shown in Fig. 4.4). Fat emulsification is promoted by bile salts secreted by the liver. Bile salts mix with fat droplets, breaking them down into minute globules that can be easily hydrolysed by pancreatic lipase and other lipolytic enzymes (colipase, sterol ester hydrolase and phospholipase). The enzymatic hydrolysis of triglycerides leads to the separation of glycerol, free FAs and monoglycerides, which remain emulsified with bile, forming microscopic micelles. These micelles move to the microvilli of the

![Fig. 4.4. Digestion and absorption of triglycerides in rabbits and other non-ruminants. NEFA, non-esterified fatty acids.](image-url)
duodenum and jejunum, which absorb the glycerol, free FAs and monoglycerides. Bile salts are left in the intestinal lumen, and are then absorbed lower down the tract (distal ileum). Fat absorption is passive (i.e. a non-energy-consuming process). When absorbed into enterocytes, glycerol and short-chain FAs (C<12) go directly into the blood, where they circulate as non-esterified FAs. Monoglycerides and medium- and long-chain FAs (C>12) are re-synthesized as triglycerides. Droplets of synthesized triglycerides are then covered by a lipoprotein membrane, forming chylomicrons that pass to the lymph circulation system.

Long-chain FAs that are esterified in the triglycerides of chylomicrons can be metabolized as energy sources or either incorporated directly into fat tissue or transferred unchanged to the milk. For this reason, the composition of the dietary fat can significantly influence fat characteristics in the rabbit carcass (Hernández, 2008) or the FA composition of the milk fat (Pascual et al., 2003).

FAs that are not digested can pass through the lowest part of gut and be excreted in the faeces as soaps or enter the caecum, where UFAs are hydrogenated by the caecal microflora. A bacterial de novo FA synthesis also occurs in caecotrophs: SFAs are the most abundant, followed by monounsaturated FAs and PUFAs; a rather high proportion of branched-chain FAs is also observed (0.07–0.13 of FAs) (Leiber et al., 2008). In addition, an increase of FAs with odd numbers of carbon atoms (C15 and C17) has been observed (Fernández et al., 1994).

### 4.4 Effect of the Analytical Method on Digestibility Determination

The precise determination of EE digestibility (EEd) is essential for a correct energy evaluation of complete diets and raw materials for rabbits. The digestible energy content of rabbit feeds can be calculated with good precision (1% residual standard deviation) whenever the digestible EE and other digestible components (crude protein, crude fibre CF and nitrogen-free extract) are known (Jentsch et al., 1963; Maertens et al., 1988; Villamide et al., 2009). Despite the considerable amount of experimental data available on fat digestion efficiency in rabbits, however, the results often conflict, with EEd ranging from 0.40 to 0.95.

Parigi Bini et al. (1974) demonstrated the presence of soaps (salts of FAs and calcium ions) in rabbit faeces, which was favoured by a high level of dietary calcium (mostly present in lucerne meal). Such soaps are only partially detected by ether extraction analysis, therefore providing an underestimation of the undigested lipids (faecal lipids) and consequently an overestimation of EEd (Table 4.2). These authors suggested submitting the faecal samples to acid hydrolysis treatment (in 5N hydrochloric acid) before extraction with ether in order to remove the FAs from the soap bonds. Using this method, Maertens et al. (1986) were able to recalculate the EEd values previously found for different types of fat (0.87–0.88) and obtain the correct values of 0.64 (beef tallow), 0.74 (lard), 0.75 (mixed

<table>
<thead>
<tr>
<th>Type of fat</th>
<th>Added fat in the diet (g kg⁻¹)</th>
<th>EE in the diet (g kg⁻¹)</th>
<th>Before HCl treatment</th>
<th>After HCl treatment</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Basal diet</td>
<td>0</td>
<td>37</td>
<td>0.72</td>
<td>0.52</td>
<td>Parigi Bini et al. (1974)</td>
</tr>
<tr>
<td>Beef tallow</td>
<td>50</td>
<td>92</td>
<td>0.85</td>
<td>0.67</td>
<td></td>
</tr>
<tr>
<td></td>
<td>100</td>
<td>137</td>
<td>0.89</td>
<td>0.69</td>
<td></td>
</tr>
<tr>
<td>Basal diet</td>
<td>0</td>
<td>22</td>
<td>0.69</td>
<td>0.57</td>
<td>Maertens et al. (1986)</td>
</tr>
<tr>
<td>Beef tallow</td>
<td>60</td>
<td>81</td>
<td>0.88</td>
<td>0.64</td>
<td></td>
</tr>
<tr>
<td>Lard</td>
<td>60</td>
<td>84</td>
<td>0.87</td>
<td>0.74</td>
<td></td>
</tr>
<tr>
<td>Mixed fat</td>
<td>60</td>
<td>84</td>
<td>0.88</td>
<td>0.75</td>
<td></td>
</tr>
<tr>
<td>Soybean oil</td>
<td>60</td>
<td>81</td>
<td>0.87</td>
<td>0.83</td>
<td></td>
</tr>
</tbody>
</table>

Table 4.2. Digestibility coefficients of ether extract (EEd) before and after acid hydrolysis of faeces.
fat) and 0.83 (soybean oil) after acid hydrolysis pre-treatment (Table 4.2).

The European Group on Rabbit Nutrition (EGRAN) has performed various ring-tests on the chemical analyses of rabbit diets and faeces (Xiccato et al., 1996; EGRAN, 2001). It demonstrated poor reproducibility among laboratories for EE values of feed and faeces; the EEd calculated in different laboratories ranged from 0.57 to 0.73 for the same diet.

### 4.5 Effect of the Level and Source of Fat

Lipid digestibility depends primarily on the level and source of added fats. The EEd of a non-added-fat diet, which contains 25–30 g structural lipids kg⁻¹ is rather low (0.45–0.65), while the EEd of added-fat diets is higher because of the higher digestibility (0.85–0.95) of pure fats (Tables 4.3 and 4.4). In three diets with 0 (control), 30 and 60 g added fat kg⁻¹, Santomá et al. (1987) observed a significant increase in the EEd as the fat level increased (0.64, 0.75 and 0.79, respectively), without any significant difference among fat sources (see Tables 4.3 and 4.4 for more information).

The increase in EEd with higher levels of dietary fat could also be ascribed to a reduction in dry matter (DM) intake. This usually occurs when feed of a higher dietary energy value is given, as a consequence of the chemostatic regulation of appetite (Forbes, 1995; Xiccato, 1996). The decrease of DM intake is associated with a lower transit of digesta and consequently leads to increased digestion efficiency (Falcão e Cunha et al., 2004).

On the other hand, when the inclusion of fat is high (e.g. >60 g kg⁻¹) EEd may decrease (Table 4.3), probably because both digestible energy and microflora activity in the caecum are negatively affected by the excessive fat (Maertens et al., 1986; Falcão e Cunha et al., 1996). Falcão e Cunha et al. (2004) observed reduced cellulolytic and pectinolytic activity in the caecum and caecotrophes of rabbits fed high-fat diets. Similar negative effects of high dietary fat supplementation have been reported in ruminants (Van Soest, 1982; Hess et al.,

### Table 4.3. Effect of the inclusion of added fat on the digestibility of ether extract (EEd).

<table>
<thead>
<tr>
<th>Type of full-fat seed</th>
<th>Inclusion level (g kg⁻¹)</th>
<th>EE in the diet (g kg⁻¹)</th>
<th>EEd of diets</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Basal diet</td>
<td>0</td>
<td>22</td>
<td>0.57</td>
<td>Maertens et al. (1986)</td>
</tr>
<tr>
<td>Beef tallow</td>
<td>60</td>
<td>81</td>
<td>0.64</td>
<td></td>
</tr>
<tr>
<td></td>
<td>120</td>
<td>133</td>
<td>0.52</td>
<td></td>
</tr>
<tr>
<td>Lard</td>
<td>60</td>
<td>84</td>
<td>0.74</td>
<td></td>
</tr>
<tr>
<td></td>
<td>120</td>
<td>136</td>
<td>0.71</td>
<td></td>
</tr>
<tr>
<td>Basal diet</td>
<td>0</td>
<td>46</td>
<td>0.82</td>
<td>Falcão e Cunha et al. (1996)</td>
</tr>
<tr>
<td>Beef tallow</td>
<td>40</td>
<td>83</td>
<td>0.86</td>
<td></td>
</tr>
<tr>
<td></td>
<td>80</td>
<td>113</td>
<td>0.84</td>
<td></td>
</tr>
</tbody>
</table>

### Table 4.4. Effect of the inclusion of full-fat oilseed on the digestibility of ether extract (EEd).

<table>
<thead>
<tr>
<th>Type of fat</th>
<th>Inclusion level (g kg⁻¹)</th>
<th>EE in the diet (g kg⁻¹)</th>
<th>EEd of diets</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Basal diet</td>
<td>0</td>
<td>28</td>
<td>0.70</td>
<td>Cavani et al. (1996)</td>
</tr>
<tr>
<td>Soybean</td>
<td>30</td>
<td>32</td>
<td>0.82</td>
<td></td>
</tr>
<tr>
<td></td>
<td>60</td>
<td>38</td>
<td>0.85</td>
<td></td>
</tr>
<tr>
<td>Basal diet</td>
<td>0</td>
<td>29</td>
<td>0.71</td>
<td>Maertens et al. (1996)</td>
</tr>
<tr>
<td>Oilseed rape</td>
<td>300</td>
<td>156</td>
<td>0.89</td>
<td></td>
</tr>
<tr>
<td>Basal diet</td>
<td>0</td>
<td>48</td>
<td>0.83</td>
<td>Peiretti and Meineri (2008)</td>
</tr>
<tr>
<td>Golden flax seed</td>
<td>80</td>
<td>66</td>
<td>0.87</td>
<td></td>
</tr>
<tr>
<td></td>
<td>160</td>
<td>89</td>
<td>0.91</td>
<td></td>
</tr>
</tbody>
</table>
poultry (Wiseman, 1984) and horses (Jansen et al., 2007).

The differences observed in EEd among various sources of fats are mostly attributed to their molecular structure and chemical bonds. The fat contained in conventional raw materials is linked to plant structures and is therefore poorly digested. Pure added fats are much more easily digestible, and this is also true for the fat contained in heated (or extruded) full-fat oil seeds, such as full-fat soybean or golden flax seed (Table 4.4). The digestibility coefficients (calculated by difference) of pure fats are 0.86 (beef tallow), 0.90 (oleins) and 0.98 (soybean oil) (Fernández et al., 1994). These values are similar to those listed by Maertens et al. (1990) for animal fat (0.90) and soybean oil (0.95). The EEd of full-fat soybean has been found to be very high (0.97), and only slightly higher than that of full-fat rapeseed (0.93) (Maertens et al., 1996).

It is unclear whether EEd variation depends on the proportion of the different FAs in the various sources of fat. As in other species, a negative relationship has been reported between the degree of saturation and fat digestibility in rabbits: more saturated fats (e.g. beef tallow, lard) are less digestible than unsaturated fats (e.g. sunflower or soybean oils), probably because the latter are more easily emulsified and therefore digested in the gut (Maertens et al., 1986; Santomá et al., 1987).

Fernández et al. (1994) found that the digestibility of different FAs depends more on the source of fat than the degree of saturation. In two diets – diet T containing 30 g beef tallow kg⁻¹ and diet S containing 30 g soybean oil kg⁻¹ – the digestibility coefficients of the two principal saturated FAs (i.e. C16:0, C18:0) were higher (0.67 and 0.71) in the T diet than in the S diet (0.57 and 0.31). On the other hand, the PUFAs (i.e. C18:2, C18:3) were more digestible in the more unsaturated diet (0.69 and 0.80 in the T diet versus 0.84 and 0.84 in the S diet). The authors concluded that UFA:SFA ratio in dietary fats may not be the most appropriate predictor of fat digestibility.

The digestibility evaluation of specific FAs in rabbits is probably affected by a systematic bias due to the lipid metabolism of caecal microflora. This changes the composition of faecal fat and modifies the ratio between digestible SFAs and UFAs (Fernández et al., 1994; Fernández-Carmona et al., 2000; Leiber et al., 2008).

### 4.6 Effect of Age, Physiological State and Nutritive Level

The digestion efficiency for fat, as well as for other nutrients, varies during the life of a rabbit. Rabbit milk contains a high quantity of lipids (100–150 g kg⁻¹, depending on lactation period) that are easily digested and absorbed by suckling rabbits, which show high gastric lipase activity (Marounek et al., 1995; Dojana et al., 1998; Maertens et al., 2006). Parigi Bini et al. (1991b) estimated the digestibility of milk and solid feed during weaning (from 21 to 26 days of age) by multiple regression: the EEd of milk was found to be practically complete (0.97), while the EEd of pelleted food was much lower (0.74).

When kits begin to consume solid feed, fat digestion occurs in the small intestine. Lipase activity in the total proteic extract of the gastric mucosa decreases from 15 to 43 days of age and is quite low or nearly absent in older rabbits (Marounek et al., 1995; Dojana et al., 1998). In contrast, the lipase activity of the pancreas, intestinal mucosa and small intestinal contents increases from 25 to 32 and 42 days of age (Debray et al., 2003; Gidenne et al., 2007; Gallois et al., 2008). Similarly, lipase activity significantly increases in the colon of rabbits from 28 to 90 days of age (Marounek et al., 1995), but remains unchanged in the caecum of kits from 15 to 35 days of age (Zita et al., 2008).

Several studies have compared digestibility efficiency in growing and adult rabbits. Digestibility coefficients of different components tend either to decrease or remain constant with age, but EEd seems to follow an opposite trend. Evans and Jebelian (1982) observed increasing EEd from 0.78 at 5 weeks to 0.82 at 8 weeks. Xiccato and
Cinetto (1988) confirmed these results, with EEd rising from 0.72 at 7 weeks to 0.79 at 12 weeks. Conversely, other authors have observed higher EEd values in recently weaned rabbits (4–5 weeks) than in older rabbits (7–10 weeks) (Fernández et al., 1994; Debray et al., 2003; Gidenne et al., 2007).

Comparing digestibility efficiency in growing rabbits and adult does fed a non-added-fat diet, Xiccato et al. (1992) observed a significantly lower EEd in young rabbits than in adult rabbits (0.58 versus 0.64), but no differences between the sexes in growing rabbits or between physiological states (pregnant or not pregnant) in adult does. The latter results confirm an absence of any effect attributable to reproductive status, as was previously observed by Parigi Bini et al. (1991a) in does during late pregnancy, early lactation and late lactation.

The influence of age and physiological state on EEd may be attributed to variations in feed intake, as suggested by Fernández et al. (1994). However, this hypothesis does not agree with the results achieved by other studies involving growing rabbits (Xiccato and Cinetto, 1988; Xiccato et al., 1992) and lactating does (Parigi Bini et al., 1992) on either ad libitum or restricted feeding diets. Parigi Bini (1971) found a very significant negative correlation between the dietary CF level and both DM digestibility (DMd) and EEd:

$$\text{DMd} = 0.812 - 1.17 \times 10^{-3} \text{CF (g kg}^{-1} \text{DM)}, \quad r = -0.929.$$  
$$\text{EEd} = 0.993 - 2.08 \times 10^{-3} \text{CF (g kg}^{-1} \text{DM}), \quad r = -0.936.$$  

The decrease in both DMd and EEd is linked to the poorer diet quality, higher feed intake and faster transit rate that occur when higher fibre levels are given. However, even if this research was unable to distinguish between the simultaneous effects of the crude fibre level on DMd and EEd, it appears that the decrease of EEd with increasing CF levels is probably accentuated by a negative interaction between fibre and crude fat. The latter is strictly associated with cell walls in non-added-fat diets.

### References


5 Fibre Digestion

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5.1 Introduction

Dietary fibre (DF) the major fraction of rabbit diets, where it accounts for 0.40–0.50 of the total diet (Table 5.1). The importance of fibre is due to its influence on the rate of passage of digesta and mucosa functionality, and its role as a substrate for microbiota. All of these factors are related to rabbit health (see Chapter 10) and performance. The concept of fibre, its quantification and its characterization as either the total fraction or different constituents have been discussed extensively. The difficulty in reaching agreement on the concept of DF is based on its complex physical structure and the chemical composition of cell walls, the considerable diversity of cells types (and, accordingly, of cell walls) that constitute different plant tissues and the wide and different physiological effects of the different constituents. This all implies that the quantitative analysis of the whole components of this fraction cannot be obtained by any analytical method or combination of methods.

This chapter initially considers the definition and structure of the different classes of fibre and of cell wall constituents, followed by a description of some analytical methods employed for animal or human feeds. Second, the effects of fibre on rabbit digestion are described.

5.2 Dietary Fibre in Animal Feeds: Definition, Physicochemical Properties and Analysis

5.2.1 Plant cell wall and dietary fibre: definition

The terms ‘cell wall’ and ‘dietary fibre’ are often imprecisely used because they refer to a common plant structure. However, they do not describe the same chemical components and therefore do not have the same meaning. Accordingly, it is useful to define separately these two terms. The term ‘plant cell walls’ (PCWs) must be employed when describing the structure of the plant cell, which is extremely complex. PCWs are not uniform: the type, size and shape of the walls are closely linked to the function of the cell within the plant (e.g. skeletal tissue, seeds). In general, PCWs consist of a series of polysaccharides often associated and/or substituted with glycoproteins (extensin), phenolic compounds and acetic acid, together with, in some cells, the phenolic polymer lignin. Cutin and silica are also found in the walls and/or in the middle lamella. A growing plant cell is gradually enveloped by a primary wall that contains a few cellulosic microfibrils and some non-cellulosic components such as pectic substances. During plant
ageing, some cells develop a thick secondary cell wall consisting of cellulose embedded in a polysaccharide and lignin matrix (Selvendran et al., 1987; McDougall et al., 1996). Thus, in brief, the PCW is formed of cellulose microfibrils (the backbone) embedded in a matrix of lignins, hemicelluloses, pectins and proteins (Fig. 5.1).

The concept of DF used in human nutrition, and extended to all mammals, is defined as the feed components resistant to mammalian endogenous enzyme digestion and absorption, and that can be partially or totally fermented in the gut. This empirical ‘catch-all’ definition describes mainly PCW constituents, but also other substances including resistant starch, oligosaccharides, fructans, protein linked to the cell wall (De Vries and Rader, 2005). Another approximation is the DF for herbivores defined by Mertens (2003) as the indigestible or slowly digested organic matter of feeds that occupies space in the gastrointestinal tract, mainly insoluble fibre. It excludes rapidly fermenting and soluble carbohydrates (e.g. oligosaccharides, fructans).

Table 5.1. Levels of fibre (g kg⁻¹ dry matter) in complete experimental feeds used for the growing rabbit (n = 111) (Villamide et al., 2009).

<table>
<thead>
<tr>
<th>Residue analysed</th>
<th>Mean</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Neutral detergent fibre (aNDFom)</td>
<td>368</td>
<td>248–443</td>
</tr>
<tr>
<td>Acid detergent fibre (ADFom)</td>
<td>196</td>
<td>135–284</td>
</tr>
<tr>
<td>Acid detergent lignin</td>
<td>56</td>
<td>27–195</td>
</tr>
<tr>
<td>Hemicelluloses</td>
<td>172</td>
<td>59–251</td>
</tr>
<tr>
<td>Cellulose</td>
<td>140</td>
<td>42–220</td>
</tr>
<tr>
<td>Crude fibre</td>
<td>166</td>
<td>122–244</td>
</tr>
<tr>
<td>Soluble fibre&lt;sup&gt;a&lt;/sup&gt;</td>
<td>109</td>
<td>61–188</td>
</tr>
<tr>
<td>Total dietary fibre&lt;sup&gt;b&lt;/sup&gt;</td>
<td>478</td>
<td>352–560</td>
</tr>
<tr>
<td>Other feed constituents</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Starch</td>
<td>176</td>
<td>82–324</td>
</tr>
<tr>
<td>Sugars&lt;sup&gt;a&lt;/sup&gt;</td>
<td>53</td>
<td>31–163</td>
</tr>
<tr>
<td>Crude protein</td>
<td>176</td>
<td>134–232</td>
</tr>
<tr>
<td>Ether extract</td>
<td>32</td>
<td>10–71</td>
</tr>
</tbody>
</table>

---

<sup>a</sup>Calculated as: OM – CP – EE – aNDFom – starch – sugars.

<sup>b</sup>Calculated as: aNDFom + soluble fibre.

<sup>c</sup>Estimated according to ingredient composition (FEDNA, 2003).

---

Fig. 5.1. Schematic representation of plant cell walls and their main constituents.
5.2.2 Biochemical characteristics of dietary fibre

The chemical features of DF are highly variable, depending on many factors such as molecular weight, the nature of the monomers and types of linkages. Accordingly, the chemical features of DF are one of the main factors responsible for variations in digestibility; thus, it is important to describe them. With the exception of lignin, cell wall constituents are predominantly polysaccharides composed of neutral and/or acidic sugars. They can be determined using sophisticated extraction techniques, and examples of their concentration in some feedstuffs are given in the Table 5.2.

There are two main groups of DF components according to their location, chemical structure and properties (Fig. 5.2):

- Cell wall components:
  - Water-insoluble polymers: lignin, cellulose, hemicelluloses and pectic substances.
  - Cytoplasm components:
    - Oligosaccharides, fructans, resistant starch and mannans.

Water-soluble polysaccharides and oligosaccharides include several classes of molecules with a degree of polymerization ranging from about 15 to >2000 (β-glucans). Most of them are insoluble in ethanol (80% v/v). Examples include soluble hemicelluloses such as arabinoxylans (in wheat, oats and barley, approximately 20–40 g kg⁻¹ dry matter (DM)) and β-glucans (in barley or oat, approximately 10–30 g kg⁻¹ DM), oligosaccharides such as α-galactosides (in lupin, pea or soya seeds, 50–80 g kg⁻¹ DM) and soluble pectic substances (fruit or beet pulp, from 100 to 400 g kg⁻¹ DM). Because of their highly variable structures, no satisfactory method is at present available to determine precisely the amount of these compounds in animal feeds.

### Table 5.2. Proximate composition of cell wall constituents (g kg⁻¹ DM) in some raw materials used in rabbit feeds, according to several methods of analysis.

<table>
<thead>
<tr>
<th>Ingredients</th>
<th>Wheat straw</th>
<th>Wheat bran</th>
<th>Dehydrated lucerne</th>
<th>Sugarbeet pulp</th>
<th>Sunflower meal</th>
<th>Soybean hulls</th>
<th>Grape pomace</th>
</tr>
</thead>
<tbody>
<tr>
<td>aNDFom</td>
<td>800</td>
<td>450</td>
<td>450</td>
<td>460</td>
<td>420</td>
<td>620</td>
<td>640</td>
</tr>
<tr>
<td>ADFom</td>
<td>540</td>
<td>110</td>
<td>340</td>
<td>220</td>
<td>310</td>
<td>440</td>
<td>540</td>
</tr>
<tr>
<td>ADL</td>
<td>160</td>
<td>30</td>
<td>80</td>
<td>20</td>
<td>100</td>
<td>20</td>
<td>340</td>
</tr>
<tr>
<td>NDSF</td>
<td>–</td>
<td>30</td>
<td>180</td>
<td>300</td>
<td>–</td>
<td>220</td>
<td>–</td>
</tr>
<tr>
<td>Crude fibre&lt;sup&gt;a&lt;/sup&gt;</td>
<td>400</td>
<td>100</td>
<td>270</td>
<td>190</td>
<td>260</td>
<td>360</td>
<td>260</td>
</tr>
<tr>
<td>WICW</td>
<td>840</td>
<td>450</td>
<td>470</td>
<td>500</td>
<td>380</td>
<td>720</td>
<td>690</td>
</tr>
<tr>
<td>INSP</td>
<td>550</td>
<td>360</td>
<td>330</td>
<td>640</td>
<td>260</td>
<td>550</td>
<td>360</td>
</tr>
<tr>
<td>Rhamnose</td>
<td>&lt;10</td>
<td>&lt;10</td>
<td>&lt;10</td>
<td>110</td>
<td>&lt;10</td>
<td>110</td>
<td>&lt;10</td>
</tr>
<tr>
<td>Arabinose</td>
<td>20</td>
<td>80</td>
<td>20</td>
<td>180</td>
<td>30</td>
<td>40</td>
<td>&lt;10</td>
</tr>
<tr>
<td>Xylose</td>
<td>180</td>
<td>160</td>
<td>60</td>
<td>20</td>
<td>50</td>
<td>70</td>
<td>80</td>
</tr>
<tr>
<td>Mannose</td>
<td>&lt;10</td>
<td>&lt;10</td>
<td>&lt;10</td>
<td>10</td>
<td>10</td>
<td>60</td>
<td>20</td>
</tr>
<tr>
<td>Galactose</td>
<td>&lt;10</td>
<td>&lt;10</td>
<td>&lt;10</td>
<td>40</td>
<td>10</td>
<td>20</td>
<td>20</td>
</tr>
<tr>
<td>Glucose</td>
<td>330</td>
<td>90</td>
<td>190</td>
<td>190</td>
<td>110</td>
<td>290</td>
<td>190</td>
</tr>
<tr>
<td>Uronic acids</td>
<td>20</td>
<td>20</td>
<td>70</td>
<td>180</td>
<td>50</td>
<td>60</td>
<td>50</td>
</tr>
<tr>
<td>SNSP</td>
<td>10</td>
<td>30</td>
<td>30</td>
<td>100</td>
<td>10</td>
<td>20</td>
<td>10</td>
</tr>
<tr>
<td>Crude protein</td>
<td>30</td>
<td>150</td>
<td>160</td>
<td>90</td>
<td>340</td>
<td>110</td>
<td>130</td>
</tr>
</tbody>
</table>

ADFom, acid detergent fibre expressed free of ash; ADL, acid detergent lignin (Van Soest et al., 1991); aNDFom, neutral detergent fibre assayed with a heat stable amylase and expressed free of ash; INSP, insoluble non-starch polysaccharides (not including the lignin, determined by direct monomeric analysis of cell wall polysaccharides) (Englyst, 1989; Barry et al., 1990); NDSF, neutral detergent soluble fibre (Hall et al., 1997, 1999); SNSP, water-soluble non-starch polysaccharides (Brilouet et al., 1988; Englyst, 1989); WICW, water-insoluble cell wall (including lignin) (Carré and Brillouet, 1989).

<sup>a</sup>According to the Weende method (AOAC, 2000: official method 962.10).
Pectic substances are a group of polysaccharides present in the middle lamellae and closely associated with the primary cell wall, especially in the primary cells (young tissues) of dicotyledonous plants, such as in legume seeds (40–140 g kg\(^{-1}\) DM in soybean, pea, faba bean and white lupin), and also in fruit and pulp. Pectic substances correspond to several classes of polymers, including pectins (rhamnogalacturonan backbone and side chains of arabinose and galactose) and neutral polysaccharides (arabinans, galactans, arabinogalactans) frequently associated with pectins. Their extraction requires the use of a chelating agent such as ammonium oxalate or ethylene diamine tetra-acetic acid (EDTA) (present in the solution for determining neutral detergent fibre (NDF) so pectins are not completely recovered in NDF analysis, as described below). Pectins of the middle lamellae serve as an adhesive in plant tissue, cementing plant cells together.

Cellulose is the major structural polysaccharide of the PCW and the most widespread polymer on earth. It is a homopolymer (in contrast to hemicelluloses and pectins), formed from linear chains of \(\beta[1\rightarrow4]\) linked D-glucopyranosyl units (whereas starch is formed of \(\alpha[1\rightarrow4]\) linked D-glucopyranosyl chains). The degree of polymerization is usually around 8000–10,000. Individual glucan chains aggregate (hydrogen bonding) to form microfibrils and may serve as the backbone of the plant. Thus, cellulose is only soluble in strong acid solutions (i.e. 72% sulphuric acid), where it is hydrolysed. Quantitatively, cellulose represents 400–500 g kg\(^{-1}\) DM in the hulls of legume and oilseeds, 100–300 g kg\(^{-1}\) DM in forages and beet pulp and 30–150 g kg\(^{-1}\) DM in oilseeds or legume seeds. Most cereal grains contain small quantities of cellulose (10–50 g kg\(^{-1}\) DM), except for oats (100 g kg\(^{-1}\) DM).

The hemicelluloses are a group of several polysaccharides, with a lower degree of polymerization than cellulose. They have a \(\beta[1\rightarrow4]\) linked backbone of xylose, mannose or glucose residues that can form extensive hydrogen bonds with cellulose. Xyloglucans are the major hemicelluloses of the primary cell wall in dicotyledonous plants (legumes, seeds), whereas mixed linked glucans (\(\beta[1\rightarrow3,4]\)) and arabinoxylans are the predominant hemicelluloses in cereal seeds (the latter two include partly water-soluble and water-insoluble polymers, described above). Hemicelluloses include other branched heteropolymers (units linked \(\beta[1\rightarrow3], \beta[1\rightarrow6]\),

---

**Fig. 5.2.** Dietary fibre constituents and their quantification by different methods (adapted from Hall, 2003).

ADFom, acid detergent fibre expressed free of ash; ADL, acid detergent lignin; aNDFom, neutral detergent fibre assayed with a heat stable amylase and expressed free of ash; NDSF, neutral detergent soluble fibre; NSP, non-starch polysaccharides. *Includes other associated compounds: proteins, tannins, waxes, saponins, suberin, phytates, phytosterols.*
Polymers formed of linear chains of pentose (linked $\beta[1 \rightarrow 4]$) such as xylans (in secondary walls) or hexose such as mannans (in palm kernel meal) are also considered as hemicelluloses. Pentosans such as xylans and arabinoxylans are soluble in weak basic solutions (5–10%) or in hot dilute acids (5% sulphuric acid). Hexosans such as mannans, glucomannans or galactans can only be dissolved in strong basic solutions (17–24%).

Quantitatively, hemicelluloses constitute of 100–250 g kg$^{-1}$ DM in forages and agro-industrial by-products (brans, oilseeds and legume seeds, hulls and pulp) and about 20–120 g kg$^{-1}$ DM in grains and roots.

Lignin is a non-carbohydrate constituent of the cell wall. It can be described as a highly branched and complex three-dimensional network (with a high molecular weight), built up from three phenylpropane units (coniferic, coumarilic and sinapinic acid). Lignin networks tend to fix the other polymers in place, exclude water and make the cell wall more rigid and resistant to various agents, such as bacterial enzymes. Most concentrate feeds and young forages contain less than 50 g lignin kg$^{-1}$. The degree of lignification of the PCW may reach 120 g kg$^{-1}$ with ageing in forages or up to 590 g kg$^{-1}$ in grape-seed meal.

Other constituents are also present in PCWs, but in smaller quantities. Minerals, such as silica, are essentially found in graminaceous leaves. Phenolic acids are chemically linked to hemicelluloses and lignin in graminaceous plants. Some proteins are linked to cell walls through intermolecular bonds from amino acids such as tyrosine, and thus resist standard extractions. In addition, plant epidermal cells may be covered by a complex lipid (cutin for aerial parts, suberin for underground structures), which can encrust and embed the cell walls, making them impermeable to water.

Other phenolic compounds can also be mentioned – for example, condensed tannins, which may exist in higher plants. They form cross-linkages with protein and other molecules. They may be included in the sum of indigestible polysaccharides plus lignin. However, condensed tannins, lignins and indigestible proteins are closely related because indigestible complexes of these substances are common in plants (Van Soest, 1994).

Methods for estimating the dietary fibre content of animal feeds

According to the DF definition, DF can only be truly measured by the digestive process of the animal. Currently no method is totally adequate to quantify or fractionate DF due to its complexity. Although many methods have been developed to estimate the DF content in animal feeds, none of them corresponds to a precise DF fraction. Detailed methods for estimating the dietary fibre content of animal feeds

Fig. 5.3. Gravimetric methods for the determination of dietary fibre and identification of the residue of analysis. ADF, acid detergent fibre; ADL, acid detergent lignin (Van-Soest et al., 1991); NDF, neutral detergent fibre; NSP, non-starch polysaccharides; TDF, total dietary fibre (Lee et al., 1992; Li, 1995); WICW, water-insoluble cell wall (Carré and Brillouet, 1989). *According to the Weende technique (AOAC, 2000: official method 962.10).
reviews have been published on this subject (Hall, 2003; Mertens, 2003; De Vries and Rader, 2005). Accordingly, only those techniques currently used in rabbit feeding are described here (Fig. 5.3).

Initially, the crude fibre method (AOAC, 2000: official method 962.10) must be mentioned because it is highly reproducible, quick, simple, cheap and frequently used all over the world. This technique extracts a fibrous residue after acidic followed by basic hydrolysis. The main drawback of this method lies in the high variability in the chemical composition of its residue as, depending on the feed, it can dissolve up to 60% cellulose, 80% pentosans and 95% lignin. As a consequence, crude fibre digestibility was higher than that of nitrogen-free extract in 25% of the feeds studied by Morrison (1956). For these reasons, this method is not very useful in explaining the effects exerted by fibre on the animal. However, it has been demonstrated to be very useful in predicting dietary energy value (Wiseman et al., 1992) or within a raw material to verify the fibre content compared to tables.

The main alternative to the crude fibre method is the sequential procedure of Van Soest, developed in 1967 and successively updated (Mertens, 2003). The NDF method was designed to isolate insoluble DF components in PCWs by using a hot neutral detergent solution – cellulose, hemicelluloses and lignin (Mertens, 2002) – as the majority of pectin substances are partially solubilized. This method has been criticized due to its variability among laboratories, especially when the results are compared with those obtained with other feed constituents (Xiccato et al., 1996). This variability is partially due to the different procedures that can be used to perform the method (with heat-stable amylase and/or sodium sulfite or not, ash free or not), but usually described with the same reference (Uden et al., 2005).

The acid detergent fibre (ADF) (AOAC, 2000: official method 973.18) method isolates cellulose and lignin, the worst digested fibrous fractions, using a hot acid detergent solution. It is designed to be performed after NDF analysis, as pectins are retained when it is performed directly. As with the crude fibre method, the ADF method is very useful in predicting dietary energy value (Wiseman et al., 1992). Finally, the lignin fraction is isolated from the ADF residue after removal of the cellulose by using a strong acid solution at room temperature (Robertson and Van Soest, 1981).

The main advantage of this sequential methodology is that it is possible to obtain an approximate estimation of lignin (ADL), cellulose (ADF-ADL) and hemicellulose (NDF-ADF) content. In addition, it is relatively quick, simple and economical, and has an acceptable reproducibility when used in a standardized methodology (EGRAN, 2001). Furthermore, it improves the fractionation of the cell wall. These methods have been complemented by the estimation of the fibre dissolved by the neutral detergent solution (NDSF: neutral detergent soluble fibre) (Hall et al., 1997), which mainly includes fructans, galactans, β-glucans and pectic substances. However, the determination of NDSF is too difficult to be used as routine analysis, as occurs with other methods used to estimate soluble fibre.

Another approach is to estimate DF as the sum of non-starch polysaccharides (NSP) and lignin. Several methods are available to estimate total, soluble and insoluble NSP (Bach Knudsen, 2001; De Vries and Rader, 2005), where the non-fibrous components are extracted by solubilization, enzymatic hydrolysis or a combination of both procedures. Once isolated, the fibre residue can be quantified gravimetrically (by weighing the residue) or chemically (by hydrolysing the residue and determining its single constituents: sugars and lignin). According to these procedures, there are three types of methodologies: chemical-gravimetric, enzymatic-gravimetric and enzymatic-chemical. In this way the total DF can be quantified (NSP and lignin) and separated into insoluble and soluble fibre (in aqueous solution), and the monosaccharide composition obtained. The combination of the
monosaccharide composition of fibre with additional chemical information may allow a better description of fibre structure that influence its physicochemical properties and, accordingly, the effect exerted on an animal’s digestive physiology and digestibility. However, these methodologies are complex, expensive and have relatively low reproducibility (especially for monomers determination). They are difficult to implement as routine analysis.

Dietary insoluble fibre can also be estimated by using near infra-red (NIR) technology. NIR technology has demonstrated usefulness in predicting dietary DM, protein, fat, starch and even digestible energy value. However, ADF is the only fibre fraction that can be adequately estimated by this technique, whereas both NDF and ADL are estimated with lower precision (Xiccato et al., 2003).

In conclusion, the determination of the fibre content of a compound feed (Table 5.1) or raw material (Table 5.2) is highly variable, depending on the analytical method of estimation. The choice of which definition is to be used by the nutritionist thus depends on the type of information required (to relate to digestive processes, predict the nutritive value).

### 5.2.3 Physicochemical properties of fibre related to digestion: particle size, water-holding capacity and buffering capacity

As described below, part of the fibre requirements of rabbits are related to the effect of the large-size fibre particles on the passage rate of digesta through the gut. Particle size can be measured by dry or wet sieving and varies largely depending on the fibre source. Table 5.3 shows the distribution of particle size of several commercial sources of fibre, once pelleted. Part of this variation can be explained by differences in chemical composition, hydration capacity or previous processing. Dietary particle size is modified considerably during feed manufacturing (see Chapter 11) and it is essential to determine the particle size profile on pellets (Lebas and Lamboley, 1999) instead of the meal. Particle size is reduced by pelleting and by successive millings, even using sieves of the same diameter. In this way Morisse (1982), by milling a feed one or three times with the same sieve size (4 mm), observed an increase in the proportion of fine particles (<0.25 mm) from 0.31 to 0.74. On the other hand, fibre composition is not homogeneous among particles of different size within the same feed: the proportion of

<table>
<thead>
<tr>
<th>Particle size, mm</th>
<th>Paprika meal</th>
<th>Olive leaves</th>
<th>Lucerne hay</th>
<th>Soybean hulls</th>
<th>NaOH-barley straw</th>
<th>Sunflower husk</th>
<th>Grape-seed meal</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt;0.160</td>
<td>0.84</td>
<td>0.54</td>
<td>0.54</td>
<td>0.24</td>
<td>0.23</td>
<td>0.02</td>
<td>0.31</td>
</tr>
<tr>
<td>&gt;0.315</td>
<td>0.07</td>
<td>0.38</td>
<td>0.29</td>
<td>0.53</td>
<td>0.54</td>
<td>0.74</td>
<td>0.45</td>
</tr>
<tr>
<td>&gt;1.250</td>
<td>0.00</td>
<td>0.09</td>
<td>0.02</td>
<td>0.04</td>
<td>0.11</td>
<td>0.04</td>
<td>0.02</td>
</tr>
</tbody>
</table>

**Table 5.3.** Particle size determined by wet sieving, hydration and buffering capacity of some commercial sources of fibre after pelleting (García et al., 1999, 2002a).

<table>
<thead>
<tr>
<th></th>
<th>Paprika meal</th>
<th>Olive leaves</th>
<th>Lucerne hay</th>
<th>Soybean hulls</th>
<th>NaOH-barley straw</th>
<th>Sunflower husk</th>
<th>Grape-seed meal</th>
</tr>
</thead>
<tbody>
<tr>
<td>Water-holding capacity, %</td>
<td>389</td>
<td>408</td>
<td>581</td>
<td>600</td>
<td>652</td>
<td>654</td>
<td>192</td>
</tr>
<tr>
<td>Acid-buffering capacitya</td>
<td>210</td>
<td>93</td>
<td>151</td>
<td>88</td>
<td>57</td>
<td>64</td>
<td>–</td>
</tr>
<tr>
<td>NDF</td>
<td>13</td>
<td>32</td>
<td>24</td>
<td>0</td>
<td>22</td>
<td>19</td>
<td>–</td>
</tr>
<tr>
<td>Base-buffering capacitya</td>
<td>121</td>
<td>47</td>
<td>54</td>
<td>27</td>
<td>0</td>
<td>27</td>
<td>–</td>
</tr>
<tr>
<td>NDF</td>
<td>12</td>
<td>24</td>
<td>17</td>
<td>33</td>
<td>13</td>
<td>20</td>
<td>–</td>
</tr>
</tbody>
</table>

NDF, neutral detergent fibre.

*Microequivalents of HCl/NaOH required to lower/increase the pH of 0.5 g dry matter suspended in 50 ml water to pH 4/9, divided by total pH change.
lignin tends to increase with particle size, because the force required to shear the fibrous particles increases with lignification (Van Soest, 1994).

Some PCW constituents, such as β-glucans, pentosans and pectins, are hydrophilic, tending to form gels in solution, whereas lignin is more hydrophobic. These gel-forming substances may increase digesta viscosity, as observed with sugarbeet pulp (Volek et al., 2005), but their consequences have not been studied in rabbits. On the other hand, hydration is negatively related to the size of the fibre particles (Van Soest, 1994).

The cation-exchange capacity of fibre is dependent on its concentration of carboxyl, amino and hydroxyl groups (Van Soest et al., 1991). Accordingly, buffering capacity is high in feeds containing pectins (e.g. 70 mEq 100 g⁻¹ for beet pulp) and is also significantly higher in legumes than in grasses (50 versus 13 mEq 100 g⁻¹). This is in agreement with the lower buffering capacity of the insoluble fibre fraction (NDF) compared to the complete raw material (Table 5.3). The type of fibre would interact with the acidity of caecal contents, as the base-buffering capacity of fibrous sources is positively related to that of dry caecal content, which is also related to the pH of dry caecal content (Garcia et al., 2000a).

5.3 Degradation of Dietary Fibre in the Rabbit Digestive Tract

5.3.1 Precaecal digestion of fibre

Traditionally, fermentation of DF has been considered to be a post-ileal activity of the endogenous microbiota. However, there is evidence that some components of structural carbohydrates are degraded prior to entering the caecum of rabbits. This has also been observed in other non-ruminant species such as pigs and poultry.

The extent of precaecal fibre digestion in rabbits varies from 0.07 to 0.19 for crude fibre (Yu et al., 1987), from 0.05 to 0.43 for NDF (Gidenne and Ruckebusch, 1989; Merino and Carabaño, 1992) and from 0 to 0.37 for NSP (Gidenne, 1992; Carabaño et al., 2001). It must be pointed out that the values obtained using NDF and crude fibre with respect to those obtained with NSP might be overestimated due to solubilization and filtration of cell wall components that would be considered digested. When NSPs have been analysed, arabinose and uronic acids, typical monomers of pectic substances, have been found to be largely digested before the ileum (from 0.2 to 0.5). On the other hand, glucose and xylose, the major monomers in most fibre sources, showed a much lower ileal digestibility (0–0.2). These results imply that around 0.4 (from 0.2 to 0.8) of total digestible fibre (including water-soluble NSP) is degraded before the caecum, which is similar to that observed in pigs (Bach Knudsen, 2001). This could be explained by the ‘remaining’ fibrolytic activity from microbiota (Gómez-Conde et al., 2007, 2009) supplied by soft faeces, and observed in the stomach and small intestine (Marounek et al., 1995) by the established microbiota.

5.3.2 Caecal digestion of fibre

Fibre degradation is ultimately determined by microbial activity, digesta retention time in the caecum and fibre chemical composition and structure.

Microbial activity

Most of the effects exerted by fibre on the rabbit digestive physiology depend on its hydrolysis and fermentation by the digestive microbiota. However, it is difficult to study the influence of any dietary component on the microbiota, as traditional cultivation techniques only recover around one-quarter of the intestinal microbiota. For this reason, other indirect techniques have been used, such as the volatile fatty acid (VFA) concentration, microbial nitrogen synthesized or fibrolytic activity. The caecal microbial population secretes enzymes capable of hydrolysing the main compo-
ponents of DF. Greater enzymatic activity for degrading pectins and hemicelluloses than for degrading cellulose has been detected in several studies (Marounek et al., 1995; Jehl and Gidenne, 1996; Falcão e Cunha et al., 2004). These results are parallel to the faecal digestibility of the corresponding DF constituents in rabbits (Table 5.4), and are also consistent with the smaller counts of cellulytic bacteria in the rabbit caecum compared with xylanolytic or pectinolytic bacteria (Boulahrouf et al., 1991).

The dietary factors affecting the variability of fibrolytic activity have not been extensively studied, but it seems that low-fibre diets might reduce or have no effect on fibrinolytic activity at the caecum (Gidenne et al., 2000, 2002). The type of fibre influences fibrolytic activity, with sugarbeet pulp increasing caecal pectinolytic and cellulytic activity, and wheat-bran-based diets increasing xylanolytic activity (Falcão e Cunha et al., 2004).

In many situations, indirect methods do not seem to reflect adequately the changes produced in the microbiota population (Abecia et al., 2007). The development of new molecular tools to characterize intestinal microbiota will improve our knowledge of nutrition and digestive microbiota functions (Gómez-Conde et al., 2007, 2009; Michelland et al., 2010). Table 5.5 presents a summary of some recent results obtained with restriction fragment length polymorphism.

Table 5.4. Mean apparent faecal digestibility coefficient of dietary fibre in experimental diets.a

<table>
<thead>
<tr>
<th>Class of dietary fibre</th>
<th>n</th>
<th>Mean</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Neutral detergent fibre (aNDFom)</td>
<td>127</td>
<td>0.34</td>
<td>0.03–0.71</td>
</tr>
<tr>
<td>Uronic acids</td>
<td>7</td>
<td>0.58</td>
<td>0.30–0.85</td>
</tr>
<tr>
<td>Hemicelluloses (aNDFom – ADF)</td>
<td>127</td>
<td>0.46</td>
<td>0.00–0.82</td>
</tr>
<tr>
<td>Cellulose (ADFom – ADL)</td>
<td>52</td>
<td>0.27</td>
<td>0.01–0.59</td>
</tr>
<tr>
<td>Lignin (ADL)</td>
<td>34</td>
<td>0.11</td>
<td>0.08 to 0.25</td>
</tr>
</tbody>
</table>

AFom, acid detergent fibre expressed exclusive of residual ash; ADL, acid detergent lignin; aNDFom, neutral detergent fibre assayed with a heat stable amylase and expressed free of ash.

Table 5.5. Effect of type of diet on biodiversity, frequency of detection of some bacteria and mortality in rabbits 10 days after weaning (Nicodemus et al., 2004; Gómez-Conde et al., 2007, 2009).

<table>
<thead>
<tr>
<th>Site</th>
<th>Decrease in fibre level (300 versus 250 g NDF kg⁻¹)</th>
<th>Increase in particle size (normal versus large)</th>
<th>Increase in soluble fibre</th>
</tr>
</thead>
<tbody>
<tr>
<td>Biodiversity</td>
<td>Ileum</td>
<td>Increase</td>
<td>Decrease</td>
</tr>
<tr>
<td></td>
<td>Caecum</td>
<td>Decrease</td>
<td>Decrease</td>
</tr>
<tr>
<td>Clostridium perfringens</td>
<td>Ileum</td>
<td>No effect</td>
<td>No effect</td>
</tr>
<tr>
<td></td>
<td>Caecum</td>
<td>No effect</td>
<td>No effect</td>
</tr>
<tr>
<td></td>
<td>Ileum</td>
<td>Increase</td>
<td>Bacteroides</td>
</tr>
<tr>
<td>Other bacteria</td>
<td>Caecum</td>
<td>Decrease</td>
<td>Bacteroides, Ruminococcus</td>
</tr>
<tr>
<td></td>
<td>Ileum</td>
<td>Increase</td>
<td>Ruminococcus</td>
</tr>
<tr>
<td>Mortality</td>
<td>Caecum</td>
<td>Decrease</td>
<td>Bacteroides, Ruminococcus</td>
</tr>
<tr>
<td></td>
<td>–</td>
<td>Increase</td>
<td>No effect</td>
</tr>
</tbody>
</table>

NDF, neutral detergent fibre.
Fibre Digestion

Fermentation time

The retention time of digesta in the caecocolic segments can be estimated from the difference in ileo-rectal mean retention time (i-r MRT, h) and minimal transit time (TTm, h) obtained using ileally cannulated animals. The latter value is relatively constant with a range from 3.5 to 4.5 h, averaging 3.7 h (Gidenne, 1994; García et al., 1999). Several studies (Gidenne et al., 1991b; Gidenne and Perez, 1993; Gidenne, 1994; García et al., 1999) have measured the i-r MRT for diets based on lucerne hay, wheat bran and fibrous by-products. This trait was linear and negatively correlated with dietary NDF content, which varied from 220 to 470 g kg⁻¹ (DM basis). The regression equation obtained was:

\[
i-r \text{ MRT} = 26.5(\pm4.9) - 0.0368(\pm0.015) \text{ NDF (DM)}, \quad R^2 = 0.35, \quad n = 13, \quad P = 0.03.
\]

According to this equation, the i-r MRT of an average rabbit diet containing 360 g NDF kg⁻¹ diet DM would be 13.2 h. The time of fermentation (i.e. retention in the caecum and proximal colon) could be estimated as 9.5 h (13.2–3.7 h).

Ileo-rectal MRT is also related to the weight of the caecal contents (CCW as a proportion of body weight; \( P = 0.04 \)), according to studies where both traits have been determined (Gidenne, 1992; García et al., 1999, 2000a). CCW is easier to determine than retention time, and the amount of information available in the literature is much larger. Some results are shown in Fig. 5.4, where CCW has been related to dietary NDF content, but the type of fibre (particle size and lignin content) also influences CCW (Nicodemus et al., 1999, 2006). Sampling time significantly affects this trait (see Chapter 1), so that only results obtained using the same methodology have been chosen (García et al., 2002b). The response shown in this figure indicates that, when a wide range of level and sources of fibre is considered, the dietary NDF content exerts a quadratic effect on CCW. From this equation, CCW is minimal for a dietary NDF content of 393 g kg⁻¹ DM. The additional effect of the degree of lignification of NDF on CCW indicates an additional influence of source of fibre. Diets containing low-lignified beet pulp or high-lignified sunflower husk tended to give, respectively, higher and lower CCW values at the same NDF level.

Another factor related to fermentation time is particle size. As was observed by Björnhag (1972), the particle size of fibre influences the entry of digesta in the caecum. Also, Gidenne (1993) observed that particles <0.3 mm were retained for longer (≥10 h, on average) than particles >0.3 mm.

---

**Fig. 5.4.** Effect of dietary neutral detergent fibre (NDF) content on the weight of caecal contents (CCW) (reviewed by García et al., 2002b). \[
\text{CCW} = 19.1(\pm2.0) - 0.070 \text{ NDF}(\pm0.11) + 0.000089(\pm0.0015) \text{ NDF}^2 - 0.0031(\pm0.0091) \text{ ADL}, \quad n = 52, \quad R^2 = 0.57, \quad P < 0.001. \]
\( \text{ADL} \), acid detergent lignin; DM, dry matter.
**Digestion rate**

The rate of fermentation of PCW constituents is a primary factor influencing their digestion efficiency in rabbits, because of the relatively short mean retention time (about 10 h) within the fermentative region. The caecal microbial NDF degradation rate may be derived from *in situ* rumen measurements (García *et al.*, 1995; Escalona *et al.*, 1999). From these data, it can be concluded that the relative value of fibre is highly dependent on the time of fermentation. For instance, paprika meal has a relatively high degradation rate at 10 h and a low degradation rate at 72 h, whereas the opposite occurs for NaOH-treated wheat straw.

The PCW composition is the main factor affecting the degradation rate. Hemicelluloses show a higher digestibility than cellulose (Table 5.4) and accordingly these diets contained higher average levels of digestible hemicelluloses than cellulose (68 versus 47 g kg\(^{-1}\), respectively). However, it must be stated that around one-third of the diets contained higher digestible cellulose content than digestible hemicelluloses. Lignin and cutin are considered almost totally undegradable, although positive values for lignin digestibility have been obtained that might indicate a solubilization rather than digestion. Lignin is covalently linked to hemicelluloses (Van Soest, 1994) and, consequently, the degree of lignification of NDF negatively affects the level of digestible hemicelluloses (*n* = 127; *r* = −0.57; *P* < 0.001), but not that of cellulose. The two raw materials that increase the digestible hemicellulose level in the diet are sugar-beet pulp (low lignified and with a high hemicellulose to cellulose ratio of 1.1 compared to lucerne at 0.4) and wheat bran (with the highest hemicellulose to cellulose ratio at 3.2). Uronic acids, an important constituent of pectins (and, depending on the source of fibre, also of hemicelluloses) and more soluble than other cell wall components, are the substrate more easily fermented (Table 5.4). This would suggest that other components of soluble fibre (e.g. pentosans, mannans, galactans) might have a similar or even higher degradability than uronic acids.

The faecal NDF digestibility of several fibrous feedstuffs is presented in Table 5.6. The highest value (0.845) was obtained for beet pulp. Fibre in this feed is poorly lignified and would have a lengthy fermentation time in the caecum. The lowest NDF digestibilities (0.086 and 0.100) were found for grape-seed meal and sunflower husk. Both of these are highly lignified (590 and 210 g kg\(^{-1}\)), and the latter has a low proportion (0.262) of fine particles (<0.3 mm). Similar NDF digestibility was observed for paprika meal and soybean hulls. The lower lignin content in soybean hulls (150 versus 210 g kg\(^{-1}\), respectively) was compensated for by its lower proportion of fine particles (0.932 versus 0.469, respectively) and a shorter fermentation time.

Fibre digestibility is frequently not affected by the DF concentration. In fact, it may be concluded that the quantity of fibre entering the caecum is not a limiting factor for the fermentation processes as the digesta retention time in the caecum is relatively short, allowing, predominantly, degradation

<table>
<thead>
<tr>
<th>Feedstuff</th>
<th>NDFd</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dehydrated lucerne</td>
<td>0.15–0.18</td>
<td>Gidenne <em>et al.</em> (1991a)</td>
</tr>
<tr>
<td>Dehydrated lucerne (<em>n</em> = 12)</td>
<td>0.255–0.407</td>
<td>Perez (1994)</td>
</tr>
<tr>
<td>Lucerne hay (<em>n</em> = 6)</td>
<td>0.175–0.276</td>
<td>García <em>et al.</em> (1995, 1999)</td>
</tr>
<tr>
<td>Beet pulp</td>
<td>0.845</td>
<td>Gidenne (1987)</td>
</tr>
<tr>
<td>Paprika meal</td>
<td>0.351</td>
<td>García <em>et al.</em> (1999)</td>
</tr>
<tr>
<td>Soybean hulls</td>
<td>0.282</td>
<td>García <em>et al.</em> (1999)</td>
</tr>
<tr>
<td>Sunflower husk</td>
<td>0.100</td>
<td>García <em>et al.</em> (1999)</td>
</tr>
<tr>
<td>Barley straw, NaOH-treated</td>
<td>0.167</td>
<td>García <em>et al.</em> (1999)</td>
</tr>
<tr>
<td>Grape-seed meal</td>
<td>0.086</td>
<td>García <em>et al.</em> (2002a)</td>
</tr>
</tbody>
</table>
of the more easily digestible fibre fractions such as pectins and hemicelluloses.

**Fermentation pattern**

**Volatile fatty acids.** VFAs are the main products of carbohydrate microbial fermentation. Their concentration in the caecum has been used as an indirect estimation of microbial activity, although great dietary changes are required to significantly modify VFAs due to their high variability. VFAs are rapidly absorbed in the hindgut and provide a regular source of energy for the rabbit. Butyrate seems to be a preferential source of energy for the hindgut, whereas acetate is mainly metabolized in the liver for lipogenesis and cholesterolgenesis (Vernay, 1987). Furthermore, VFAs have been suggested to enhance colon mucosal growth (Chiou et al., 1994). Although VFAs have been proposed as a protective factor against pathogen microbiota (Escherichia coli) infections *in vitro* (Prohaszka, 1980; Wallace et al., 1989), no clear effects have been observed in rabbits *in vivo* (Gidenne and Licois, 2005).

Carbohydrate uptake by the gut microbiota includes most of the cell wall constituents, in addition to starch not digested in the small intestine and endogenous mucopolysaccharides. Additionally, protein residues from the ileal digesta (undigested dietary protein, mucosal-cell protein, enzymes) can be utilized (after deamination) as an energy source for the microbial population. In this way, Vernay and Raynaud (1975) observed a caecal VFA concentration of 17.8 mmol 1⁻¹ in fasted rabbits, suggesting that a significant amount of endogenous materials can be fermented in the caecum. In fact, a decrease of ileal protein digestibility increased caecal acidity, suggesting an important role of protein in caecal fermentation (Gidenne and García, 2006). However, the relative contribution of these sources to total caecal VFA production is unknown.

The caecal VFA concentration determined in 78 experimental diets averaged 57.4 mmol 1⁻¹ and ranged from 18.1 to 99.8 mmol 1⁻¹. It increased with dietary uronic acid and NDF levels and decreased with the degree of lignification of NDF (García et al., 2002b). Chiou et al. (1994), using isolated components of DF (cellulose, pectins and lignin) and lucerne hay, also observed a negative effect of lignin on caecal VFA concentration.

The caecal VFA profile is specific to the rabbit, with a predominance of acetate (77 mmol 100 ml⁻¹ on average, range 65–87 mmol 100 ml⁻¹), followed by butyrate (17 mmol 100 ml⁻¹ on average, range 6–28 mmol 100 ml⁻¹) and then propionate (6 mmol 100 ml⁻¹ on average, range 3–11 mmol 100 ml⁻¹). These molar proportions are affected by fibre level. For instance, the proportion of acetate increases and that of butyrate generally decreases significantly when the fibre level increases, whereas the propionic acid proportion is only positively correlated to dietary uronic acids concentration (García et al., 2002b).

**Caecal pH.** Caecal pH is frequently determined in digestion studies because it gives an estimation of the extent of the fermentation. Caecal pH is negatively related to both dietary uronic acid and digestible NDF concentrations (Fig. 5.5) (García et al., 2002b), as it decreases with the inclusion of ingredients such as sugar beet pulp, soy hulls and lucerne in the diet; the opposite occurs with cereal straw and grape-seed meal.

From a chemical point of view, caecal pH is expected to be related to the main sources of hydrogen ions, hydroxide ions, VFAs and ammoniacal nitrogen. However, a poor or absent relationship has been found between these variables, which only account for 12% of the variability observed in caecal pH (García et al., 2002b). This may due to the presence of buffer substances in the caecum from endogenous or feed origin, which may also explain the stability of caecal pH among animals fed different diets. In fact, 68% of the variability of caecal pH is explained by the pH of the dry caecal contents (free from VFA and ammoniacal nitrogen), which is negatively related to the base-buffering capacity of the dry caecal contents (García et al., 2000a).
Fig. 5.5. Effect of dietary digestible neutral detergent fibre (NDF) and of increasing levels of sources of fibre rich in soluble fibre on caecal pH (reviewed by García et al., 2002b). DM, dry matter; INRA, Institut National de la Recherche Agronomique; UPM, Universidad Politécnica de Madrid; UTL, Universidade Técnica de Lisboa.

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6 Energy and Protein Metabolism and Requirements

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6.1 Energy Units and their Measurement

Energy is the potential ability to produce work and the Joule (J), with its multiples, is the international unit used to measure all forms of energy, including feed energy. The standard calorie (cal), equivalent to the energy cost of increasing 1 g of distilled water by 1°C, is commonly used in practice to measure energy and may be converted into J by multiplying by 4.184.

In the nutrition and feeding of rabbits, as in other species, the following energy parameters are used to express energy requirements and the nutritive value of feeds: gross energy (GE), digestible energy (DE), metabolizable energy (ME) and net energy (NE) (Fig. 6.1).

6.1.1 Gross energy

GE is the quantity of chemical energy lost as heat when organic matter is completely oxidized, forming water and carbon dioxide as the main products. In feed, the GE content depends on the chemical composition of the organic matter: the caloric values of the individual components are approximately 22–24 kJ g⁻¹ for crude protein, 38–39 kJ g⁻¹ for ether extract and 16–17 kJ g⁻¹ for carbohydrates. The GE concentration in complete diets or raw materials does not provide any useful information on the availability and utilization of dietary energy by the animal. For this reason, it is not a relevant unit in the energy evaluation of feeds or of animal energy requirements.

6.1.2 Digestible energy

DE can be measured in vivo by subtracting the quantity of energy recovered in the faeces from GE; in other words, the energy of undigested nutrients. In compound feeds for rabbits, the DE usually varies from 0.50 to 0.80 of the GE and offers a sufficiently precise estimation of the energy value of feeds.

6.1.3 Metabolizable energy

ME is calculated from DE by subtracting the energy loss associated with urine (UE) and intestinal fermentation gases (GasE), primarily methane. In ruminants, GasE accounts for an important part of DE. In rabbits, however, it is practically negligible, as is the heat loss from caecal fermentation. On the other hand, the energy loss in urine is substantial and depends on feed protein concentration (Maertens et al., 2002; Xiccato et al., 2007). Nitrogen losses (and consequently the energy...
associated with urea and other nitrogen catabolites) increase as dietary protein increases. The UE can be calculated from the quantity of nitrogen excreted daily in the urine (UN) (Parigi Bini and Cesselli, 1977):

\[
\text{UE (kJ day}^{-1}\text{)} = 51.76 \text{ UN (g day}^{-1}\text{)} - 3.01
\]

residual standard deviation (RSD) = 3.93, \( r = 0.90 \)

6.1.4 Net energy

NE is the fraction of GE that is actually utilized by the animal for maintenance and productive purposes and is, therefore, the most precise estimate of feed energy value and animal energy requirements. The actual feed value within an NE unit is related to the specific energy utilization: NE for maintenance (NE\(_m\)), growth (NE\(_g\)), milk production (NE\(_l\)) and so on.

The experimental development of an NE system for rabbits (which proved extremely complicated and expensive) was abandoned some time ago (Parigi Bini et al., 1974, 1978), but the choice between the DE and ME systems is still under discussion. ME is preferred for poultry, because birds excrete urine and faeces together, but the collection and measurement of urine energy values in rabbits is difficult and expensive. Although ME is more precise than DE, urinary energy losses are closely linked to the total intake of digestible protein (DP). Therefore, in common compound diets with 120–150 g DP kg\(^{-1}\), DE and ME are closely correlated and ME can be easily estimated as 0.95 DE (Parigi Bini and Cesselli, 1977; Partridge et al., 1986b; Ortiz et al., 1989; Santomà et al., 1989). For a more precise estimation of the ME concentration of diets (or raw materials), the following equations can be utilized to calculate the ME content for nitrogen equilibrium (Maertens et al., 2002):

\[
\text{ME (MJ kg}^{-1}\text{)} = \text{DE (MJ kg}^{-1}\text{)} \times \frac{\text{ME}}{\text{DE}}
\]

where:

\[
\text{ME/DE} = 0.995 - 0.0048 \times \text{DP (g kg}^{-1}\text{)} / \text{DE (MJ kg}^{-1}\text{)}
\]

For the reasons outlined above, DE values are still commonly used both in studies on energy metabolism and in practical rabbit feeding. Since GE digestibility is closely correlated with dry matter (DM) digestibility, an international standardized method (Perez et al., 1995) capable of offering repeatable and reproducible measurements of in vivo DM digestibility (and consequently energy digestibility) has been adopted by the scientific community.

6.2 Methods for Estimating Energy Requirements

The principal methods used for the measurement of energy requirements (for further details see Blaxter, 1989; Webster, 1989; Close, 1990) are as follows:
1. Long-term feeding experiments, carried out to establish the energy needed to maintain constant live weight or, on the other hand, to measure the variations in live weight (or milk production or fetal growth) induced by a certain quantity of energy. These experiments permit the breeding of high numbers of animals for long periods under conditions similar to those on farms. However, they do not provide any useful information on the body composition changes that affect rabbits during growth, lactation or pregnancy.

2. Calorimetric methods, which measure the heat lost by animals. Measurement is direct (direct calorimetry) when calorimeters are used and indirect (indirect calorimetry) when based on the gaseous exchanges measured in respiratory chambers of various types (open or closed circuit). These methods allow the direct measurement of ME intake (MEI) and energy lost as heat (HE). The retained energy (RE) in either the body or products (e.g. milk, fetal body, wool) is calculated by the difference (RE = ME – HE). Calorimetric methods require very complex and expensive equipment and can be utilized on only a few animals and in short-term experiments. Measurements are highly accurate and repeatable on the same animal in subsequent moments, but scarcely comparable to those obtained under practical rearing conditions. In addition, as in feeding experiments, calorimetric methods do not permit the identification of the origin of heat lost from different physiological functions (e.g. whether from feed digestion or body tissue utilization) or the partition of RE (e.g. energy retained in maternal or fetal tissues).

3. Comparative slaughter technique, which measures the variation of the energy contained in the body. This method constitutes the basis of the California Net Energy System developed for beef cattle (Lofgreen and Garrett, 1968) and has been largely applied to rabbits (Parigi Bini et al., 1974, 1978, 1990a, 1992; Parigi Bini and Xiccato, 1986; Partridge et al., 1989; Xiccato et al., 1992b, 1995, 2004, 2005b; Fortun et al., 1993; Nizza et al., 1995; Pascual et al., 2000b). This technique allows the direct measurement of MEI and RE, while HE is calculated by difference (HE = ME – RE). Body energy change is measured by first analysing the empty body (EB = live body – gut contents) of a reference group of animals (initial slaughter group). A second group of animals is fed a diet in which the ME (or DE) content is measured experimentally and their EBs are then analysed (final slaughter group). In growing rabbits, the RE is calculated by subtracting the body energy found in the final group from the body energy in the initial group – that is, the RE for growth (RE₉). Similarly, the energy excreted in the milk of lactating does (Eₘilk) and/or retained in the fetuses in pregnant does (Eₐetus) can be measured during the entire lactation or pregnancy. The comparative slaughter technique is based on the assumption that the body composition of the initial slaughter group is very similar to the body composition of the final slaughter group at the beginning of the experiment. The difference in body composition at the beginning and the end of the experiment is a good estimate of RE when the animals in the initial and the final groups are homogeneous, their number is relatively high and the length of experiment is long enough (e.g. a complete growing period or an entire pregnancy or lactation) (Close, 1990). Comparative slaughter thus permits the partition of RE between the energy retained (or lost) as protein (RE₉) and fat (RE₉).

4. Non-destructive methods for body composition measurement, which measure the variation of body composition and then body RE without slaughter. Several methods have been proposed for rabbits, including dilution methods, nuclear magnetic resonance, computerized tomography and total body electrical conductivity (as reviewed by Fekete, 1992; Pascual et al., 2006). These methods often need very expensive equipment and their efficacy is not completely proven. More recently, ultrasound scanning of perirenal fat thickness has been used to measure body-fat changes in the same animal during the reproductive period (Pascual et al., 2000a,
2002b, 2004; Castellini et al., 2003, 2006; Cardinali et al., 2008), although with varying success depending on the doe’s physiological state.

6.3 Energy Metabolism and Requirements

Several factors influence the energy metabolism and consequently the energy requirements in rabbits. The most important are: (i) body size, which depends on breed, age and sex; (ii) vital and productive functions, such as maintenance, growth, lactation and pregnancy; and (iii) environment (i.e. temperature, humidity, air speed).

Only those aspects of energy metabolism related to vital and productive functions are discussed here.

6.3.1 Voluntary feed and energy intake

Appetite in rabbits is mostly regulated by a chemostatic mechanism. Because of this, the total quantity of energy ingested daily tends to be constant. Growing rabbits in good sanitary conditions naturally consume sufficient feed to meet their energy requirements. However, reproducing does have high energy requirements for pregnancy, lactation and concurrent pregnancy and lactation that are often not covered by an adequate voluntary intake.

Voluntary energy intake is proportional to metabolic live weight ($LW^{0.75}$). In growing rabbits, voluntary intake is about 900–1000 kJ DE day$^{-1}$ kg$^{-1}$ $LW^{0.75}$ and chemostatic regulation appears only with a DE concentration in the diet of >9 MJ kg$^{-1}$ (Lebas et al., 1984; Partridge, 1986; Cheeke, 1987; Parigi Bini, 1988; Lebas, 1989; Santomá et al., 1989).

Below this level a physical-type regulation is prevalent, which is linked to the filling of the gut with dietary material (Fig. 6.2). Reproducing females can ingest on average 1100–1300 kJ DE day$^{-1}$ kg$^{-1}$ $LW^{0.75}$ during lactation, with the lowest value recorded by primiparous females (Maertens and De Groote, 1988; Lebas, 1989; Parigi Bini et al., 1990b, 1992; Xiccato et al., 1992b, 1995, 2004; Pascual et al., 1998), and have a different energetic limit of chemostatic regulation compared to growing rabbits. An increase in DE concentration >9–9.5 MJ kg$^{-1}$ permits a further increase in the daily energy intake of lactating females (Maertens and De Groote, 1988; Fraga et al., 1989; Castellini and Battaglini, 1991; Xiccato et al., 1995; Pascual et al., 1998, 2000b). In these animals, the regulation limit probably varies by around 10.5–11 MJ kg$^{-1}$ and also depends on the dietary energy source, tending to be higher in added-fat diets than in high-starch diets (Fraga et al.,

![Fig. 6.2. Influence of dietary digestible energy (DE) concentration on voluntary feed and energy intake in lactating does and growing rabbits.](image)
6.3.2 Energy for maintenance and efficiency of energy utilization

By varying the quantity of DE or MEI, it is possible to modify both the quantity of RE in the bodies of growing rabbits (RE$_g$) and the quantity of energy excreted in the milk (E$_{\text{milk}}$) or retained in the fetal tissues (E$_{\text{fetus}}$).

When the energy system is based on ME units, ME requirement for maintenance (ME$_m$) is the MEI that permits the maintenance of energy equilibrium in the body (RE$_g$ = 0).

Once the needs for maintenance have been covered, the efficiency of utilization (k) of MEI is different for energy retained in the body tissues (k$_g$ = RE$_g$/MEI), milk (k$_l$ = E$_{\text{milk}}$/MEI) or fetal tissues (k$_{\text{fetus}}$ = E$_{\text{fetus}}$/MEI).

When the energy system is based on DE, as with rabbits, energy retained in the body, milk or fetal tissue can be related to DE intake (DEI) instead of MEI. In different studies on rabbit energy metabolism, the efficiencies of utilization of DEI for maintenance, growth, lactation or pregnancy (RE/DEI) have been estimated instead of the k coefficients (de Blas et al., 1985; Parigi Bini and Xiccato, 1986; Partridge et al., 1989; Xiccato et al., 1995). Assuming a constant ratio of ME = 0.95 DE, the efficiency of DEI utilization can be easily transformed into k values by dividing by 0.95. For example, using data from de Blas et al. (1985):

\[ k_g = \frac{\text{RE}_g}{\text{DEI}} / 0.95 = \frac{0.53}{0.95} = 0.56 \]

Table 6.1 summarizes average values from the literature for energy requirements for the maintenance and efficiency of energy utilization for different categories of rabbits.

6.3.3 Energy requirements for maintenance

In all animals, energy losses for maintenance (basal metabolism and voluntary activity) are related to metabolic weight and physiological state.

Different estimates of DE requirements for the maintenance (DE$_m$) of growing rabbits have been found (see previous reviews of Parigi Bini, 1988 and Lebas, 1989), varying

| Table 6.1. Digestible energy requirements for the maintenance (DE$_m$) and efficiency of utilization of DE intake (DEI) and body energy reserves. |
|-------------------------|-----------------|----------------|-----------------|-----------------|
|                         | Young rabbits   | Pregnant does  | Lactating does  | Pregnant and lactating does |
| DE$_m$ (kJ day$^{-1}$ kg$^{-1}$ LW$^{0.75}$) | 430             | 430            | 430             | 470             | 400             |
| Efficiency of energy utilization: |                    |                |                 |                  |
| Body retained energy (RE$_g$/DEI) | 0.50            | 0.50           | –               | –               | 0.50            |
| RE as protein (RE$_p$/DEI) | 0.40            | –              | –               | –               | –               |
| RE as fat (RE$_f$/DEI) | 0.65            | –              | –               | –               | –               |
| RE as fetuses (E$_{\text{fetus}}$/DEI) | –              | 0.30           | –               | 0.30            | –               |
| Milk energy from DEI (E$_{\text{milk}}$/DEI) | –              | –              | 0.65            | 0.65            | –               |
| Milk energy from doe body reserves (E$_{\text{milk}}$/RE) | –              | –              | 0.80            | 0.80            | –               |

LW, live weight; RE, retained energy.
from 381 kJ day\(^{-1}\) kg\(^{-1}\) LW\(^{0.75}\) in New Zealand White rabbits (Partridge et al., 1989) to 552 kJ day\(^{-1}\) kg\(^{-1}\) LW\(^{0.75}\) in Giant Spanish growing rabbits (de Blas et al., 1985). These estimates vary depending on both the breeds, characterized by very different daily gain and body composition, and the measurement methods used (calorimetric methods usually give a lower \(\text{DE}_m\) than comparative slaughter). On the basis of a review of homogeneous studies on growing New Zealand White pure-breed or derived rabbits (Table 6.2), an average \(\text{DE}_m\) of 430 kJ day\(^{-1}\) kg\(^{-1}\) LW\(^{0.75}\) and an average \(\text{ME}_m\) of 410 kJ day\(^{-1}\) kg\(^{-1}\) LW\(^{0.75}\) might be proposed.

Similarly to in growing rabbits, experimental estimates of \(\text{DE}_m\) in reproducing does are often inconsistent (Table 6.3). Based on available data, \(\text{DE}_m\) may be proposed as 400 kJ day\(^{-1}\) kg\(^{-1}\) LW\(^{0.75}\) for non-reproducing does, 430 kJ day\(^{-1}\) kg\(^{-1}\) LW\(^{0.75}\) for pregnant or lactating does and 470 kJ day\(^{-1}\) kg\(^{-1}\) LW\(^{0.75}\) for concurrently pregnant and lactating does.

### 6.3.4 Energy requirements for growth

Figure 6.3 shows the response in terms of daily gain and energy intake to an increase in feed DE density when the DP to DE ratio is held constant and protein contains the major amino acids in satisfactory equilibrium (Partridge et al., 1989). This typical growth-response curve shows that the maximum average daily growth is achieved when the dietary DE concentration is about 10–10.5 MJ kg\(^{-1}\).

An increase in the level of dietary energy intake also affects body gain composition and the partition of energy retained as protein and fat. The body composition changes are not linearly correlated

---

**Table 6.2. Energy requirements (kJ day\(^{-1}\) kg\(^{-1}\) LW\(^{0.75}\)) for maintenance of energy equilibrium (retained energy = 0) in New Zealand White or hybrid growing rabbits.**

<table>
<thead>
<tr>
<th>Authors</th>
<th>(\text{DE}_m)</th>
<th>(\text{ME}_m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Isar (1981)</td>
<td>470</td>
<td>446</td>
</tr>
<tr>
<td>Scheele et al. (1985)</td>
<td>413</td>
<td>392</td>
</tr>
<tr>
<td>Partridge et al. (1989)</td>
<td>381</td>
<td>362</td>
</tr>
<tr>
<td>Nizza et al. (1995)</td>
<td>441–454</td>
<td>419–432</td>
</tr>
</tbody>
</table>

\(\text{DE}_m\): digestible energy requirement for maintenance; \(\text{ME}_m\): metabolizable energy requirement for maintenance.

\(^a\)Calculated from \(\text{DE}_m\) by assuming ME = 0.95 DE.

\(^b\)Recalculated values from original data expressed on metabolic empty body weight (EBW\(^{0.75}\)).

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**Table 6.3. Digestible energy requirements for maintenance in rabbit does (kJ day\(^{-1}\) kg\(^{-1}\) LW\(^{0.75}\)).**

<table>
<thead>
<tr>
<th>Author</th>
<th>Non-lactating does</th>
<th>Lactating does</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Non-pregnant</td>
<td>Pregnant</td>
</tr>
<tr>
<td>Partridge et al. (1983)</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Partridge et al. (1986b)</td>
<td>326</td>
<td>352</td>
</tr>
<tr>
<td>Fraga et al. (1989)</td>
<td>–</td>
<td>452</td>
</tr>
<tr>
<td>Parigi Bini et al. (1990a)</td>
<td>398</td>
<td>431</td>
</tr>
<tr>
<td>Parigi Bini et al. (1991a)</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Xiccato et al. (1992b)</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Lebas (1989)</td>
<td>–</td>
<td>400</td>
</tr>
<tr>
<td>Maertens (1992)</td>
<td>–</td>
<td>420</td>
</tr>
<tr>
<td>Toschi et al. (2003)</td>
<td>439</td>
<td>–</td>
</tr>
<tr>
<td>Toschi et al. (2004)</td>
<td>–</td>
<td>458</td>
</tr>
</tbody>
</table>
Energy and Protein Metabolism

with DEI, because some constituents (i.e. fat) tend to increase more than proportionally. The following quadratic regression equations estimate the daily gains (g day⁻¹ kg⁻¹ LW⁰.⁷⁵) of EB (EBG), water (WG), protein (PG), fat (FG) and ash (AG) from DEI (MJ day⁻¹ kg⁻¹ LW⁰.⁷⁵; Parigi Bini and Xiccato, 1986):

\[
\text{EBG} = -12.61 + 48.50 \text{ DEI} - 8.15 \text{ DEI}^2,
\]

\[
RSD = 1.64, r = 0.93
\]

\[
\text{WG} = -6.52 + 33.59 \text{ DEI} - 10.69 \text{ DEI}^2,
\]

\[
RSD = 0.61, r = 0.96
\]

\[
\text{PG} = -2.42 + 10.01 \text{ DEI} - 1.70 \text{ DEI}^2,
\]

\[
RSD = 0.38, r = 0.91
\]

\[
\text{FG} = -2.76 + 1.69 \text{ DEI} + 5.75 \text{ DEI}^2,
\]

\[
RSD = 0.45, r = 0.94
\]

\[
\text{AG} = -0.91 + 3.21 \text{ DEI} - 1.51 \text{ DEI}^2,
\]

\[
RSD = 0.12, r = 0.67
\]

The same equations may be transformed to formulate other equations that estimate retained energy as protein (REₚ) and total RE (RE₉) as a function of DEI (all data are expressed as MJ day⁻¹ kg⁻¹ LW⁰.⁷⁵):

\[
\text{REₚ} = -0.098 + 0.060 \text{ DEI} + 0.204 \text{ DEI}^2,
\]

\[
RSD = 0.016, r = 0.94
\]

\[
\text{RE₉} = -0.155 + 0.294 \text{ DEI} + 0.164 \text{ DEI}^2,
\]

\[
RSD = 0.012, r = 0.96
\]

In fact, body protein and fat have specific caloric values, namely 23.2 and 35.6 MJ kg⁻¹, respectively, as determined by bomb calorimeter (Parigi Bini and Dalle Rive, 1978). Nizza et al. (1995) found similar caloric values (23.1 and 35.7 MJ kg⁻¹), thereby confirming that the caloric value of rabbit fat is lower than that of other animal fats (average 38–40 MJ kg⁻¹) (Close, 1990). The caloric value of fat was found to be higher in reproducing does (36–37 MJ kg⁻¹) than in growing animals, probably related to the lower content of phospholipids in older and fatter animals (Cambero et al., 1991; Hulot et al., 1992).

These equations can be used to calculate the daily gain composition throughout the entire growing period (e.g. from 0.8 to 2.4 kg LW). During this interval, the average LW⁰.⁷⁵ is about 1.42 kg. An increase in EBG and a strong modification of the chemical composition of EBG (and consequently its energy value) occurs as DEI increases (Table 6.4).

When DEI = 0, substantial losses of body weight and body tissues occur and

![Fig. 6.3. Effect of dietary energy density on growth rate (◆) and total digestible energy (DE) intake (▲) (from Partridge et al., 1989).](image_url)
the body loses 155 kJ day\(^{-1}\) kg\(^{-1}\) LW\(^{0.75}\). This loss is called ‘fasting metabolism’, which means the loss of body energy at fasting. The requirements for the maintenance of energy equilibrium (RE\(_g\) = 0) and the maintenance of live body weight (live weight gain, LWG = 0) are different: DE\(_m\) has been measured at 425 kJ day\(^{-1}\) kg\(^{-1}\) LW\(^{0.75}\) at RE\(_g\) = 0 and only 273 kJ day\(^{-1}\) kg\(^{-1}\) LW\(^{0.75}\) when LWG = 0. When LWG = 0, the rabbit exhibits an energy deficit as a consequence of the loss of fat primarily compensated by water gain.

When DE\(_I\) is 273 kJ day\(^{-1}\) kg\(^{-1}\) LW\(^{0.75}\), the EB weight is maintained (EBG = 0), but losses of fat (−1.9 g day\(^{-1}\) kg\(^{-1}\) LW\(^{0.75}\)) and energy (−62 kJ day\(^{-1}\) kg\(^{-1}\) LW\(^{0.75}\)) are observed. When DE\(_I\) = DE\(_m\) (425 kJ day\(^{-1}\) kg\(^{-1}\) LW\(^{0.75}\)), the energy equilibrium is reached as a consequence of a gain in energy (36 kJ day\(^{-1}\) kg\(^{-1}\) LW\(^{0.75}\)) as protein (1.5 g day\(^{-1}\) kg\(^{-1}\) LW\(^{0.75}\)) and an equivalent loss of energy as fat (−1.0 g day\(^{-1}\) kg\(^{-1}\) LW\(^{0.75}\)). At the same time, EBG is positive (6.5 g day\(^{-1}\) kg\(^{-1}\) LW\(^{0.75}\)), primarily due to water retention.

With increasing DE\(_I\), protein gain (in weight) always remains higher than fat gain, but at DE\(_I\) = 900 kJ day\(^{-1}\) kg\(^{-1}\) LW\(^{0.75}\), RE as protein and fat become equal (RE\(_p\) = RE\(_f\) = 122 kJ day\(^{-1}\) kg\(^{-1}\) LW\(^{0.75}\)).

With non-restricted feeding (DE\(_I\) = 1000 kJ day\(^{-1}\) kg\(^{-1}\) LW\(^{0.75}\)), EBG is 39.5 g day\(^{-1}\) (27.8 g day\(^{-1}\) kg\(^{-1}\) LW\(^{0.75}\) \(\times\) 1.42) and LWG is 45.2 g day\(^{-1}\) (assuming EB weight = 0.87 LW). Daily EBG is then composed of 23.3 g (590 g kg\(^{-1}\)) water, 8.4 g (212 g kg\(^{-1}\)) protein, 6.7 g (169 g kg\(^{-1}\)) fat and 1.1 g (29 g kg\(^{-1}\)) ash. At the voluntary intake, RE\(_I\) > RE\(_p\) and total RE reaches the maximum level (RE\(_g\) = 303 kJ day\(^{-1}\) kg\(^{-1}\) LW\(^{0.75}\)). Daily RE\(_I\) is 430 kJ day\(^{-1}\) and the energy concentration of growth is 10.9 kJ g\(^{-1}\) EBG and 9.5 kJ g\(^{-1}\) LWG. These chemical composition and energy partitions of daily growth are typical of a young, rapidly growing rabbit.

The above-listed regression equations of RE from DE\(_I\) are not linear. From the same data set, the following linear regression equation can be estimated (data are expressed in kJ day\(^{-1}\) kg\(^{-1}\) LW\(^{0.75}\)):

\[
RE_g = -235 + 0.527 \times DE_I, \\
RSD = 22, r = 0.97
\]

This indicates that DE\(_m\) = 446 kJ day\(^{-1}\) kg\(^{-1}\) LW\(^{0.75}\) and gives an efficiency of utilization of DE for growth of 0.53, which is close to the values found by de Blas et al. (1985), Partridge et al. (1989) and others (Table 6.5).

The efficiency of energy utilization for growth is clearly influenced by the composition of growth, because energy is retained as protein less efficiently than energy retained as fat (Blaxter, 1989; Close, 1990). On the basis of the literature, we can utilize average values of efficiencies of DE utilization for total energy retention, energy retained as protein and energy retained as fat of 0.50, 0.40 and 0.65, respectively.

Using the above-mentioned coefficients of energy utilization and DE\(_m\) values, the DE requirement and energy and material balance in growing rabbits can be estimated. An example regarding rabbits from 0.8 to 2.4 kg is provided in Box 6.1.

### Table 6.4. Empty body gain (EBG) composition and retained energy (RE) partition as influenced by digestible energy intake (DEI) (all data are in kJ or g day\(^{-1}\) kg\(^{-1}\) LW\(^{0.75}\)) (recalculated from Parigi Bini and Xiccato, 1986).

<table>
<thead>
<tr>
<th>DEI (kJ)</th>
<th>EBG (g)</th>
<th>WG (g)</th>
<th>PG (g)</th>
<th>FG (g)</th>
<th>AG (g)</th>
<th>RE(_p) (kJ)</th>
<th>RE(_f) (kJ)</th>
<th>RE(_g) (kJ)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>−12.6</td>
<td>−6.5</td>
<td>−2.4</td>
<td>−2.8</td>
<td>−0.9</td>
<td>−57</td>
<td>−98</td>
<td>−155</td>
</tr>
<tr>
<td>273</td>
<td>0.0</td>
<td>1.8</td>
<td>0.2</td>
<td>−1.9</td>
<td>−0.1</td>
<td>4</td>
<td>−66</td>
<td>−62</td>
</tr>
<tr>
<td>425</td>
<td>6.5</td>
<td>5.8</td>
<td>1.5</td>
<td>−1.0</td>
<td>0.2</td>
<td>36</td>
<td>−36</td>
<td>0</td>
</tr>
<tr>
<td>900</td>
<td>24.4</td>
<td>15.0</td>
<td>5.2</td>
<td>3.4</td>
<td>0.8</td>
<td>122</td>
<td>122</td>
<td>244</td>
</tr>
<tr>
<td>1000</td>
<td>27.8</td>
<td>16.4</td>
<td>5.9</td>
<td>4.7</td>
<td>0.8</td>
<td>137</td>
<td>166</td>
<td>303</td>
</tr>
</tbody>
</table>

AG, FG, PG, WG, daily gains of ash, fat, protein and water, respectively; RE\(_p\), RE\(_f\), RE\(_g\), retained energy as protein, fat and total RE, respectively.
**Table 6.5.** Efficiency of utilization of digestible energy for energy retained for growth (RE\textsubscript{g}) and RE as protein (RE\textsubscript{p}) and fat (RE\textsubscript{f}).

<table>
<thead>
<tr>
<th>Authors</th>
<th>RE\textsubscript{g}/DEI</th>
<th>RE\textsubscript{p}/DEI</th>
<th>RE\textsubscript{f}/DEI</th>
</tr>
</thead>
<tbody>
<tr>
<td>de Blas et al. (1985)</td>
<td>0.52</td>
<td>0.38</td>
<td>0.65</td>
</tr>
<tr>
<td>Parigi Bini and Xiccato (1986)</td>
<td>0.53</td>
<td>0.44</td>
<td>0.70</td>
</tr>
<tr>
<td>Partridge et al. (1989)</td>
<td>0.47</td>
<td>0.39</td>
<td>0.60</td>
</tr>
<tr>
<td>Nizza et al. (1995)</td>
<td>0.51\textsuperscript{a}</td>
<td>0.39–0.41</td>
<td>0.64–0.66</td>
</tr>
</tbody>
</table>

DEI, digestible energy intake.
\textsuperscript{a}Calculated value.

**Box 6.1.** Estimate of digestible energy (DE) requirements and body energy partition in growing rabbits.

Reference data
- Age at weaning = 32 days
- Age at slaughter = 72 days
- Live weight (LW) at weaning = 0.8 kg
- LW at slaughter = 2.4 kg
- Empty body gain (EBG) = 0.87 LW gain (LWG)
- EBG composition = water 610 g kg\textsuperscript{-1}; protein 210 g kg\textsuperscript{-1}; fat 150 g kg\textsuperscript{-1}; ash 30 g kg\textsuperscript{-1}
- Caloric value of body protein = 23.2 MJ kg\textsuperscript{-1} = 23.2 kJ g\textsuperscript{-1}
- Caloric value of body fat = 35.6 MJ kg\textsuperscript{-1} = 35.6 kJ g\textsuperscript{-1}
- DE required for maintenance (DE\textsubscript{m}) = 430 kJ day\textsuperscript{-1} kg\textsuperscript{-1} LW\textsuperscript{0.75}
- Efficiency of DE utilization for retained energy (RE) as protein = 0.40
- Efficiency of DE utilization for RE as fat = 0.65
- Dietary DE concentration = 10.0 MJ kg\textsuperscript{-1} = 10.0 kJ g\textsuperscript{-1}

Calculated data
- Growing period = 40 days
- LWG = 1.6 kg
- Daily LWG = 40 g day\textsuperscript{-1}
- EBG = 0.87 × 40 g day\textsuperscript{-1} = 34.8 g day\textsuperscript{-1}
- Protein gain = 34.8 g day\textsuperscript{-1} × 0.21 = 7.3 g day\textsuperscript{-1}
- Fat gain = 34.8 g day\textsuperscript{-1} × 0.15 = 5.2 g day\textsuperscript{-1}
- Average metabolite LW = ((0.8 + 2.4) / 2)\textsuperscript{0.75} = 1.42 kg LW\textsuperscript{0.75}
- RE as protein (RE\textsubscript{p}) = 7.3 g day\textsuperscript{-1} × 23.2 kJ g\textsuperscript{-1} = 169 kJ day\textsuperscript{-1}
- RE as fat (RE\textsubscript{f}) = 5.2 g day\textsuperscript{-1} × 35.6 kJ g\textsuperscript{-1} = 185 kJ day\textsuperscript{-1}
- Total RE (RE\textsubscript{g}) = 169 + 185 = 354 kJ day\textsuperscript{-1}
- Caloric value of EBG = 354 kJ day\textsuperscript{-1} / 34.8 g day\textsuperscript{-1} = 10.2 kJ g\textsuperscript{-1}
- Caloric value of LWG = 354 kJ day\textsuperscript{-1} / 40 g day\textsuperscript{-1} = 8.9 kJ g\textsuperscript{-1}

DE requirement and efficiency for growth
- DE\textsubscript{m} requirement = 430 kJ day\textsuperscript{-1} kg\textsuperscript{-1} LW\textsuperscript{0.75} × 1.42 kg LW\textsuperscript{0.75} = 611 kJ day\textsuperscript{-1}
- DE requirement for RE\textsubscript{p} = 169 kJ day\textsuperscript{-1} / 0.40 = 423 kJ day\textsuperscript{-1}
- DE requirement for RE\textsubscript{f} = 185 kJ day\textsuperscript{-1} / 0.65 = 285 kJ day\textsuperscript{-1}
- DE requirement for growth (DE\textsubscript{g}) = 423 + 285 = 708 kJ day\textsuperscript{-1}
- Efficiency of DE utilization for growth (DE\textsubscript{g}) = 354 kJ day\textsuperscript{-1} / 708 kJ day\textsuperscript{-1} = 0.50
- Total DE requirement = DE\textsubscript{m} + DE\textsubscript{g} = 611 + 708 = 1319 kJ day\textsuperscript{-1} (929 kJ day\textsuperscript{-1} kg\textsuperscript{-1} LW\textsuperscript{0.75})
- Required feed intake = 1319 kJ day\textsuperscript{-1} / 10 kJ g\textsuperscript{-1} = 132 g day\textsuperscript{-1}

### 6.3.5 Energy requirements for reproduction and lactation

Investigations on the energy metabolism of rabbit does were started over 20 years ago by Partridge and co-workers in a well-known series of experiments (Partridge, 1986). Information on the changes of body composition in reproducing does and on the partition and utilization of dietary energy for maternal and fetal tissues synthesis and for milk production was obtained in a successive series of
experiments carried out by Parigi Bini, Xiccato and co-workers using the comparative slaughter technique (Parigi Bini and Xiccato, 1993, 1998; Xiccato et al., 1995, 1999, 2004, 2005b; Xiccato, 1996). The research groups of Toulouse, France (Lebas and Fortun-Lamothe), Perugia, Italy (Castellini and Dal Bosco), Valencia, Spain (Pascual and Cervera) and Kaposvár, Hungary (Szendrő, Milisits) further contributed to a more precise definition of the energy requirements and the utilization and partition of dietary energy in rabbit does, also utilizing other techniques to estimate energy requirements and body composition (ultrasound scanning, total body electrical conductivity, computerized tomography).

6.3.6 Pregnancy

Nulliparous does experience considerable variations in body composition, tissue deposition and energy retention during their first pregnancy (Parigi Bini et al., 1990a, 1991a; Xiccato et al., 1995; Fortun-Lamothe and Lebas, 1996; Milisits et al., 1996, 1999). During early and mid-gestation (0–21 days), the LW increases similarly to that of non-pregnant does (Table 6.6).

During late pregnancy (21–30 days), the EB weight decreases as a result of protein and fat losses and a transfer of energy to the rapidly growing fetuses. At the same time, non-pregnant does continue to gain weight and retain body energy, primarily in the form of fat.

Changes in various blood plasma metabolites confirm the intense modification of energy metabolism in late pregnancy (Parigi Bini et al., 1990a; Fortun et al., 1994; Xiccato et al., 2005b; Pascual et al., 2006). In the last period of pregnancy, the glucagon level increases, while glucose, triglyceride, cholesterol and leptin levels decrease. Glucagon is involved in the control of catabolic utilization of body reserves and a similar increase in level was reported by Jean-Blain and Durix (1985). The transfer of energy from the body of doe to the fetuses leads to an energy deficit that is especially concentrated in the last 10 days of pregnancy, as reported for sows (Noblet and Close, 1980) and ewes (Rattray et al., 1980). The low circulating levels of leptin and glucose immediately after kindling suggest either that body energy stores are depleted by pregnancy or that no energy is available for body tissue deposition due to the very low feed intake at kindling (Parigi Bini et al., 1990a; Housekneckt and Spurlock, 2003; Xiccato et al., 2005b).

The body composition of newborn kits (born dead included) can vary according to litter size, average weight of kits, parity order, physiological state and the feeding

| Table 6.6. Variations in empty body (EB) composition in non-pregnant and pregnant nulliparous does (Parigi Bini et al., 1990a). |
|-----------------|-----------------|-----------------|
|                  | Days on trial   |                  |
| **Non-pregnant does** |                  |                  |
| EB weight (kg)  | 2.97            | 3.16            | 3.27            |
| Water (g kg⁻¹)  | 611             | 597             | 576             |
| Protein (g kg⁻¹)| 215             | 208             | 205             |
| Fat (g kg⁻¹)    | 146             | 162             | 187             |
| EB energy (MJ kg⁻¹) | 10.2           | 10.6           | 11.4           |
| **Pregnant does** |                  |                  |
| EB weight (kg)  | 2.97            | 3.15            | 2.98            |
| Water (g kg⁻¹)  | 611             | 592             | 596             |
| Protein (g kg⁻¹)| 215             | 217             | 218             |
| Fat (g kg⁻¹)    | 146             | 160             | 156             |
| EB energy (MJ kg⁻¹) | 10.2           | 10.7           | 10.6           |

*Excluding pregnant uterus.*
The body composition of newborn kits from does fed ad libitum is 800 (790–818) g water kg$^{-1}$, 120 (113–130) g protein kg$^{-1}$, 55 (48–61) g fat kg$^{-1}$, 22 (19–26) g ash kg$^{-1}$ and 5.0 (4.3–5.6) kJ energy kg$^{-1}$ (Parigi Bini et al., 1992; Parigi Bini and Xiccato, 1993; Xiccato et al., 1995; Fortun-Lamothe et al., 1999). Feeding restriction of the doe reduces body fat and energy concentration and increases water of newborn kits (Xiccato et al., 1992b; Fortun-Lamothe and Lebas, 1996; Fortun-Lamothe et al., 1999).

The efficiency of DE utilization for maternal tissue accretion in pregnant or non-pregnant does (REg/DEI) has been estimated at 0.49 (Parigi Bini et al., 1991a) to 0.55 (Toschi et al., 2004), similarly to efficiency in growing rabbits. Lower efficiencies of dietary DE utilization for fetal growth (Efetus/DEI) have been found, namely 0.31 in pregnant nulliparous does and 0.27 in lactating and pregnant does (Parigi Bini et al., 1991a, 1992; Xiccato et al., 1992b) (Table 6.7).

Similar or lower efficiencies (0.20–0.30) for fetal growth have been observed in pigs (Walach-Janiak et al., 1986). An explanation for the high energy cost of fetal growth may come from the very high protein content of the fetal tissues and the extremely rapid turnover of fetal protein (Young, 1979).

### 6.3.7 Lactation and concurrent pregnancy

The energy output in milk (Emilk) during lactation is exceptionally high in rabbits, compared to other species, due to the considerable milk production (200–300 g day$^{-1}$) and the high concentration in DM (300–350 g kg$^{-1}$), protein (100–150 g kg$^{-1}$) and fat (120–150 g kg$^{-1}$; Lebas, 1971; Partridge et al., 1983, 1986b; Fraga et al., 1989; Parigi Bini et al., 1992; Pascual et al., 1999a, 2002b; Maertens et al., 2006). The chemical composition of rabbit milk changes substantially during lactation (Lebas, 1971; Pascual et al., 1999a). In particular, the DM content decreases in the first 1–3 days, when colostrum becomes milk, then remains constant for about 3 weeks and finally increases as milk yield decreases. On the other hand, the composition of milk DM tends to remain unchanged, except for a constant reduction in lactose, and therefore the caloric value of milk is strictly dependent on the variation of DM content (Parigi Bini et al., 1991b; Xiccato et al., 1995).

Different measurements of milk energy concentration and variation during lactation are listed in Table 6.8. The average caloric value of 8.5 MJ kg$^{-1}$ is close to the value of 8.53 MJ kg$^{-1}$ reported by Blaxter (1989) and is about 2.9 times higher than that of cow milk (2.97 MJ kg$^{-1}$).

If the daily excretion of energy as milk is expressed in terms of metabolic weight, however, the average milk energy output is higher in rabbits than in cows. For example, a 4 kg doe producing 250 g milk day$^{-1}$ excretes 751 kJ Emilk day$^{-1}$ kg$^{-1}$ LW$^{0.75}$, while a 600 kg cow producing 25 kg

### Table 6.7. Efficiency of utilization of digestible energy and the doe’s body energy reserves (RE) for fetal growth (Efetus) and milk production (Emilk).

<table>
<thead>
<tr>
<th>Authors</th>
<th>Efetus/DEI</th>
<th>Emilk/DEI</th>
<th>Emilk/REr</th>
</tr>
</thead>
<tbody>
<tr>
<td>Partridge et al. (1983, 1986b)</td>
<td>–</td>
<td>0.68–0.84$^a$</td>
<td>0.94</td>
</tr>
<tr>
<td>Partridge et al. (1986a)</td>
<td>–</td>
<td>0.62</td>
<td>–</td>
</tr>
<tr>
<td>Fraga et al. (1989)</td>
<td>–</td>
<td>0.71</td>
<td>–</td>
</tr>
<tr>
<td>Parigi Bini et al. (1991a, b, 1992)</td>
<td>0.27–0.31</td>
<td>0.63</td>
<td>0.76–0.81</td>
</tr>
<tr>
<td>Xiccato et al. (1992b, 1995)</td>
<td>0.30</td>
<td>0.63</td>
<td>0.76</td>
</tr>
<tr>
<td>Pascual et al. (2000b)</td>
<td>–</td>
<td>0.71–0.79$^a$</td>
<td>–</td>
</tr>
</tbody>
</table>

$^a$DEI, Digestible energy intake.

$^a$The highest values were found in does fed with high-fat-added diets.
Table 6.8. Energy concentration (MJ kg\textsuperscript{-1}) and variation of rabbit milk during lactation.

<table>
<thead>
<tr>
<th>Authors</th>
<th>Week 1</th>
<th>Week ≥2</th>
<th>Final week</th>
<th>Average</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lebas (1971)\textsuperscript{a}</td>
<td>8.10</td>
<td>7.11</td>
<td>10.22</td>
<td>8.02</td>
</tr>
<tr>
<td>Parigi Bini \textit{et al.} (1991b)</td>
<td>–</td>
<td>7.75</td>
<td>9.84</td>
<td>8.27</td>
</tr>
<tr>
<td>Maertens (1992)</td>
<td>–</td>
<td>8.0</td>
<td>9.0–12.0</td>
<td>–</td>
</tr>
<tr>
<td>Pascual \textit{et al.} (1999a)\textsuperscript{b}</td>
<td>9.28</td>
<td>9.18</td>
<td>11.59</td>
<td>–</td>
</tr>
<tr>
<td>Pascual \textit{et al.} (2002b)\textsuperscript{c}</td>
<td>–</td>
<td>8.85</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Maertens \textit{et al.} (2006)</td>
<td>8.4</td>
<td>8.7</td>
<td>10.5</td>
<td>–</td>
</tr>
<tr>
<td>Average</td>
<td>8.5</td>
<td>8.3</td>
<td>10.5</td>
<td>8.5</td>
</tr>
</tbody>
</table>

\textsuperscript{a}Estimated energy values from chemical composition.
\textsuperscript{b}Average of does fed diets with ether extract: 26, 99 and 117 g kg\textsuperscript{-1} dry matter.
\textsuperscript{c}Average of does fed diets with ether extract: 28, 71 and 91 g kg\textsuperscript{-1} dry matter.

Milk day\textsuperscript{-1} excretes only 612 kJ E\textsubscript{milk day\textsuperscript{-1} kg\textsuperscript{-1} LW\textsuperscript{0.75}}.

The dietary DE is utilized very efficiently by lactating does. Based on literature (see Table 6.7), the coefficient of utilization of DE for milk production in lactating non-pregnant and lactating and concurrent pregnant does ranges from 0.60 to 0.70. The highest values (>0.75) found by Partridge \textit{et al.} (1983, 1986b) and Pascual \textit{et al.} (2000b) may be explained by the particular diets (high fat, high protein) used in those experiments, which could have permitted the direct passage of long-chain fatty acids from feed to milk.

The efficiency of utilization of energy retained in the doe’s body reserves (RE,) for milk production is 0.81 in lactating does (Parigi Bini \textit{et al.}, 1991a,b) and 0.76 in lactating and pregnant does (Parigi Bini \textit{et al.}, 1992; Xiccato \textit{et al.}, 1992b).

The average values proposed for the utilization of dietary DE (0.65) and maternal body energy for milk production (0.78) agree with the results from other species (cattle and pigs) and the theoretical calculations by Blaxter (1989).

A calculation of the energy requirements and body balance for multiparous, lactating and non-pregnant does is provided in Box 6.2.

6.3.8 Energy and material balance during reproduction

The significant energy excretion through milk in lactating does, which is even more pronounced in selected ‘hybrid’ does, is not completely compensated by voluntary DEI, especially in primiparous does. This causes a consistent deficit in both body tissues and energy. During the first pregnancy, DEI decreases from 600 to 650 kJ day\textsuperscript{-1} kg\textsuperscript{-1} LW\textsuperscript{0.75} in the first 25 days until 400–450 kJ day\textsuperscript{-1} kg\textsuperscript{-1} LW\textsuperscript{0.75} in the last 5 days, due to the increasing volume of fetuses in the abdomen. On the day of kindling, the doe ingests only a small amount of feed or even nothing (Fig. 6.4).

Voluntary DE consumption is much higher in lactating females, which can ingest 1500–1800 kJ day\textsuperscript{-1} kg\textsuperscript{-1} LW\textsuperscript{0.75} at the lactation peak and 1100–1300 kJ day\textsuperscript{-1} kg\textsuperscript{-1} LW\textsuperscript{0.75} on average. The highest values are recorded by multiparous does.

After litter weaning, does quickly decrease their energy intake in a week to about 0.35–0.45 of the lactation level; that is, 500–600 kJ DE day\textsuperscript{-1} kg\textsuperscript{-1} LW\textsuperscript{0.75} (Xiccato \textit{et al.}, 2004, 2005b).

During lactation, therefore, the doe’s body is subjected to a marked reduction in energy reserves following the mobilization of fat deposits (Fig. 6.5) (Parigi Bini \textit{et al.},
Box 6.2. Estimate of digestible energy (DE) requirements and body energy and fat balance in multiparous, non-pregnant and lactating does (assuming protein balance is in equilibrium).

Reference data
- Average live weight (LW) = 4.25 kg
- Empty body (EB) weight at kindling = 0.92 LW = 3.91 kg
- Days of lactation = 30 days
- Milk production = 220 g day\(^{-1}\)
- Caloric value of milk = 8.5 MJ kg\(^{-1}\) = 8.5 kJ g\(^{-1}\)
- Energy concentration of EB at kindling = 10.5 MJ kg\(^{-1}\)
- Fat concentration of EB at kindling = 160 g kg\(^{-1}\)
- Caloric value of EB fat = 36.5 kJ g\(^{-1}\)
- DE required for maintenance (DE\(_m\)) = 430 kJ day\(^{-1}\) kg\(^{-1}\) LW\(^{0.75}\)
- Efficiency of utilization of DE for milk energy (E\(_{milk}\)) = 0.65
- Efficiency of utilization of body energy reserves (RE\(_r\)) for E\(_{milk}\) = 0.80
- Dietary DE concentration = 11.0 MJ kg\(^{-1}\) = 11.0 kJ g\(^{-1}\)
- Maximum DE intake (DEI) = 1250 kJ day\(^{-1}\) kg\(^{-1}\) LW\(^{0.75}\)
- Protein balance = 0

Calculated data
- Average LW\(^{0.75}\) = 4.25\(^{0.75}\) kg = 2.96 kg LW\(^{0.75}\)
- E\(_{milk}\) = 220 g day\(^{-1}\) × 8.5 kJ g\(^{-1}\) = 1870 kJ day\(^{-1}\)
- Total EB energy at kindling = 3.91 kg × 10.5 MJ kg\(^{-1}\) = 41.05 MJ
- Total EB fat at kindling = 3.91 kg × 160 g kg\(^{-1}\) = 626 g

DE requirements and intake
- DE requirement for maintenance = 430 kJ day\(^{-1}\) kg\(^{-1}\) LW\(^{0.75}\) × 2.96 kg LW\(^{0.75}\) = 1273 kJ day\(^{-1}\)
- DE requirement for milk production (DE\(_{milk}\)) = 1870 kJ day\(^{-1}\) / 0.65 = 2877 kJ day\(^{-1}\)
- Total DE requirement = 1273 + 2877 = 4150 kJ day\(^{-1}\)
- Maximum DEI = 1250 kJ day\(^{-1}\) kg\(^{-1}\) LW\(^{0.75}\) × 2.96 kg LW\(^{0.75}\) = 3700 kJ day\(^{-1}\) 11.0 kJg\(^{-1}\)
- Maximum feed intake = 336 g day\(^{-1}\)
- DEI deficit = 4150 – 3700 = −450 kJ day\(^{-1}\)

Body energy and tissue balance
- DEI for milk production = DEI – DE\(_{m}\) = 3700 – 1273 = 2427 kJ day\(^{-1}\)
- E\(_{milk}\) from dietary DE = 2427 kJ day\(^{-1}\) × 0.65 = 1578 kJ day\(^{-1}\)
- E\(_{milk}\) from body energy reserves = 1870 – 1578 = 292 kJ day\(^{-1}\)
- Daily EB energy loss (RE\(_r\)) = −292 kJ day\(^{-1}\) / 0.80 = −365 kJ day\(^{-1}\)
- Total EB energy loss during lactation = −365 kJ day\(^{-1}\) × 30 days = −10.95 MJ
- EB energy balance = −10.95 MJ / 41.05 MJ × 100 = −26.7%
- Daily EB fat loss = −365 kJ day\(^{-1}\) / 36.5 kJ g\(^{-1}\) = −10.0 g day\(^{-1}\)
- Total EB fat loss during lactation = −10.0 g day\(^{-1}\) × 30 days = −300 g
- EB fat balance = −300 g / 626 g × 100 = −47.9%

1990b, 1991b, 1992; Xiccato et al., 1992b, 1995, 1999, 2004, 2005b; Pascual et al., 2000b, 2003). Unlike in other species, this energy loss remains constant throughout lactation (Parigi Bini et al., 1990b) and no recovery is observed during the final phase due to the milk energy output, which remains high even after 25–30 days of lactation.

The simultaneous condition of pregnancy is responsible for a further reduction in fat content and body energy levels. It prevents the return to normal body conditions (Fortun et al., 1993; Parigi Bini and Xiccato, 1993; Fortun-Lamothe and Lebas, 1996; Xiccato et al., 2005b) and increases protein requirements in response to the elevated demand for protein by the fetuses and the rapid turnover of fetal protein (Parigi Bini et al., 1992; Xiccato et al., 1992b, 1995).

The emergence of high-performance hybrid lines with higher nutritional needs, but that are unable to ingest sufficient dietary energy, has increased rabbit doe susceptibility to the energy deficit. The
Fig. 6.4. Evolution of voluntary feed intake (g day\(^{-1}\)) (solid line) and digestible energy intake (kJ day\(^{-1}\) kg\(^{-1}\) LW\(^{0.75}\)) (dotted line) from the first insemination to the fourth kindling in does submitted to a 12-day post-partum remating programme (from Xiccato and Trocino, 2008). I1, I2, I3, I4: 1st, 2nd, 3rd, 4th insemination; K1, K2, K3, K4: 1st, 2nd, 3rd, 4th kindling; W1, W2, W3: 1st, 2nd, 3rd weaning.

6.3.9 Nutritional strategies to reduce energy deficit

Feeding young does

Young does should face their first mating, pregnancy and lactation with an adequate body energy condition to support the high nutritional requirements of reproduction. From weaning (30–35 days) to puberty (10–12 weeks) and LW from 0.8 to 2.4 kg, feeding programmes and growth performance are similar to those of rabbits kept for meat production. Later, from puberty to first mating (16–18 weeks of age) and LW until 3.2–3.5 kg, the feeding programme should aim to permit correct morphologic and reproductive development and avoid overfattening (Pascual et al., 2006; Rommers et al., 2006; Xiccato and Trocino, 2008). In this period, voluntary feed intake decreases slightly from 800 to 700 kJ DE day\(^{-1}\) kg\(^{-1}\) LW\(^{0.75}\) and daily weight gain decreases from 35 to 20 g day\(^{-1}\) (Xiccato et al., 1999).

At 17 weeks of age, breeding rabbits given *ad libitum* access to a diet containing 10 MJ DE kg\(^{-1}\) may reach about 3.4 kg LW and 180 g body fat kg\(^{-1}\) LW. This condition may be excessive if the further fattening during pregnancy or the rapid overfattening (>200 g fat kg\(^{-1}\)) in 2–3 weeks in case of failure of pregnancy are considered. Overfattening can...
provoke subsequent dystocia and impaired reproductive performance (Partridge et al., 1986a; Parigi Bini et al., 1989; Viudes-de-Castro et al., 1991). On the other hand, an earlier insemination (e.g. 15 weeks) is not advisable due to the still incomplete development of the endocrine and reproductive systems (Matics et al., 2008).

For these reasons, feeding restriction (0.8–0.9 of ad libitum intake) may be applied to young does for different periods before mating to obtain a target weight at insemination. In restricted does, flushing with a lactation diet given ad libitum is usually performed 4–7 days before the first insemination to avoid a reduction in sexual receptivity at this time (Rommers et al., 2001, 2002, 2004a,b, 2006; Bonannò et al., 2004).

Feed restriction can continue also in the first part of pregnancy, especially when LW exceeds target weight, while ad libitum feeding with a lactation diet is recommended during the last 2 weeks of pregnancy to take into account increasing pregnancy requirements and decreasing feed intake around kindling (Rommers et al., 2004b). However, restricting feed during the entire pregnancy to maintenance needs or even less (0.75) reduces body fat and energy reserves (Table 6.9) to a level that may negatively influence reproductive performance (Fortun et al., 1994).

In young does, feeding restriction may also reduce voluntary feed intake in the following pregnancy and lactation and accentuate the risk of a negative energy balance between reproductive cycles (Parigi Bini et al., 1991a; Maertens, 1992; Fortun-Lamothe, 1998). On the other hand, the administration of high-fibre, low-energy diets to young females before the first mating increases voluntary feed intake during growth and pregnancy, and partially decreases the body fat and energy deficit at the end of first lactation (Table 6.10) (Xiccato et al.,

| Table 6.9. Body composition and energy concentration of primiparous does slaughtered at 28 days’ of gestation. The does had been fed ad libitum (C), at a maintenance level (M) or at 0.75 of the maintenance level (R) during pregnancy (Fortun et al., 1994). |
|-----------------|-----------------|-----------------|
|                 | C does          | M does          | R does          |
| Water (g kg⁻¹) | 590<sup>a</sup> | 620<sup>b</sup> | 640<sup>c</sup> |
| Protein (g kg⁻¹)| 189             | 192             | 189             |
| Fat (g kg⁻¹)   | 193<sup>a</sup> | 156<sup>b</sup>| 134<sup>b</sup> |
| Energy (MJ kg⁻¹)| 11.8<sup>a</sup> | 10.5<sup>b</sup> | 9.6<sup>c</sup> |

<sup>a,b,c</sup>Means on the same row with different subscript differ (P < 0.05).

| Table 6.10. Influence of a high-fibre, low-energy diet given from weaning until first insemination of young does on the ensuing lactation and empty body (EB) balance (Xiccato et al., 1999). |
|-----------------|-----------------|-----------------|
| Diet fed before first insemination | Control diet | Low-energy diet | P |
| LW at kindling (g) | 3846 | 3833 | NS |
| LW at end of lactation (g) | 3939 | 3848 | NS |
| Milk production (g day⁻¹) | 206 | 204 | NS |
| Feed intake (g day⁻¹) | 331 | 340 | NS |
| DE intake (kJ day⁻¹ kg⁻¹ LW<sup>0.75</sup>) | 1203 | 1245 | NS |
| EB gain (g) | −233 | −221 | NS |
| DE, digestible energy; LW, live weight; NS, not significant. | | | |

| EB balance (variation on the composition at kindling): | | | |
| Water (%) | 11 | 7 | 0.09 |
| Protein (%) | 7 | 6 | NS |
| Fat (%) | −68 | −59 | <0.01 |
| Energy (%) | −41 | −36 | <0.01 |
A similar feeding regime does not affect reproductive performance at birth, but stimulates feed intake during lactation with consequent higher litter sizes and weights at weaning (Nizza et al., 1997; Pascual et al., 2002a).

**Feeding reproducing does**

High-energy diets have been widely tested in reproducing does to meet their high energy requirements. The effects of increasing dietary energy concentration on reproductive performance and body chemical and energy balance have been reviewed by Pascual et al. (2003).

During early pregnancy, increasing dietary DE concentration usually reduces DMI and does not change DEI significantly (Pascual et al., 1998, 1999a, b, 2002b). During the last week of pregnancy, voluntary feed intake is limited by physical intake capacity (Pascual et al., 2003).

During lactation, feeding highly digestible diets increases DEI (Partridge, 1986; Maertens and De Groote, 1988; Fraga et al., 1989; Castellini and Battaglini, 1991; Barreto and de Blas, 1993; Cervera et al., 1993), especially when added-fat diets are used in comparison with high-starch diets (Xiccato et al., 1995; Fortun-Lamothe and Lebas, 1996; Parigi Bini et al., 1996; Pascual et al., 1998, 2002b). The body energy balance of does, however, is always negative and is not statistically affected by dietary treatments (Fig. 6.6). In fact, a higher dietary energy supply determines an increase of milk production, impairing its potential beneficial effect on body condition both in primiparous (Table 6.11) (Xiccato et al., 1995; Fortun-Lamothe and Lebas, 1996) and multiparous does (Table 6.12) (Pascual et al., 2000b).

Therefore, the limiting factor on doe productivity is not milk production, but voluntary feed intake: as DEI increases, milk production also tends to increase, thereby impairing – at least partially – the effect of increased DEI on body energy balance. An increase of 1 kJ in the DEI leads to a proportional increase in milk energy output (0.434 kJ) and a more limited reduction in the energy deficit (−0.203 kJ) (Fig. 6.7) (Xiccato, 1996).

This trend, linear throughout the interval tested, shows a DEI capable of obtaining the doe’s body energy equilibrium (REr = 0) at 1585 kJ day⁻¹ kg⁻¹ LW⁰.⁷⁵. At this DEI level, the energy milk output is 711 kJ day⁻¹ kg⁻¹ LW⁰.⁷⁵, which corresponds to about 250 g day⁻¹ of milk in a 4.25 kg rabbit (assuming a milk energy density of 8.5 MJ kg⁻¹). Using a

![Fig. 6.6. Empty body energy balance (percentage variation on energy content at initial kindling) of does at different physiological states, given diets with increasing digestible energy (DE) concentrations (Xiccato et al., 1995). DM, dry matter.](image)
Table 6.11. Effect of dietary energy level on reproductive performance and empty body (EB) composition at day 28 of the first lactation in concurrently lactating and pregnant does (Fortun-Lamothe and Lebas, 1996).

<table>
<thead>
<tr>
<th>Dietary DE (MJ kg⁻¹ DM)</th>
<th>Total milk production (0–21 days) (kg)</th>
<th>Litter weight at day 28 (kg)</th>
<th>EB energy (MJ kg⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>9.9 (control diet)</td>
<td>3.8ab</td>
<td>3.9a</td>
<td>7.85b</td>
</tr>
<tr>
<td>12.1 (added-fat diet)</td>
<td>4.2a</td>
<td>4.5a</td>
<td>8.76a</td>
</tr>
<tr>
<td>12.2 (starch diet)</td>
<td>3.6b</td>
<td>3.8a</td>
<td>9.22a</td>
</tr>
</tbody>
</table>

DE, digestible energy; EB, empty body; abMeans on the same row with different subscript differ (P < 0.05).

Table 6.12. Effect of dietary energy level on reproductive performance and energy balance of rabbit does at day 28 of the second lactation (Pascual et al., 2000b).

<table>
<thead>
<tr>
<th>Dietary DE (MJ kg⁻¹ DM)</th>
<th>DE intake (kJ day⁻¹ kg⁻¹ LW⁰.⁷⁵)</th>
<th>Milk production (g day⁻¹)</th>
<th>Litter weight at weaning (kg)</th>
<th>EB energy gain (MJ)</th>
</tr>
</thead>
<tbody>
<tr>
<td>11.0 (control diet)</td>
<td>1296</td>
<td>191</td>
<td>3.93</td>
<td>−3.33</td>
</tr>
<tr>
<td>12.4 (added-fat diet)</td>
<td>1445</td>
<td>237</td>
<td>4.69</td>
<td>−3.42</td>
</tr>
</tbody>
</table>

DE, digestible energy; EB, empty body; LW, live weight; NS, not significant.

Fig. 6.7. Effect of digestible energy intake (DEI) on the energy excreted during milk production (Emilk) and the energy retained in the doe body (REr) (data expressed in kJ day⁻¹ kg⁻¹ LW⁰.⁷⁵) (Xiccato, 1996).

diet with 10.5 MJ DE kg⁻¹, this female must be able to ingest at least 150 g day⁻¹ kg⁻¹ LW⁰.⁷⁵ (i.e. about 450 g day⁻¹). Such an average voluntary intake during the entire period of lactation is unusual in primiparous and secundiparous does. Therefore, any intervention performed to stimulate energy intake will rarely provide a substantial reduction in the body energy deficit. In some cases, a contemporary increase in daily
energy intake and milk production does not modify the rabbit’s nutritional state.

In addition to stimulating milk production, any increase in DEI is generally associated with an increased feed intake. This leads to a faster digestive transit and a consequent reduction in the digestive utilization of the dietary energy, which makes the objective of solving the energy deficit even more difficult to achieve (Xiccato et al., 1992a; de Blas et al., 1995; Xiccato, 1996).

The nutritional deficit provoked by lactation also seems to be responsible for the decreased reproductive efficiency of concurrently lactating and pregnant does, and consequently for the reduction in fetal developmental viability (Viudes-de-Castro et al., 1991; Parigi Bini et al., 1992; Fortun et al., 1993; Fortun-Lamothe and Bolet, 1995; Fortun-Lamothe and Lebas, 1996). Similar negative effects have been described when feed restriction is used in reproducing rabbit does before mating and during pregnancy to avoid overfattening (Fortun et al., 1994; Fortun-Lamothe, 1998).

### 6.3.10 Management strategies

#### Parity order

The occurrence of doe body energy deficit has been largely proven during the first lactation (Simplicio et al., 1988; Parigi Bini et al., 1989; Battaglini and Grandi, 1991; Castellini and Battaglini, 1991). Multiparous does are usually considered capable of ingesting higher amounts of feed therefore of achieving body energy and protein equilibrium. Substantial body fat and energy mobilization has, however, been observed in multiparous lactating does (Table 6.13) (Partridge et al., 1983, 1986a; Pascual et al., 2000b; Castellini et al., 2003, 2006; Xiccato et al., 2004, 2005b). Several authors have described significant increases (5–15%) in feed intake from the first to the second and from the second to the third kindling, followed by lower but not significant increases for successive parities (Parigi Bini et al., 1989; Battaglini and Grandi, 1991; Castellini and Battaglini, 1991). DEI rises by 9% between the first and the second lactation, but only by 3% from

<table>
<thead>
<tr>
<th>Parity order</th>
<th>1st</th>
<th>2nd</th>
<th>3rd</th>
<th>Probability</th>
</tr>
</thead>
<tbody>
<tr>
<td>1st</td>
<td>22</td>
<td>20</td>
<td>27</td>
<td></td>
</tr>
<tr>
<td>Total milk production (g)</td>
<td>4548</td>
<td>5023</td>
<td>5410</td>
<td>&lt;0.001 NS</td>
</tr>
<tr>
<td>Total feed intake (g)</td>
<td>7276</td>
<td>7993</td>
<td>8313</td>
<td>&lt;0.001 NS</td>
</tr>
<tr>
<td>From weaning to kindling</td>
<td>2721</td>
<td>2945</td>
<td>2888</td>
<td>NS NS</td>
</tr>
<tr>
<td>DE intake (kJ d(^{-1}) kg(^{-1}) LW(^{−0.75}))</td>
<td>1099</td>
<td>1203</td>
<td>1237</td>
<td>&lt;0.001 NS</td>
</tr>
<tr>
<td>From weaning to kindling</td>
<td>685</td>
<td>757</td>
<td>726</td>
<td>NS NS</td>
</tr>
<tr>
<td>Chemical and energy balance (^{c})</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Water (%)</td>
<td>10.5</td>
<td>2.6</td>
<td>3.8</td>
<td>&lt;0.001 &lt;0.01</td>
</tr>
<tr>
<td>Protein (%)</td>
<td>−0.2</td>
<td>1.8</td>
<td>−1.1</td>
<td>NS NS</td>
</tr>
<tr>
<td>Fat (%)</td>
<td>−33.0</td>
<td>−23.3</td>
<td>−20.2</td>
<td>&lt;0.05 NS</td>
</tr>
<tr>
<td>Energy (%)</td>
<td>−20.5</td>
<td>−11.2</td>
<td>−9.2</td>
<td>&lt;0.001 NS</td>
</tr>
</tbody>
</table>

DE, digestible energy; LW, live weight; NS, not significant.

\(^{a}\) Linear component of variance.

\(^{b}\) Quadratic component of variance.

\(^{c}\) Change in body composition at initial kindling.
the second to the third lactation, while milk production increases by 10% and 8%, respectively (Xiccato et al., 2004).

The unchanged substantial gap between dietary energy intake and milk energy output accounts for the body deficit that is also maintained at higher parities (Pascual et al., 2000b; Castellini et al., 2003, 2006; Xiccato et al., 2004, 2005b). The total body energy of rabbit does lowers during the first lactation and remains constant until the third kindling in pregnant and lactating does, while it increases in non-pregnant does (Fig. 6.8) (Bolet and Fortun-Lamothe, 2002). In does submitted to a semi-intensive rhythm and traditional weaning, however, the body energy deficit not longer appears in females after their third kindling (Quevedo et al., 2004). Different results may be ascribed to the rabbit strain (commercial hybrids or selected pure breeds) and the body balance measurement method (comparative slaughter, ultrasound technique, total body electric conductivity).

Breeding rhythm

On commercial farms, rabbit does are usually mated on a fixed day in the first weeks post-partum (PP); that is, 3–5 days PP (intensive rhythm), 10–12 or 17–19 days PP (semi-intensive rhythms) or 24–26 days PP (extensive rhythm). This determines exact theoretical intervals between two kindlings of 5, 6, 7 or 8 weeks, respectively. New schedules are now under study (post-weaning insemination associated with early weaning, alternate PP and post-weaning insemination, rhythms based on doe body condition score) that better fit doe physiology (Castellini et al., 2003, 2006; Castellini, 2007; Bonanno et al., 2008; Brecchia et al., 2008; Cardinali et al., 2008), but the most diffuse remating programme remains the semi-intensive rhythm. This rhythm is a compromise between the doe’s need to recover energy between one reproductive cycle and the next and the economic demand of increasing the number of kits weaned per year (Fig. 6.9) (Mendez et al., 1986; Parigi Bini et al., 1989; Cervera et al., 1993; Xiccato et al., 2005b; Rebollar et al., 2009). In fact, intensive PP insemination implies an excessive exploitation of the doe, which finally results in a reduction in reproductive performance and career length. On the other hand, extensive rhythms allow a too-low number of kindlings per year and can

![Fig. 6.8. Evolution of total empty body (EB) energy concentration (total body electrical conductivity measurements) in rabbit does from the first to third kindling, and according to their physiological state (I2, I3: 2nd, 3rd insemination; K1, K2, K3: 1st, 2nd, 3rd kindling; W1, W2: 1st, 2nd weaning) (from Bolet and Fortun-Lamothe, 2002).](image-url)
cause doe overfattening, higher embryonic mortality and impairment of reproductive performance (Parigi Bini et al., 1996).

The breeding system greatly affects the energy balance of lactating does, influencing both milk production and feed intake (Fig. 6.10). Does submitted to intensive reproductive rhythms begin showing decreased milk production after 15–17 days of lactation, with a sharper decrease in the last week of pregnancy (Lebas, 1972; Partridge et al., 1986b; Fraga et al., 1989) due to the exponential development of fetuses and hormonal changes caused by the imminent kindling that compromise milk production (Fortun-Lamothe et al., 1999). The role of high prolactin and low progesterone levels in lactating does in reducing the fetal survival rate has been elucidated, and may interact with the effects of the nutritional deficit caused by

![Fig. 6.9. Evolution of digestible energy (DE) requirement (full line) and of DE intake (dotted line) in does submitted to 12 days post-partum (PP) insemination. Areas with horizontal tracts indicate periods during which the female is in negative energy balance and utilizes body reserves; areas with vertical tracts indicate phases of positive balance and body energy recovery (Xiccato, 1996).](image)

![Fig. 6.10. Effect of breeding rhythm on (a) milk production and (b) feed intake (Xiccato, 1996). PP, post-partum.](image)
lactation (Fortun-Lamothe and Prunier, 1999; Fortun-Lamothe et al., 1999).

Lengthening the interval between kindlings prolongs the dry period and should permit body energy reserves to recover (Partridge et al., 1984; Cervera et al., 1993). In primiparous does, a severe body energy deficit has been observed within the first and second kindlings with insemination at 12 days PP (−26% of initial body energy content), but a less serious deficit (−15%) with insemination at 28 days PP (Fig. 6.11a) (Parigi Bini et al., 1996). When multiparous does were submitted to early weaning (21 or 25 days), the body energy deficit disappeared in those submitted to semi-intensive (insemination at 12 days PP) and extensive (26 days PP) rhythms, but was severe in rabbits submitted to an intensive reproductive rhythm (2 days PP) (Fig. 6.11b) (Xiccato et al., 2005b). The better body condition observed in this latter study, in which only the intensive rhythm provoked a substantial energy deficit, might be ascribed to the concurrent action of high parity order and early weaning age.

In primiparous and multiparous does submitted to standard (insemination at 11 days PP) or extended (insemination post-weaning at 27 days PP) reproductive rhythms, a body energy deficit was found in all does and did not change significantly with the insemination programme (Castellini et al., 2006). However, the post-weaning rhythm improved reproductive performances and appeared more adapted to the doe physiology (Table 6.14).

**Litter weaning age**

Under field conditions, kits are usually separated from their mothers at around 32–35 days of age or even later. Previous research, in fact, reported a negative correlation between weaning weight and post-weaning mortality (Morisse, 1987; Lebas, 1993) and induced breeders to increase weight by delaying weaning age. On the other hand, more recent studies have demonstrated the possibility of successfully anticipating litter weaning age (de Blas et al., 1999; Pascual, 2001; Xiccato et al., 2003).

The greatest interest in early weaning lies in the possibility of reducing the doe body energy deficit by shortening the lactation length (the period of energy deficit with body energy utilized for milk synthesis) and prolonging the dry period (the period of energy surplus, with body energy restoration). In does at their first, second and third kindling, however, reducing weaning age from 32 to 21 days of age improved body energy balance (from −19% to −8% of the initial body energy content), but was unable to achieve equilibrium (Table 6.15) (Xiccato et al., 2004). In multiparous does, weaning at 25 days did not prevent body energy deficit (−8% of the initial energy content), while weaning at 21 days resulted in a balance that

**Fig. 6.11.** Effect of reproductive rhythm on body protein, fat and energy balance (percentage variation between two successive kindling) at kindling in reproducing does: (a) primiparous does with litter weaning at 28 days (Parigi Bini et al., 1996); (b) multiparous does, with an average of litter weaning at 21 and 25 days (Xiccato et al., 2005b). PP, post-partum.
approached equilibrium (~3%) (Xiccato et al., 2005b).

Early weaning failed definitively to avoid the energy deficit in these does because of the substantial decrease in feed intake after weaning (about 0.4–0.5 of lactation period). With standard weaning, in fact, feed intake remains at the highest levels during the last 10 days of lactation, thus partially permitting recovery of the body energy lost during the first 20 days. The sudden decrease in feed intake that occurs after early weaning reduces the daily energy surplus and delays the complete restoration of body reserves.

A negative effect on reproductive performance has also been described with a lower number of kits born and kits born alive per litter in multiparous does with weaning at 21 days (Xiccato et al., 2004, 2005b). This could be ascribed to the marked effect of weaning on the metabolic and hormonal pattern at the time of fetus implantation (7–11 days of pregnancy) (Fortun-Lamothe and Bolet, 1995).

### Table 6.14. Body energy balance and some productive traits in rabbit does inseminated at 11 days post-partum (control, C) or in the post-weaning (PW) period, 27 days post-partum (Castellini et al., 2006).

<table>
<thead>
<tr>
<th>Reproductive rhythm</th>
<th>Primiparous does</th>
<th>Multiparous does</th>
<th>Probability</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>C</td>
<td>PW</td>
<td>C</td>
</tr>
<tr>
<td>DE intake during lactation (kJ day⁻¹ kg⁻¹ LW^(0.75))</td>
<td>1046</td>
<td>1042</td>
<td>1220</td>
</tr>
<tr>
<td>DE requirements¹ (kJ day⁻¹ kg⁻¹ LW^(0.75))</td>
<td>1246</td>
<td>1228</td>
<td>1306</td>
</tr>
<tr>
<td>Energy deficit (kJ day⁻¹ kg⁻¹ LW^(0.75))a</td>
<td>162</td>
<td>149</td>
<td>86</td>
</tr>
<tr>
<td>Milk production (g day⁻¹)</td>
<td>172</td>
<td>170</td>
<td>185</td>
</tr>
<tr>
<td>Sexual receptivity (%)</td>
<td>30.9</td>
<td>58.1</td>
<td>45.0</td>
</tr>
<tr>
<td>Fertility (%)</td>
<td>48.8</td>
<td>76.8</td>
<td>60.2</td>
</tr>
<tr>
<td>Live born (no.)</td>
<td>7.0</td>
<td>7.0</td>
<td>8.3</td>
</tr>
<tr>
<td>Litter size at weaning (no.)</td>
<td>6.2</td>
<td>6.0</td>
<td>6.9</td>
</tr>
</tbody>
</table>

DE, digestible energy; LW, live weight; NS, not significant.

¹Estimated according to Parigi Bini and Xiccato (1998).

### Table 6.15. Empty body balance of lactating and pregnant does between initial and final kindling (Xiccato et al., 2004).

<table>
<thead>
<tr>
<th>Weaning age</th>
<th>21 days</th>
<th>26 days</th>
<th>32 days</th>
<th>Probabilitya</th>
</tr>
</thead>
<tbody>
<tr>
<td>Protein (%)</td>
<td>1.8</td>
<td>−0.5</td>
<td>−0.8</td>
<td>NS</td>
</tr>
<tr>
<td>Fat (%)</td>
<td>−16.9</td>
<td>−24.5</td>
<td>−35.3</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Energy (%)</td>
<td>−8.0</td>
<td>−13.4</td>
<td>−19.4</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

NS, not significant.

aProbability of the linear component of variance.

6.4 Protein Units and their Measurement

When speaking about nitrogen nutrition in rabbits, various units are available for expressing requirements (de Blas and Mateos, 1998; Fraga, 1998; Carabaño et al., 2000, 2008; García et al., 2005). Crude protein (CP) and apparent DP are the most commonly used units, for which both requirements and raw material composition are largely available (Villamide et al., 1998; Maertens et al., 2002). In reality, rabbits have specific amino acid requirements and apparent faecal and true ileal digestible amino acids would be more reliable units. However, even if increasing information is given on the amino acid con-
centrations of the most common raw materials, digestible amino acid requirements and concentration in feeds are barely known and even less information exists on ileal digestible amino acid (Carabaño et al., 2008). In practice, due to the chemostatic regulation of appetite in rabbits, nitrogen requirements are expressed in relation to dietary energy by the DP to DE ratio, which is directly correlated to body nitrogen retention and excretion.

Besides optimizing productive performance, a correct dietary supply of protein and amino acids in growing and reproducing rabbits permits the maximization of nitrogen retention and reduces nitrogen excretion, which is of growing importance in view of controlling environmental pollution (Maertens et al., 2005; Xiccato et al., 2005a, 2006; Calvet et al., 2008).

Table 6.16 summarizes literature data on DP requirements for maintenance (DPₘ) and the efficiency of utilization of DP intake (DPI) and body protein reserves (Rₚᵣ) in the different categories of rabbits.

### 6.4.1 Maintenance requirements

In growing rabbits, DPₘ is estimated to be 2.9 g DP day⁻¹ kg⁻¹ LW⁰.⁷⁵ (Partridge et al., 1989; Fernández and Fraga, 1996; Motta Ferreira et al., 1996; Fraga, 1998). Lower DPₘ has been found in a new strain of laboratory rabbits (2.11–2.14 DP day⁻¹ kg⁻¹ LW⁰.⁷⁵), which was attributed to a lower basic metabolic rate (Lv et al., 2009). In non-reproducing adult rabbits, since specific information is lacking, the same figures as for growing rabbits may be used for DPₘ.

In lactating and concurrently lactating and pregnant does, protein requirements for maintenance have been estimated by using the comparative slaughter technique equal to 3.73 and 3.76–3.80 g DP kg⁻¹ LW⁰.⁷⁵ (Parigi Bini et al., 1991a, 1992; Xiccato et al., 1992b; Parigi Bini and Xiccato, 1993).

### 6.4.2 Growth requirements

DP requirements vary according to the growth rate. The EB protein concentration changes from 120 g kg⁻¹ (610 g kg⁻¹ DM) at birth to 170 g kg⁻¹ (680 g kg⁻¹ DM) at weaning (35 days of age) and about 200 g kg⁻¹ (590 g kg⁻¹ DM) at 10–12 weeks of age. Afterwards, the body protein concentration is quite constant (200 g kg⁻¹ of EBW, i.e. about 180 g kg⁻¹ LW).

The efficiency of utilization of DPI for growth is estimated to be 0.56 (Partridge et al., 1989; Fernández and Fraga, 1996; Motta Ferreira et al., 1996; Fraga, 1998). Overall DP retention (RP/DPI) decreases linearly from 0.40 to 0.10 with increasing live weight, due to the increase in DP used for maintenance (Xiccato and Cinetto, 1988; Maertens et al., 1997; Trocino et al., 2000, 2001).

### 6.4.3 Pregnancy and lactation requirements

During the first pregnancy, rabbit does retain protein in their body in the early gestation (0–21 days), while they transfer some protein from their body to the rapidly growing fetuses in the late period of pregnancy (21–30 days) (Table 6.17)

<table>
<thead>
<tr>
<th>Growing rabbits</th>
<th>Pregnant and/or lactating does</th>
<th>Non-reproducing does and bucks</th>
</tr>
</thead>
<tbody>
<tr>
<td>DPₘ (g day⁻¹ kg⁻¹ LW⁰.⁷⁵)</td>
<td>2.9</td>
<td>3.7</td>
</tr>
<tr>
<td>Efficiency of protein utilization:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Body retained protein (RP/DPI)</td>
<td>0.56</td>
<td>–</td>
</tr>
<tr>
<td>RP as fetuses (Pₘᵣᵣ/DPI)</td>
<td>–</td>
<td>0.44</td>
</tr>
<tr>
<td>Milk protein from DP (Pₘᵣᵣ/DPI)</td>
<td>–</td>
<td>0.78</td>
</tr>
<tr>
<td>Milk protein from body reserves (Pₘᵣᵣ/Rₚᵣ)</td>
<td>–</td>
<td>0.60</td>
</tr>
</tbody>
</table>

LW, live weight.

### Table 6.16. Digestible protein (DP) requirements for maintenance (DPₘ) and the efficiency of utilization of DP intake (DPI) and body protein reserves (RP).
Table 6.17. Partition of empty body gain and protein retention in pregnant does (Parigi Bini et al., 1990a).

<table>
<thead>
<tr>
<th></th>
<th>0–21 days of pregnancy</th>
<th>21–30 days of pregnancy</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Does</td>
<td>Pregnant uterus</td>
</tr>
<tr>
<td>Empty body gain (g)</td>
<td>180</td>
<td>193</td>
</tr>
<tr>
<td>Retained protein (g)</td>
<td>44</td>
<td>18</td>
</tr>
</tbody>
</table>

(Parigi Bini et al., 1990a). This is due to the exponentially increasing protein requirements of the fetuses and the intense fetal protein turnover, which has been shown to be five times higher than that of maternal tissue, as observed in sheep by Young (1979). The efficiency of DP utilization for fetal protein synthesis is 0.42 and 0.46 in lactating and concurrently lactating and pregnant does, respectively (Parigi Bini et al., 1992; Xiccato et al., 1992b).

In lactating does, the coefficients of utilization of DP and maternal body protein for milk protein are estimated at 0.77 and 0.59, respectively. Similarly, in concurrently lactating and pregnant does the coefficients of utilization of DP and maternal body protein for milk protein are estimated at 0.76–0.80 and 0.60–0.61, respectively.

The high milk production and high milk protein concentration (110–130 g kg\(^{-1}\)) accounts for the high protein requirements for milk synthesis (Maertens et al., 2006). When lactation and pregnancy overlap, as already described for energy, protein requirements also increase to a different extent depending on the reproductive rhythm. In concurrently pregnant and lactating does that are subjected to an intensive reproductive rhythm, limited body protein losses (5–10% of initial content) have been found (Table 6.18) (Parigi Bini et al., 1992; Xiccato et al., 1995, 2004). Sometimes, a negative protein balance has been reported in multiparous lactating does (Partridge et al., 1986b; Pascual et al., 2000b; Xiccato et al., 2005b).

6.4.4 DP to DE ratio

The dietary protein levels recommended for growing rabbits, young females and bucks range from 150 to 160 g CP kg\(^{-1}\) and from 105 to 110 g DP kg\(^{-1}\). In reproducing does, CP from 175 to 190 g kg\(^{-1}\) and DP from 125 to 138 g kg\(^{-1}\) are recommended. These values correspond to a DP to DE ratio of 10.5–11.0 g MJ\(^{-1}\) for young rabbits and bucks and 11.5 to 12.5 g MJ\(^{-1}\) for reproducing does. The higher values are recommended for does under intensive breeding rhythms (Lebas, 1989; Maertens, 1992; Xiccato, 1996; de Blas and Mateos, 1998).

On the basis of more recent studies, the standard CP concentration of commercial diets seems to exceed rabbits’ requirements around weaning and during growth (Maertens et al., 1997; Trocino et al., 2000, 2001; García-Palomares et al., 2006a, b; Eiben et al., 2008). In pregnant and lactating does, a reduction of the DP to DE ratio from 12.5 to 11.2 may decrease litter weight and size, while having less effect on the protein body balance (Table 6.19) (Xiccato et al., 1992b). However, when milk production decreases (from 21 days of lactation to weaning) and the diet is adequately integrated for the most limiting amino acid, the DP to DE ratio may be lowered to 11.5 g MJ\(^{-1}\) (161 g CP kg\(^{-1}\)) without negative effects on the performance of rabbit does and their litters (García-Palomares et al., 2006a).

Table 6.18. Protein balance during the first lactation of does according to their physiological status (Xiccato et al., 1995).

<table>
<thead>
<tr>
<th></th>
<th>Lactating does</th>
<th>Lactating and pregnant does</th>
</tr>
</thead>
<tbody>
<tr>
<td>Empty body gain (g)</td>
<td>184</td>
<td>−131</td>
</tr>
<tr>
<td>Retained protein (g)</td>
<td>75</td>
<td>−38</td>
</tr>
<tr>
<td>Protein balance (%)</td>
<td>11</td>
<td>−6</td>
</tr>
</tbody>
</table>
Table 6.19. Effect of digestible protein (DP) to digestible energy (DE) ratio on reproductive performance and composition of empty body gain between first and second kindling (Xiccato et al., 1992b).

<table>
<thead>
<tr>
<th>DP to DE ratio (g MJ⁻¹)</th>
<th>12.5</th>
<th>11.2</th>
<th>Probability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Milk production (g day⁻¹)</td>
<td>154</td>
<td>151</td>
<td>NS</td>
</tr>
<tr>
<td>Litter weight at 30 days (g)</td>
<td>4479</td>
<td>4367</td>
<td>NS</td>
</tr>
<tr>
<td>No. of kits born per litter</td>
<td>8.0</td>
<td>6.4</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>Weight of kits born per litter (g)</td>
<td>474</td>
<td>351</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>No. of kits born alive per litter</td>
<td>7.6</td>
<td>5.6</td>
<td>&lt;0.10</td>
</tr>
<tr>
<td>Weight kits born alive per litter (g)</td>
<td>455</td>
<td>313</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>Doe body protein gain (g)</td>
<td>+17</td>
<td>+4</td>
<td>NS</td>
</tr>
</tbody>
</table>

NS, not significant.

6.5 Amino Acid Requirements

The amino acid supply through caecotrophy has for a long time been considered adequate to support essential amino acid requirements in rabbits (de Blas and Mateos, 1998). In reality, in rabbits fed conventional diets, the contribution of soft faeces to total CP intake is only 0.15–0.18 (Fraga, 1998; Carabaño et al., 2000), while limited information is available for the different amino acids. In lactating does, the contribution of caecotrophy has been found to make up 0.17 of the supply of sulphur amino acid, 0.18 of lysine and 0.21 of threonine (Nicodemus et al., 1999). Recently, the microbial contribution through caecotrophy has been measured as equal to 0.23 for both tissue lysine in growing rabbits (Belenguer et al., 2005) and milk lysine in lactating does (Abecia et al., 2008).

On the whole, the literature on rabbit amino acid requirements is rather old and restricted to the most limiting amino acids in the diet (lysine, sulphur-containing amino acids, threonine and arginine). Therefore, the amino acid levels actually recommended are still those provided by Lebas (1989) and revised by de Blas and Mateos (1998).

The total amino acid requirements of rabbits have been mainly studied through dose–response trials (Fig. 6.12) or by using the amino acid pattern in body tissue and milk in relation to lysine according to the ideal protein concept (Table 6.20) (de Blas and Mateos, 1998; Fraga, 1998; Ball et al., 2007). However, little attention has been paid to the amino acid partition and efficiency of utilization for maintenance and reproduction. More recently, specific needs for certain essential and non-essential amino acids (threonine, arginine, glutamate) have been hypothesized in order to optimize the defence mechanisms of the intestinal barrier against pathogens (Baylos et al., 2008; Carabaño et al., 2008; Chamorro et al., 2010).

The most limiting essential amino acids in rabbit diets are methionine (and/or cystine) and lysine, immediately followed by threonine. A minimum level of 5.4 g total sulphur-containing amino acid kg⁻¹ (4.0 g digestible amino acid kg⁻¹) is required to obtain adequate productivity in growing and non-reproducing rabbits. A higher level (6.3 g total amino acid kg⁻¹ and 4.9 g digestible sulphur-containing amino acid kg⁻¹) is recommended for reproducing females to increase milk production, reduce the interval between parturitions and improve feed utilization efficiency (Taboada et al., 1996). Recommended levels of lysine (for lactation diets with 10.5–11 MJ DE kg⁻¹) are 6.8 g total lysine kg⁻¹ (5.2 g digestible lysine kg⁻¹) for maximum reproductive performance and 7.6–8.0 g total lysine (6.0–6.4 g kg⁻¹ digestible lysine) kg⁻¹ for maximum milk production and litter growth (Fig. 6.13) (Taboada et al., 1994).

During the lactation peak (10–20 days), a minimum dietary concentration of 5.8 g total threonine kg⁻¹ or 3.8 g digestible threonine kg⁻¹ is necessary to maximize feed intake and
milk production. The optimum supply is 6.4 g total threonine kg\(^{-1}\) and 4.4 g digestible threonine kg\(^{-1}\), while higher or lower values impair both the number of weaned kits and feed efficiency (de Blas et al., 1998).

### 6.6 Protein Retention and Nitrogen Excretion

In highly populated areas, vulnerable from a hydrogeologic point of view, animal waste can represent a potential contaminant of water and soil. The European Directive 91/676/EC aims to prevent or reduce the nitrate pollution of surface and underground water, and asks each member to state reference values for nitrogen excretion of all livestock as well as to define feeding and management strategies to control environmental pollution.

Nitrogen excretion cannot be measured directly because of the considerable loss of nitrogen (through volatile ammonia) from urine and faeces during waste stocking and treatment. According to the official methodology (ERM/AB-DLO, 1999), nitrogen excretion is quantified as the difference between nitrogen consumption and nitrogen retention in animal products; that is, for rabbits, body and fetal tissues and milk. Since nitrogen concentration in the body tissues of finishing rabbits is fairly constant (29–32 g kg\(^{-1}\)) and the nitrogen of fetal tissues and milk is destined to be transferred into the body of fatterers, the farm nitrogen balance of rabbits can be calculated as the difference between the nitrogen input (dietary nitrogen) and the nitrogen output (produced rabbits) at the farm.

Various factors can affect farm nitrogen balance, both in the reproductive and in the fattening sectors (Maertens et al., 2005; Xiccato et al., 2005a). The role of feeding and management factors is discussed below.
Nitrogen excretion is strictly dependent on the dietary CP level. In fattening rabbits, once the limiting amino acid requirements are satisfied by synthetic amino acid supplementation, dietary CP may be reduced to <170 g kg\(^{-1}\), therefore decreasing nitrogen excretion without impairing productive performance (Maertens et al., 1997). Daily weight gain is impaired only at <138 g CP kg\(^{-1}\) (−0.09), but nitrogen excretion is reduced by 0.38 (Fig. 6.14).

When rabbits are fed a diet supplemented with the most limiting amino acid until slaughter at 63 days of age and 2.35 kg LW, decreasing dietary CP from 160 to 140 g kg\(^{-1}\) does not impair growth performance (García-Palomares et al., 2006b). When rabbits are slaughtered later (75–90 days) at a heavier LW (2.5–3.0 kg), feeding programmes based on decreasing dietary CP would permit a better coverage of the higher protein requirements of the first growth period and reduce excretion during fattening. In fact, in this latter period feed intake is higher and dietary nitrogen concentration can be reduced without impacting performance and meat quality (Maertens et al., 1997; Maertens and Luzi, 1998; Trocino et al., 2000, 2001). Lowering dietary CP from 160 to 140 g kg\(^{-1}\) in the first period, from 32 to 56 days of age, reduces daily growth and body nitrogen retention (−0.06) and nitrogen excretion to a similar extent (−0.07) (Trocino et al., 2000). In the second period (56–77 days), a reduction of dietary CP from 154 to 143 g kg\(^{-1}\) decreases nitrogen excretion by 0.09 without impairing daily gain and body nitrogen retention. A further decrease of dietary CP until 131 g kg\(^{-1}\) permits a lowering of nitrogen excretion by 0.15 in comparison with the control diet, while reducing growth and nitrogen retention by only 0.03.

In reproducing does, protein and amino acid requirements are largely satisfied by the current lactation diets. Therefore, as

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**6.6.1 Dietary protein level**

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**Fig. 6.13.** Effect of digestible lysine concentration of the diet (g kg\(^{-1}\)) on productive traits (4.8 g kg\(^{-1}\) = 1) (from Taboada et al., 1994).

**Fig. 6.14.** Daily weight gain and nitrogen (N) excretion in rabbits (32–74 days of age) according to dietary crude protein (CP) concentration (170 g CP kg\(^{-1}\) = 1) (Maertens et al., 1997).
mentioned above, a reduction of dietary CP during lactation until 170 g kg\(^{-1}\) does not affect doe reproductive performance, milk yield or litter growth (Xiccato et al., 1992b; García-Palomares et al., 2006a). Taking into account that the lactation diet represents about a third of the total feed consumed in a closed-cycle farm (reproduction and fattening sectors), advantages in terms of reducing nitrogen excretion are of great importance.

### 6.6.2 Dietary energy level and DP to DE ratio

High-fibre, low-starch diets with low DE concentration have been largely used in the last decade to reduce the risk of digestive diseases such as rabbit epizootic enteropathy (Gidenne, 2003; Gidenne and Garcia, 2006). However, when lowering DE concentration, feed intake increases and, if dietary CP concentration remains unchanged, the DP to DE ratio and nitrogen intake increase. Since growth rate is not modified and nitrogen retention remains constant, nitrogen excretion increases. As an example, when DE concentration decreases from 10.5 to 8.8 MJ kg\(^{-1}\) and dietary CP concentration is maintained at 150 g kg\(^{-1}\) with 0.70 digestibility, the DP to DE ratio increases from 10 to 12 g MJ\(^{-1}\). As shown in Fig. 6.15, body nitrogen retention remains unchanged while daily nitrogen excretion (faecal plus urinary) increases by 0.20.

#### 6.6.3 Numerical productivity of rabbit does and slaughter weight

Numerical productivity (i.e. the number of rabbits produced per doe per year) directly affects the amount of excreted nitrogen on a farm and is in its turn influenced by several factors. The use of more or less intensive reproductive rhythms results in great differences in reproductive efficiency (Maertens et al., 2005). The number of rabbits produced per doe per year can vary from 35–40 in does submitted to extensive rhythms (post-weaning mating) to 45–50 in those undergoing intensive rhythms (mating 5–12 days PP). In a closed-cycle farm, with both reproductive and fattening sectors, nitrogen excretion can be referred to the reproducing doe, including its offspring produced during a year. In this case, excreted nitrogen per doe per year depends both on numerical productivity and on the slaughter weight of fatteners. According to the theoretical model proposed by Maertens et al. (2005), excreted nitrogen increases from 5.24 kg year\(^{-1}\) per doe producing 35 fatteners of 2.25 kg slaughter weight to 9.25 kg year\(^{-1}\) per doe producing 50 fatteners slaughtered at 2.75 kg (Table 6.21).

![Fig. 6.15. Daily nitrogen (N) retention and excretion (faeces plus urine) according to the dietary digestible protein (DP) to digestible energy (DE) ratio (Xiccato et al., 2006). The numbers on the bars represent daily nitrogen excretion (10g DP MJ\(^{-1}\) DE = 1.0).](image)
The model above is calculated on the basis of a constant dietary CP content (on average, 165 g kg\(^{-1}\)) and feed efficiency increasing with doe numerical productivity. With an average CP concentration of feeds consumed on a farm (approximately one-third lactation diet, one-third weaning diet and one-third fattening diet) of 170 g kg\(^{-1}\) and 45 rabbits produced per doe year\(^{-1}\), nitrogen excretion of the doe and its offspring increases from 6.23 to 9.50 kg per doe year\(^{-1}\) depending on the slaughter weight (Table 6.22). A reduction in the average CP level from 170 to 160 g kg\(^{-1}\) permits a decrease of total nitrogen excretion by 0.08–0.10 (Xiccato et al., 2006).

If the nitrogen excretion values listed in Table 6.21 are divided by the number of rabbits produced per year, excreted nitrogen decreases from 150 to 127 g per rabbit of 2.25 kg LW as the doe numerical productivity increases from 35 to 50 rabbits produced per doe year\(^{-1}\). With rabbits sold at 2.75 kg LW, the nitrogen excreted varies from 241 to 185 g per rabbit as the doe numerical productivity increases. If excretion is referred to the weight (kg) of rabbits, excreted nitrogen is less variable (57–87 g N kg\(^{-1}\) rabbit produced).

The theoretical values arising from the model proposed by Maertens et al. (2005) have been confirmed by field data collected from 48 Italian closed-cycle farms (Xiccato et al., 2005a): the does and their offspring (43 rabbits produced per doe year\(^{-1}\), slaughtered at 2.65 kg LW) ingested on average 11.2 kg N year\(^{-1}\) and retained 3.8 kg N year\(^{-1}\), thus excreting 7.4 kg N year\(^{-1}\). If nitrogen excretion is expressed per rabbit or kg produced in the farm, excreted nitrogen is 173±16 g per rabbit or 65±5 g kg\(^{-1}\) (Xiccato et al., 2007). The overall nitrogen or CP efficiency (retained nitrogen/ingested nitrogen) of the Italian productive system of rabbit meat is 0.34 (3.8 kg retained nitrogen per doe year\(^{-1}\)/11.2 kg ingested nitrogen per does year\(^{-1}\)). In Spain, lower values of excreted nitrogen (48 g per rabbit and 41 g kg\(^{-1}\)) and higher overall nitrogen retention (>0.40 of ingested nitrogen) have been found, because the nitrogen ingested during the reproductive and weaning phases was not included in the balance and the slaughter LW was lower (1.8 kg) (Calvet et al., 2008).

### Table 6.21. Nitrogen excretion (kg doe year\(^{-1}\)) according to doe numerical productivity (rabbits produced doe year\(^{-1}\)) and fattener slaughter weight (Maertens et al., 2005).

<table>
<thead>
<tr>
<th>Slaughter weight (kg)</th>
<th>Rabbits produced per doe year(^{-1})</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>35</td>
</tr>
<tr>
<td>2.25</td>
<td>5.24</td>
</tr>
<tr>
<td>2.50</td>
<td>6.65</td>
</tr>
<tr>
<td>2.75</td>
<td>8.42</td>
</tr>
</tbody>
</table>

### Table 6.22. Nitrogen excretion (kg per doe year\(^{-1}\)) according to the average dietary crude protein (CP) level and slaughter weight of fattening rabbits (a closed-cycle farm with 45 rabbits produced per doe year\(^{-1}\)) (Xiccato et al., 2006).

<table>
<thead>
<tr>
<th>Slaughter weight (kg)</th>
<th>Dietary CP (g kg(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>170</td>
</tr>
<tr>
<td>2.25</td>
<td>6.23</td>
</tr>
<tr>
<td>2.50</td>
<td>7.75</td>
</tr>
<tr>
<td>2.75</td>
<td>9.50</td>
</tr>
</tbody>
</table>

References


7 Minerals, Vitamins and Additives

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7.1. Mineral Requirements of Rabbits

Rabbit meat is rich in protein and low in energy, with an ash content similar to or greater than that of other domestic species (Ouhayoun and Lebas, 1987). Publications have shown that rabbit meat is poor in sodium and iron and rich in potassium and phosphorus when compared to meat from other domestic species (Combes, 2004; Hermida et al., 2006). Mean values (mg 100 g⁻¹ fresh loin or hind leg muscles) of 55 for sodium, 400 for potassium, 9.0 for calcium, 234 for phosphorus, 28 for magnesium, 0.83 for iron, 0.89 for zinc, 0.09 for copper, 0.08 for selenium and 0.03 for manganese have been reported. For the whole carcass, Lombardi-Boccia et al. (2005) reported lower values for some of the trace minerals (0.38 for iron, 0.55 for zinc and 0.03 mg 100 g⁻¹ for copper).

Compared with that from other mammals, rabbit milk is high in ash, and especially in calcium, phosphorus and sodium. This is not surprising since the bones of the newborn pups are immature at birth and need extensive mineralization (Widdowson, 1974). In addition, the low level of lactose in rabbit milk has to be compensated for by a high sodium concentration in order to maintain, within an adequate range, the osmotic pressure values (Coates et al., 1964). The macromineral composition of rabbit milk as compared to that of other mammals is presented in Table 7.1.

7.1.1 Macrominerals

Macrominerals are defined as those elements that are required in grams per day and are expressed as g kg⁻¹. The definition includes calcium, phosphorus, magnesium, sodium, potassium, chloride and sulphur. Currently, only calcium, phosphorus and sodium are taken into account in the practical formulation of rabbit diets.

Calcium

Calcium is the main component of the skeleton. Over 0.98 of the total body calcium is present in bones and teeth. In addition, calcium plays a key role in numerous organic processes such as heart function, muscle contraction, blood coagulation and electrolyte equilibrium in serum. Furthermore, doe milk is rich in calcium. Therefore, the dietary requirements for this mineral are expected to be greater for fast-growing young animals and rabbit does in late gestation or at the peak of milk production than for later maturing rabbits or those at maintenance.
When compared to other domestic species, the metabolism of calcium in the rabbit presents important differences: (i) calcium is absorbed in direct proportion to its concentration in the diet, regardless of metabolic needs and, therefore, blood levels of calcium rise with increasing intake (Chapin and Smith, 1967); and (ii) urine is the main route used by the rabbit to eliminate any excess.

Calcium absorption is not tightly controlled in the rabbit. Intestinal absorption is very efficient (Cheeke and Amberg, 1973) and serum concentrations of ionized and total calcium (3–4 mmol l⁻¹ and 13–15 mg dl⁻¹, respectively) are high compared to those of other mammals (Warren et al., 1989). The blood calcium level is controlled by parathyroid hormone and 1,25-OH D₃, similarly to other mammalian species (Bas et al., 2005). Diets low in calcium (Barr et al., 1991) or vitamin D (Bourdeau et al., 1986) reduce urinary excretion and induce a rapid renal tubular mechanism to conserve the mineral, indicating the importance of homeostatic mechanisms within the kidneys to maintain serum calcium levels (Redrobe, 2002). Excess calcium is excreted through the urine as a white, thick, creamy precipitate that is deposited beneath the cages. Swick et al. (1981) proposed that the filtration of calcium, as well as the crystals formed in the process of eliminating excess calcium, might damage the structure of the kidneys, occasionally producing the observed red pigmentation of urine. Prolonged feeding of excess calcium (>40 g kg⁻¹) increases the risk of urolithiasis (Kamphues, 1991) and may result in calcification of the soft tissues (Lölliger and Vogt, 1980; Cheeke, 1987), particularly when vitamin D intake is high (Kamphues, 1991). Furlan et al. (1997b) estimated that, in most instances, 5 g calcium kg⁻¹ covers the nutritional requirements of rabbits from 35 to 90 days of age.

High milk-producing does might suffer a syndrome similar to that of milk fever in dairy cows. During late gestation and early lactation, does may show a drop in calcium (from 14 to <7 mg 100 ml⁻¹) and other mineral (phosphorus and magnesium) levels in plasma that results in loss of appetite, tetany, muscle tremors, ear flapping, animals lying on their sides and eventually death (Barlet, 1980). Injection of calcium gluconate induces a rapid recovery within 2 h. It is possible that a modification of the electrolyte equilibrium of the diet towards a negative balance (acidotic diets) will benefit rabbit does under these circumstances, as it does in dairy cattle and other species.

**Phosphorus**

Phosphorus is a major constituent of the bones. It also plays an important role in many reactions related to energy metabolism. In most mammalian species, inorganic phosphorus is absorbed at the duodenal and jejunal level, a mechanism that is modulated by endocrine (calcitriol, triiodothyronine) and nutritional factors (Barlet et al., 1995). However, the role of 1,25-OH D₃ and other vitamin D metabolites on phosphorus absorption in the rabbit is largely unknown. Borowitz and Granrud (1993) reported the existence of an active mechanism for phosphorus transport at the duodenum and

![Table 7.1. Macromineral composition of rabbit milk (g kg⁻¹) compared with that of other mammals.](image-url)
proximal jejunum in 3-month-old rabbits. Because horses and rabbits have a somewhat similar digestive tract, Cheeke (1987) proposed that similar absorption values should be used for both species. It is likely that phosphorus absorption is more efficient in younger animals than in adults because of the higher requirements at younger ages (Marounek et al., 2003).

A major factor influencing phosphorus availability from plant materials in non-ruminant animals is the presence of phytates and phytases. Phytates are phosphorus-rich complexes that are not degraded by endogenous enzymes. In the rabbit, phytate phosphorus is well utilized because of phytase production by the microorganisms of the caecum (Marounek et al., 2009). Most of the phosphorus is recycled through soft faeces followed by coprophagy and, therefore, should result in an almost complete utilization of phytate phosphorus. In addition, natural phytases present in wheat and other ingredients, as well as in other exogenous sources, may facilitate phytate hydrolysis and absorption of phosphorus in the upper part of the digestive tract (Marounek et al., 2003). Swick et al. (1981) found a coefficient of apparent phosphorus digestibility in rabbits fed a maize-soybean meal diet of 0.75, which indicates that the utilization of phosphorus from vegetable sources is close to that of dicalcium phosphate. The utilization of phosphorus contained in lucerne seems rather low in rabbits compared to that of pigs (Cheeke et al., 1985; Cromwell, 1992). This is surprising, since most of the phosphorus in lucerne is found in the leaves rather than in the stems. However, the absorption of soluble phosphorus in the caecum and the recycling of the phosphorus of the digesta through soft faeces and caecotrophy seem to be incomplete. Marounek et al. (2003) found that the digestibility of phytate phosphorus in rabbits fed diets containing cereals, lucerne meal, oilseed meals and sugarbeet pulp averaged 0.82. However, the apparent digestibility of total phosphorus was 0.48 at 7 weeks and 0.35 at 10 weeks of age. Similarly, Gutierrez et al. (2000) showed that the inclusion of 2000 FTU kg⁻¹ of an Aspergillus niger phytase into a diet that contained 4.2 g total phosphorus kg⁻¹ improved phosphorus digestibility by 24% in growing rabbits. Guo Xian et al. (2004) and Eiben et al. (2008) demonstrated that phytases supplemented at 800–1000 FTU kg⁻¹ to fattening rabbit diets containing 3.5 g total phosphorus kg⁻¹ resulted in similar growth and feed conversion to those obtained with conventional diets and, in fact, eliminated the need for inorganic supplements.

There is growing interest in controlling the excretion of phosphorus through feed manipulation to reduce environmental pollution. Studies conducted under commercial conditions have estimated phosphorus excretion of 4.76 kg P₂O₅ year⁻¹ doe (for a 2.5 kg doe producing 45 fatteners year⁻¹) and 26 g P₂O₅ kg⁻¹ per fattener rabbit (0.8–2.5 kg body weight) (Maertens et al., 2005). A decrease in dietary phosphorus levels (depending on the age and physiological status of the rabbits) is a promising tool to reduce phosphorus excretion. Studies conducted with fryers (Steenland, 1991) and breeding does (Lebas and Jouglar, 1990) have demonstrated that rabbit performance is not reduced when dietary phosphorus is decreased below former practical recommendations. In fact, these authors found that 5 g phosphorus kg⁻¹ was adequate for all types of production. Moreover, Ritskes-Hoitinga et al. (2004) found that 1 g phosphorus kg⁻¹, included as dicalcium phosphate in semi-purified diets, supported growth and bone development in rabbits. In addition, this low level of phosphorus prevented kidney calcification. Unfortunately, the available information on phosphorus requirements in rabbits fed commercial diets is scarce. Moreover, in order to achieve these low dietary phosphorus levels, the inclusion of some raw materials rich in phosphorus (i.e. grains, grain by-products) in the diet should be limited, an alternative that might not be economically feasible (Maertens, 1999).

A dietary relationship of calcium to available phosphorus of 2:1 to 1.5:1 is widely accepted in practical feeding (Vandelli, 1995). In fact, rabbit milk maintains a constant 2:1 calcium to phosphorus ratio
throughout the lactation period (El-Sayiad et al., 1994; Maertens et al., 2006). However, because of the renal mechanism existing in the rabbit to conserve both calcium and phosphorus and maintain mineral homeostasis (Redrobe, 2002), the need to closely maintain this relationship is not evident and, at least in fatteners, does not seem to be critical. Diets for growing rabbits with a calcium to phosphorus ratio of 12:1 have not shown any detrimental effect in terms of performance (Chapin and Smith, 1967). However, calcium in excess of requirements may decrease phosphorus absorption and, therefore, create an artificial deficiency in this mineral when low dietary phosphorus levels are used. On the other hand, an increase in dietary phosphorus levels from 4 to 8 g kg\(^{-1}\), at a constant calcium concentration (5 g kg\(^{-1}\)), changes the route of calcium excretion from urine to faeces through the formation of insoluble complexes of dicalcium phosphate. Consequently, the intestinal absorption of both minerals is reduced (Ritskes-Hoitinga et al., 2004). Under practical conditions it is more common to find dietary excesses of calcium than of phosphorus. Excess calcium is more detrimental to rabbit health if marginal levels of phosphorus are used. Assane et al. (1993) observed an increase of phosphorus and magnesium in the blood at the end of the gestation period when the calcium to phosphorus ratio in feed was 1:1 as compared with 2:1 (Table 7.2). Assane et al. (1994) reported positive calcium and phosphorus balances with dietary calcium to phosphorus ratios of 2:1 and 1:1. However, calcium retention increased in both non-pregnant and pregnant does with the higher calcium level. Moreover, the best reproductive performance was obtained when the calcium to phosphorus ratio was 2:1.

Practical recommendations on dietary levels of calcium and phosphorus vary according to age, breed, productivity and diet composition. For growing-fattening rabbits, the recommendations vary from 4 to 10 g for calcium and from 2.2 to 7 g for phosphorus (Table 7.3) (NRC, 1977; AEC, 1987; Schlolaut, 1987; INRA, 1989; Mateos, 1989; Burgi, 1993; Mateos and Piquer, 1994; Vandelli, 1995; Xiccato, 1996; Mateos and de Blas, 1998; Lebas, 2004; Maertens and Luzi, 2004). Calcium and phosphorus requirements are higher for lactating does than for growing rabbits or non-lactating does, because rabbit milk is particularly rich in both minerals. Average contents of calcium and phosphorus in rabbit milk is approximately three to five times higher than those in cow milk (Burgi, 1993; El-Sayiad et al., 1994). At maximal milk production the doe can excrete up to 2 g of calcium. Practical recommendations in doe feeds vary from 7.5 to 15 g for calcium and from 4.5 to 8 g for phosphorus, according to the same authors (Table 7.3).

### Table 7.2. Influence of the dietary calcium to phosphorus (C:P) ratio on calcium, phosphorus and magnesium levels in the serum of gestating rabbit does (Assane et al., 1993).

<table>
<thead>
<tr>
<th>C:P ratio</th>
<th>Calcaemia (mg l(^{-1}))</th>
<th>Phosphataemia (mg l(^{-1}))</th>
<th>Magnesaemia (mg l(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Premating</td>
<td>Week 3 of gestation</td>
<td>Pre-partum</td>
</tr>
<tr>
<td>1:1(^a)</td>
<td>123*</td>
<td>120**</td>
<td>111***</td>
</tr>
<tr>
<td>2:1(^b)</td>
<td>145*</td>
<td>125**</td>
<td>114***</td>
</tr>
<tr>
<td>1:1</td>
<td>38</td>
<td>39</td>
<td>41</td>
</tr>
<tr>
<td>2:1</td>
<td>43*</td>
<td>38*</td>
<td>25**</td>
</tr>
<tr>
<td>1:1</td>
<td>28</td>
<td>27</td>
<td>27</td>
</tr>
<tr>
<td>2:1</td>
<td>31*</td>
<td>23**</td>
<td>19**</td>
</tr>
</tbody>
</table>

**SEM, standard error of the mean.**

\(^a\)5.2 g calcium and 5.1 g phosphorus kg\(^{-1}\) diet.

\(^b\)8.3 g calcium and 3.9 g phosphorus kg\(^{-1}\) diet.

*Means in the same row with different superscripts differ (P< 0.05).*
Dietary calcium and phosphorus levels below requirements will lead to rickets (young rabbits), osteomalacia (adults), lack of fertility (does) and abnormal behaviour. Adequate calcium supplementation rapidly reverses the problem caused by calcium deficiency in growing rabbits (Mehrotra et al., 2006). Excess calcium (>13 g kg\(^{-1}\)) does not increase bone mass (Gilsanz et al., 1991), but might result in calcification of the soft tissues (Kamphues, 1991) and reduced phosphorus absorption. Excess phosphorus (>9 g kg\(^{-1}\)) may depress feed intake and impair prolificacy in does (Chapin and Smith, 1967; Lebas and Jouglar, 1984, 1990). In all cases, excess phosphorus has detrimental effects on the environment.

The recommended concentrations of calcium and phosphorus in complete diets for rabbits are presented in Table 7.4. These values are based on a literature review and practical experience.

### Table 7.3. Macromineral recommendations (g kg\(^{-1}\) as-fed) for intensively reared rabbits.

<table>
<thead>
<tr>
<th>Growing-fattening rabbits</th>
<th>Calcium</th>
<th>Phosphorus</th>
<th>Sodium</th>
<th>Chloride</th>
<th>Potassium</th>
</tr>
</thead>
<tbody>
<tr>
<td>NRC (1977)</td>
<td>4</td>
<td>2.2</td>
<td>2</td>
<td>3</td>
<td>6</td>
</tr>
<tr>
<td>AEC (1987)</td>
<td>8</td>
<td>5</td>
<td>3</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Schlolaut (1987)(^a)</td>
<td>10</td>
<td>5</td>
<td>–</td>
<td>–</td>
<td>10</td>
</tr>
<tr>
<td>INRA (1989)</td>
<td>4</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>6</td>
</tr>
<tr>
<td>Mateos (1989)</td>
<td>4.0–8.0</td>
<td>3.0–5.0</td>
<td>3</td>
<td>–</td>
<td>6.0–9.0</td>
</tr>
<tr>
<td>Burgi (1993)</td>
<td>5</td>
<td>3</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Mateos and Piquer (1994)</td>
<td>5.5</td>
<td>3.5</td>
<td>3.5</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Vandelli (1995)</td>
<td>4.0–8.0</td>
<td>3.0–5.0</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Xiccato (1996)(^b)</td>
<td>8.0–9.0</td>
<td>5.0–6.0</td>
<td>2</td>
<td>3</td>
<td>–</td>
</tr>
<tr>
<td>Mateos and de Blas (1998)</td>
<td>3.0–10.0</td>
<td>3.0–7.0</td>
<td>2.0–2.3</td>
<td>2.8–4.8</td>
<td>6.5–10</td>
</tr>
<tr>
<td>Lebas (2004)</td>
<td>7–8</td>
<td>4–4.5</td>
<td>2.2</td>
<td>2.8</td>
<td>&lt;15</td>
</tr>
<tr>
<td>Maertens and Luzi (2004)</td>
<td>8</td>
<td>5</td>
<td>2.5</td>
<td>3</td>
<td>8</td>
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</table>

<table>
<thead>
<tr>
<th>Lactating does</th>
<th>Calcium</th>
<th>Phosphorus</th>
<th>Sodium</th>
<th>Chloride</th>
<th>Potassium</th>
</tr>
</thead>
<tbody>
<tr>
<td>NRC (1977)</td>
<td>7.5</td>
<td>5.0</td>
<td>2.0</td>
<td>3.0</td>
<td>6.0</td>
</tr>
<tr>
<td>AEC (1987)</td>
<td>11.0</td>
<td>8.0</td>
<td>3.0</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>INRA (1989)</td>
<td>11.0</td>
<td>8.0</td>
<td>3.0</td>
<td>3.0</td>
<td>9.0</td>
</tr>
<tr>
<td>Schlolaut (1987)(^a)</td>
<td>10.0</td>
<td>5.0</td>
<td>–</td>
<td>–</td>
<td>10.0</td>
</tr>
<tr>
<td>Lebas (1990)</td>
<td>12.0</td>
<td>7.0</td>
<td>2.0</td>
<td>3.5</td>
<td>9.0</td>
</tr>
<tr>
<td>Mateos and Piquer (1994)</td>
<td>11.5</td>
<td>7.0</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Vandelli (1995)</td>
<td>11.0–13.5</td>
<td>6.0–8.0</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Maertens (1996)</td>
<td>12.0</td>
<td>5.5</td>
<td>–</td>
<td>3.0</td>
<td>–</td>
</tr>
<tr>
<td>Xiccato (1996)(^b)</td>
<td>13.0–13.5</td>
<td>6.0–6.5</td>
<td>2.5</td>
<td>3.5</td>
<td>–</td>
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<tr>
<td>Mateos and de Blas (1998)</td>
<td>10.0–15.0</td>
<td>4.5–7.5</td>
<td>2.2–2.5</td>
<td>2.8–4.8</td>
<td>6.5–10</td>
</tr>
<tr>
<td>Lebas (2004)</td>
<td>12</td>
<td>6</td>
<td>2.5</td>
<td>3.5</td>
<td>&lt;18</td>
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<tr>
<td>Maertens and Luzi (2004)</td>
<td>12</td>
<td>5.5</td>
<td>2.5</td>
<td>3</td>
<td>10</td>
</tr>
</tbody>
</table>

\(^a\) Angora rabbits.

\(^b\) Young does.

### Table 7.4. Requirements of calcium and phosphorus for rabbits (g kg\(^{-1}\) as-fed basis).

<table>
<thead>
<tr>
<th>Breeding does</th>
<th>Calcium</th>
<th>Phosphorus</th>
</tr>
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<tbody>
<tr>
<td>Recommendation</td>
<td>10.5</td>
<td>6.0</td>
</tr>
<tr>
<td>Acceptable commercial range</td>
<td>10.0–12.5</td>
<td>5.5–7.0</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Growing rabbits</th>
<th>Calcium</th>
<th>Phosphorus</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1–2 months of age)</td>
<td>6.0</td>
<td>4.0</td>
</tr>
<tr>
<td>Recommendation</td>
<td>4.5–7.6</td>
<td>3.3–4.6</td>
</tr>
<tr>
<td>Acceptable commercial range</td>
<td>4.0</td>
<td>3.0</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Finishing rabbits</th>
<th>Calcium</th>
<th>Phosphorus</th>
</tr>
</thead>
<tbody>
<tr>
<td>(&gt;2 months of age)</td>
<td>4.0</td>
<td>3.0</td>
</tr>
<tr>
<td>Recommendation</td>
<td>3.0–6.0</td>
<td>3.0–4.5</td>
</tr>
<tr>
<td>Acceptable commercial range</td>
<td></td>
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</tr>
</tbody>
</table>

Other macrominerals

Magnesium is a major component of the bones (0.7 of total body magnesium is in the
skeleton) and also acts as a cofactor in many energy metabolism reactions. Deficiency produces poor growth, alopecia, hyperexcitability, convulsions, poor fur texture and fur chewing. The magnesium requirements for growing rabbits vary from 0.3 (NRC, 1977; INRA, 1989) to 3 g kg\(^{-1}\) (Lebas, 2004; Maertens and Luzi, 2004). Evans et al. (1983a,b) found that 3.4 g kg\(^{-1}\) fulfilled requirements, but that 1.7 g kg\(^{-1}\) was insufficient. Excess dietary magnesium is eliminated through the urine. Therefore, extra supplementation with magnesium rarely induces severe side effects (Plamenac et al., 2008). The content and apparent digestibility of magnesium in most raw materials is high and the need to add extra magnesium to commercial rabbit diets has not been established.

Potassium plays a key role in the regulation of the acid–base balance in organisms and is a cofactor of numerous enzymes. Symptoms of deficiency include muscle weakness, paralysis and respiratory distress. Potassium ion (K\(^+\)) deficiency in rabbits might appear when diarrhoea is present (Licois et al., 1978). Current estimates indicate that 6 g potassium kg\(^{-1}\) avoids symptoms of deficiency. Because most of the ingredients used in rabbit diets are rich in K\(^+\) (i.e. soybean meal, lucerne, molasses), deficiency is difficult to envisage. Excess K\(^+\) (>10 g kg\(^{-1}\)) may occur when a high proportion of heavily fertilized, early mature lucerne is used. Lebas (2004) recommended dietary K\(^+\) levels for growing rabbits and lactating does of <15–20 and 18 g kg\(^{-1}\), respectively. Surdeau et al. (1976) observed a higher incidence of nephritis when the K\(^+\) level of the diet was >8 g kg\(^{-1}\). Furthermore, Evans et al. (1983a) reported reduced feed intake with K\(^+\) levels >10 g kg\(^{-1}\). In addition, excess K\(^+\) antagonizes magnesium absorption, although the importance of this problem has not been ascertained in the rabbit. Practical recommendations range between 6.0 and 10 g kg\(^{-1}\).

Sodium is involved in the regulation of pH and osmotic pressure. In contrast to K\(^+\), sodium ions (Na\(^+\)) concentrate in the plasma, outside the cells. Sodium is essential for the absorption of luminal nutrients such as glucose and amino acids (Schultz and Zalusky, 1964, 1965). Intestinal brush-border membranes contain a Na\(^+\)-phosphate co-transport system, which catalyses the entry of phosphate and Na\(^+\) into the intestinal epithelial cell. The requirements for Na\(^+\) have not been studied in breeding does. In fattening rabbits, however, Harris et al. (1984b) and Furlan et al. (1997a) reported that 1.0 g sodium kg\(^{-1}\) met the requirements for growth from 35 to 90 days. A deficit in Na\(^+\) may impair the efficiency of digestive processes and/or the absorption of amino acids, as has been demonstrated in pigs (Patience et al., 1985). Chamorro et al. (2007) observed that a reduction in Na\(^+\) from 2.6 to 1.6 g kg\(^{-1}\) impaired ileal digestibility of methionine and cystine, although dry matter and protein digestibility were not affected. Under practical conditions, 2.0–2.3 and 2.2–2.5 g sodium kg\(^{-1}\) are used for fryers and does, respectively. Excess Na\(^+\) in the feed (>8–10 kg sodium chloride (NaCl) kg\(^{-1}\) diet) or the presence of salt in the drinking water (3000 mg kg\(^{-1}\)) is detrimental to growth (Harris et al., 1984b; Marai et al., 2005).

Chloride is also involved in acid–base regulation. In addition, this ion concentrates in the gastric cells. It is secreted as hydrogen chloride and is involved in the solubility of mineral salts and protein digestion. Practical diets for high-producing rabbits are unlikely to be deficient in chloride ions (Cl\(^-\)), because NaCl and lysine hydrochloride are routinely used in feed formulations as a source of Na\(^+\) and lysine, respectively, and indirectly serve as a supplement for Cl\(^-\). The Cl\(^-\) requirements have been estimated as within the 1.7–3.2 g kg\(^{-1}\) range, but excess (4.7 g kg\(^{-1}\)) does not impair performance (Colin, 1977). Practical levels vary between 2.8 and 4.8 g kg\(^{-1}\).

It is well known that the relationship between Na\(^+\), K\(^+\) and Cl\(^-\) (the electrolyte balance) affects animal performance. In addition to influencing resistance to thermal stress, leg score, kidney function and incidence of milk fever, a large negative value may decrease feed intake, whereas a positive value may increase problems around farrowing. Chiericato and Rizzi (2004, 2005) found that increasing the electrolyte bal-
ance \((Na^+ + K^+ – Cl^-)\) of breeding rabbit diets from 270 to 350 mEq kg\(^{-1}\) tended to increase the mortality rate of does at farrowing, but did not affect milk production or feed intake up to 21 days of lactation. Similarly, Rizzi et al. (2005) did not observe any effect on the performance of bucks during three reproductive cycles with electrolyte balances of 270 or 350 mEq kg\(^{-1}\) diet. No information on variation of this balance on the productivity of growing rabbits is available. However, this species is particularly vulnerable to acid loads. In fact, rabbit urine is more alkaline than that of rats or other mammals fed diets with similar electrolyte balances. Therefore, care should be taken to avoid electrolyte imbalances that might result in nephritis and decrease feed intake.

Sulphur is one of the more abundant elements in nature. Sulphur is a component of chondroitin sulphate, a major component of cartilage, tendons, blood vessel walls and bones. In addition, sulphur is a constituent of numerous organic substances such as haemoglobin, glutathione, coenzyme A and the amino acids methionine and cystine. Practical diets include over 2.0 g sulphur kg\(^{-1}\) but, in general, no supplemental sources are used under practical conditions. There are no reports in the literature indicating any benefit of sulphur supplementation on rabbit performance, although inorganic S\(^{2-}\) can be incorporated into microbial protein in the hindgut and used for protein accretion. Furthermore, there are no reports on the effects of excess sulphur on rabbit performance. In laying hens and dairy cows, however, excess sulphur reduces performance. Consequently, care should be taken when including high levels of rapeseed meal, sunflower meal or distillers’ dried grains with solubles in rabbit diets, especially in does.

7.1.2 Trace minerals

Trace minerals are defined as those elements required in mg per day and needs are expressed as mg kg\(^{-1}\) or ppm of the diet. The definition includes iron, copper, manganese, zinc, selenium, iodine and cobalt. Other trace elements that are required by the rabbit but are not supplemented under practical conditions are molybdenum, fluorine and chromium. The trace minerals mentioned in the first group are routinely added to rabbit diet as salts through a premix.

Iron is a major constituent of enzymes involved in oxygen transport and metabolism. Therefore, deficiency may result in impaired haemoglobin formation and anaemia. The mechanisms for transporting iron to milk or to the fetus are poor, especially in the pig, but rabbits are capable of absorbing reasonable amounts of iron through the placenta. Rabbits have sufficient iron reserves at birth, provided the doe has received a properly supplemented diet. Therefore, rabbits are not as dependent as piglets on an exogenous supply of iron for survival. Even though milk is poor in iron, no deficiency is expected in young rabbits because they have free access to doe feed during the milking period. Since most ingredients used in feeds are rich in iron (i.e. soil-contaminated lucerne, macromineral sources and trace mineral premix) an iron deficiency is not expected to develop early in life. El-Masry and Nasr (1996) reported beneficial effects in does when 80 mg iron kg\(^{-1}\) was added to diets that already contained 129 mg kg\(^{-1}\) diet. Does fed the iron-supplemented diet produced more milk and had greater litter sizes and litter weights than controls. However, the low productivity and high mortality of the animals on trial, as well as the small number of replicates and the composition of the premix used, do not allow the results of this trial to be adopted with confidence.

Recommendations for iron reported in the literature vary from 30 to 100 mg kg\(^{-1}\) (Table 7.5), with greater levels for does and fur-producing animals (Schlolaut, 1987). Under commercial conditions, all of the commercial premixes supply extra iron (15–105 mg kg\(^{-1}\)) (Table 7.6) and most are within the 30–50 mg kg\(^{-1}\) diet range. At these levels, iron requirements for all types of production are easily met, especially when calcium carbonate and dicalcium phosphate are used as sources of calcium and...
phosphorus, respectively. In fact, the need for extra iron supplementation in commercial diets for fatteners is questionable.

Copper is a major component of metalloenzymes involved in energy and iron metabolism and in collagen and hair formation. Faecal excretion is the main route of copper output in rabbits (Skrivanova et al., 2002). Deficiency will manifest as retarded growth, grey hair, bone abnormalities and anaemia, among other symptoms. When fed in excess, copper is accumulated in the liver (Cavalcante et al., 2002) but not in muscle tissues. Therefore, copper has little effect on the oxidative stability status of rabbit meat (Skrivanova et al., 2001).

Published recommendations vary between 3 and 10 mg copper kg⁻¹ (Table 7.5), with higher levels recommended for fur production (25 mg kg⁻¹ diet; Schlolaut, 1987) and breeding does. Practical levels used in Iberian rabbit commercial premixes vary from 4 to 25 mg kg⁻¹ (Table 7.6). Even at the lower levels of inclusion, no deficiency

| Table 7.5. Micromineral requirements of rabbits (mg kg⁻¹ diet). |
|-----------------|----------------|----------------|----------------|----------------|----------------|
| Growing-fattening |                |                |                            |                |                |
| Copper           | 3              | 5              | 5                          | 10             | 6              |
| Iodine           | 0.2            | 0.2            | 1.1                        | 0.2            | –              |
| Iron             | –              | 50             | 35                         | 50             | 50             |
| Manganese        | 8.5            | 8.5            | 5                          | 5              | 8              |
| Zinc             | –              | 50             | 60                         | 25             | 25             |
| Cobalt           | 0              | 0.1            | 0.25                       | 0.1            | –              |
| Selenium         | 0              | –              | 0.01                       | 0.15           | –              |
| Lactating does   |                |                |                            |                |                |
| Copper           | 5              | 5              | 5                          | 10             | 10             |
| Iodine           | 1              | 0.2            | 1.1                        | 0.2            | –              |
| Iron             | 30             | 100            | 35                         | 100            | –              |
| Manganese        | 15             | 2.5            | 2.5                        | 5              | 12             |
| Zinc             | 30             | 70             | 60                         | 50             | 50             |
| Cobalt           | 1              | 0.1            | 0.25                       | 0.1            | –              |
| Selenium         | 0.08           | –              | 0.01                       | 0.15           | –              |

–, not determined.

aSame feed for does and fryers.
bYoung does.

<table>
<thead>
<tr>
<th>Table 7.6. Trace mineral recommendations for commercial rabbit diets (mg kg⁻¹ diet).</th>
</tr>
</thead>
<tbody>
<tr>
<td>Commercial premixesa</td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td>Copper</td>
</tr>
<tr>
<td>Iodine</td>
</tr>
<tr>
<td>Iron</td>
</tr>
<tr>
<td>Manganese</td>
</tr>
<tr>
<td>Zinc</td>
</tr>
<tr>
<td>Cobalt</td>
</tr>
<tr>
<td>Selenium</td>
</tr>
</tbody>
</table>

sd, standard deviation.

a n = 29 (>0.9 of total feed production for rabbits). The range indicates the maximum and minimum levels used commercially.
bAuthor recommendations under practical conditions. The higher values of the range are more appropriate for lactating rabbits.
cAccording to European Commission regulation (EC) 1134/2003.
symptoms are expected because of the high copper content of most raw materials used in rabbit feeds and the potential for accumulation in the liver. As a precaution, the use of forages high in sulphur and molybdenum should be avoided. The interaction between copper and molybdenum for absorption is well known in sheep, and the presence of sulphur exacerbates this antagonism.

In addition to its role as an essential nutrient, copper is used worldwide as a growth promoter in poultry and pigs. Indeed, several reports (Bassuny, 1991; Ayyat et al., 1995; Abbo el-Ezz et al., 1996; Onifade and Abu, 1998; Aboul-Ela et al., 2000; Skrivanova et al., 2001) have reported that supplementation with 100–400 mg CuSO₄ kg⁻¹ improves growth performance in rabbits. The beneficial effects are more noticeable in young animals under poor sanitation status and in the presence of digestive diseases such as enteritis and enterotoxaemia (Patton et al., 1982). There are, however, conflicting reports. For example, King (1975) and Harris et al. (1984a) did not find any benefit for the rabbit with supplementation of CuSO₄. Fekete et al. (1988) observed an improvement in the growth of rabbits fed a high-protein diet (180 g crude protein kg⁻¹) when 100 mg of extra copper kg⁻¹ was added, but no effects were observed when 140 g crude protein kg⁻¹ was used. Aboul-Ela et al. (2000) reported a reduction in mortality in response to copper supplementation in rabbits fed a high-fibre, low-energy diet, but not in those fed a high-energy, low-fibre diet. In any event, the use of CuSO₄ as a growth promoter is not permitted in rabbit feeds in the European Union (EU), which precludes its utilization at high levels in commercial feeds. In fact, even in the absence of supplementary manganese, its concentration in uterine tissues remains stable. Hidiroglou et al. (1978) observed that, when fed in excess, manganese concentrates in the kidney, liver and spleen, but not in the reproductive tract of rabbits. The response of rabbits to manganese is probably more similar to that of pigs than poultry. Published values on manganese requirements for rabbits vary between 2.5 and 15 mg kg⁻¹ (Table 7.5), similar to those of pigs. Commercial mineral premixes from the Iberian Peninsula include levels between 5 and 75 mg kg⁻¹ (Table 7.6). Based on field information and cost, the advisable manganese levels is around 8–15 mg kg⁻¹.

Zinc is a component of numerous enzymes and is involved in the biosynthesis of nucleic acids and in cell division processes. Higher levels of zinc are recommended for reproduction and fur and hair production than for maintenance or meat production. Because of the relatively high phytase production by hindgut microorganisms, dietary phytates are less detrimental for zinc absorption in rabbits than in other non-ruminant species. Therefore, a lower requirement must be expected for rabbits than for pigs or poultry (Swick et al., 1981). No recent trials on the zinc requirements of rabbits have been published in the literature, but levels of use vary between 25 and 60 mg kg⁻¹, with the higher values proposed for does and bucks. Practical commercial diets contain a wider range of zinc (40–140 mg kg⁻¹). Zinc oxide is the most commonly used source because it is less reactive and has a higher zinc concentration than sulfate and carbonate salts. No differences in zinc bioavailability between inorganic and organic sources have been reported in rabbits (Guimaraes and Motta, 2000). Because of zinc’s environmental impact, the maximum level allowed in the EU for rabbit feeds is 150 mg kg⁻¹. In addition, the adverse effect of high zinc intake on copper availability has to be considered (Maret and Sandstead, 2006).
Selenium was considered a toxic element but, in 1957, the essentiality of this nutrient was demonstrated. Diseases such as white muscle, liver degeneration and exudative diathesis and impaired reproduction and poor immunity have been associated with selenium deficiency. In most species the role of selenium is closely linked to vitamin E. Selenium is a constituent of the enzyme glutathione peroxidase (GSH), which plays a role in the detoxification of peroxides formed during metabolic processes. However, rabbit tissues are less dependent on selenium for the disposal of peroxides than tissues from other mammals. Lee et al. (1979) observed that, in the rabbit, most of the existing GSH does not have selenium as a cofactor. Moreover, Erdélyi et al. (2000) did not observe any relationship between selenium status and GSH activity in the liver, kidney, pancreas, genital organs and femoral muscle of rabbits. Similarly, supplementation with 0.5 mg selenium kg$^{-1}$ does not improve plasma tocopherol or the oxidative stability of spermatozoa (Castellini et al., 2002). As observed in pig and poultry meats and in eggs, feeding supplemental organic selenium (0.12–0.50 mg kg$^{-1}$) to fattening rabbits increases the selenium content of meat (95.5–395 µg kg$^{-1}$). However, extra selenium supplementation has limited potential to improve the oxidative stability status of rabbit meat (Dokoupilová et al., 2007). Therefore, the rabbit is more dependent on vitamin E and less on selenium than other mammals in reducing the oxidation load on tissues (Jenkins et al., 1970). On the other hand, Struklec et al. (1994) observed improved fetal and birth weight when does received 0.1 mg supplemental selenium kg$^{-1}$, but no further improvement was observed with 0.3 mg selenium kg$^{-1}$. Commercial premixes without supplemental selenium have been marketed for years in Europe without any evidence of impaired productivity in does or growing-fattening rabbits (Mateos, 1989; Mateos and Piquer, 1994; Robledo et al., 1999; Lebas, 2004). Since no detailed experiments have recently been conducted on this subject, and taking into account other potential effects of selenium as a constituent of various enzymes complexes, it is advisable to include a small amount of supplemental selenium (0.05 mg kg$^{-1}$) in the feeds of rabbits.

Iodine is a component of the thyroid hormones that regulates energy metabolism. No requirements for iodine have been established for any type of production in rabbits. Iodine deficiency results in goitre. The incidence of this disease increases when goitrogens are present in the diet. Brassica species, such as cabbage, turnips and rape seeds, are rich in goitrogens and therefore their use will increase iodine requirements. Does are probably more sensitive to iodine deficiency than growing-fattening rabbits. Literature requirements vary from 0.2 to 1.1 mg kg$^{-1}$ (Table 7.5). Practical premixes in Spain and Portugal include between 0.25 and 2 mg kg$^{-1}$. At these levels of inclusion, no goitre or other classic symptoms of deficiency have ever been detected. If marine salt is used as a source of iodine, the requirements are fully satisfied and a supplemental source of iodine is no longer required.

Cobalt requirements are often overestimated for non-ruminants. The only metabolic role currently accepted for cobalt is as a component of vitamin B$_{12}$. Therefore, similar symptoms of deficiency are observed in cases of cobalt or vitamin B$_{12}$ deficiency. Since animals do not have the enzymes required to attach cobalt to the molecule to form vitamin B$_{12}$, the supply of this mineral is ineffective in non-ruminants without access to faeces. Rabbits, however, depend on cobalt to produce vitamin B$_{12}$. In fact, the existing bacteria in the rabbit hindgut are more efficient than the bacteria of other non-ruminant and ruminant species in the production of vitamin B$_{12}$ (Simnett and Spray, 1965a, b). Furthermore, the requirements for cobalt are relatively greater for ruminants than for rabbits (Underwood, 1977), because rumen microorganisms use large amounts of cobalt to synthesize non-active compounds. In addition, ruminants require extra amounts of vitamin B$_{12}$ (and consequently of cobalt) for propionic acid metabolism, a volatile fatty acid that is a
major energy-yielding source for these species. In the case of cobalt deficiency, the rate of propionate clearance from the blood is depressed and, as a consequence, feed intake and productivity are decreased (McDowell, 2003).

Literature requirements for cobalt in rabbits generally vary between 0 and 0.25 mg kg\(^{-1}\), although the National Research Council (NRC, 1977) recommended 1.0 mg kg\(^{-1}\). Practical premixes for rabbits in Spain and Portugal contain between 0.1 and 0.7 mg cobalt kg\(^{-1}\), and one-third of them include >0.4 mg. Cobalt deficiency, even in unsupplemented vitamin B\(_{12}\) diets, is unlikely to occur, especially under non-intensive production systems. Based on the above data, supplementation of rabbit diets with 0.25 mg cobalt kg\(^{-1}\) is recommended.

The current trace mineral composition (average and range) of commercial premixes used in Spain and Portugal for rabbits is depicted in Table 7.6. This table also presents recommended values from the authors and the current maximum levels allowed in the EU.

### 7.2 Vitamin Requirements of Rabbits

Vitamins are defined as a group of complex organic compounds that are present in minute amounts in natural feeds and are essential for nutrient metabolism and life. Deficiency causes a decrease in performance and often pathological symptoms of disease. Vitamins and trace minerals differ in their nature: vitamins are organic and trace minerals are inorganic.

In a review of published data, Combes (2004) showed that rabbit meat contains on average the following amounts of vitamins 100 g\(^{-1}\) of product: 0.186 mg vitamin E, 0.082 mg thiamine, 0.125 mg riboflavin, 9.6 mg niacin, 0.34 mg pyridoxine, 0.60 mg pantothenic acid, 6.85 µg cobalamin, 5 µg folic acid and 0.7 µg biotin. Vitamin A was only found in trace amounts, whereas vitamin C was essentially absent. These values are similar to those found for other meats, except for thiamine and folic acid, which are higher in pig and beef meat, respectively (Dalle Zotte, 2004).

Except for choline, vitamins are required in minute amounts and requirements are expressed as IU, mg kg\(^{-1}\) or ppm. All vitamins have essential functions in the organism: most act as metabolic catalysts of organic processes. Not all vitamins are essential in a strict sense. Some can be derived from other substances obtained through metabolic changes. For example: vitamin C can be synthesized in several species including the rabbit; choline is synthesized by mammals and avian species, but often in smaller amounts than required for optimal growth; niacin can be obtained from tryptophan, although the process is quite inefficient; most B vitamins are synthesized by microorganisms of the gut and recycled into the body; and vitamin D can be obtained from precursors by the action of ultraviolet light on the skin. Therefore, many vitamins do not fit the classic definition of vitamins.

Vitamins are classified on the basis of their solubility. Vitamins A, D, E and K are soluble in fat, whereas all the others (B complex, vitamin C) are soluble in water. Fat-soluble vitamins are absorbed with dietary lipids, probably by similar mechanisms. In general, they are stored in the body (predominantly in the liver and fat tissues) in appreciable amounts. Water-soluble vitamins are not stored but rapidly excreted, the exception being vitamin B\(_{12}\). In addition, both groups differ in their excretion patterns: fat-soluble vitamins are excreted primarily in faeces via the bile, whereas water-soluble vitamins are excreted mainly through the urine. A continuous supply is therefore more important for water- than for fat-soluble vitamins. Because rabbits have a functional hindgut, the need for supplementation is much higher for fat- than for water-soluble vitamins. Because rabbits have a functional hindgut, the need for supplementation is much higher for fat- than for water-soluble vitamins. In fact, the benefits of adding B-complex vitamins to commercial rabbit feeds have not been experimentally demonstrated. However, the production of B vitamins may not meet requirements in highly producing rabbits and, thus, extra supplementation is often convenient and sometimes required.
7.2.1 Fat-soluble vitamins

Vitamin A

Vitamin A, as such, is only found in ingredients of animal origin or synthetic supplements. Plants contain a series of precursors, the carotenoids, with variable vitamin A activity. In the rabbit, β-carotene, the most important precursor of vitamin A found in vegetables, is converted into vitamin A in the intestinal mucosa. In most domestic species, the process is not very efficient. In the rabbit, Bondi and Sklan (1984) estimated a conversion efficiency of around 1700 IU vitamin A mg–1 β-carotene, similar to that of chickens. The process, which requires the presence of a copper-dependent enzyme, is more efficient at low β-carotene intakes. For this reason, vitamin A toxicity in rabbits is more likely to occur when vitamin A, rather than the precursor, is supplemented in the diet (Deeb et al., 1992). Vitamin A participates in numerous metabolic reactions and is involved in vision, bone development, maintenance of epithelial integrity, reproduction and the immunological response. A particular problem in young rabbits that responds to vitamin A supplementation is hydrocephaly. It results from defective bone growth with stenosis of the cerebral aqueduct and elevated cerebrospinal fluid pressure, which may affect nerve function. In addition, vitamin A deficiency reduces fertility and milk production in does and increases abortion rates and resorption of fetuses (Cheeke et al., 1984).

Vitamin A plasma levels in the rabbit are around 150μg 100−1 ml, a value somewhat higher than that for most domestic species (Cheeke, 1987). This value is very variable, because vitamin A is stored in the liver and released as needed. In addition, Kerti et al. (2005) showed that caecotrophy increases the retinoid blood levels in rabbits fed diets supplemented with 10,000 IU vitamin A, but that the retinoid content of the liver and kidney was not affected.

Vitamin A requirements for growth and reproduction have not been experimentally determined. Values in the literature vary from 6000 to 10,000 IU (Table 7.7). In practice, feeding levels of 6000 IU for growing-fattening rabbits and 10,000 IU for breeders appear to be sufficient under commercial conditions. The liver can store large quantities of vitamin A. If the amounts supplied are in excess of requirements, the organ becomes overloaded and toxicity symptoms may appear. The adverse effects of a high supplementation of vitamin A (50,000IU) in growing rabbits include reductions in plasma calcium, bone weight, bone ash and body weight gain (Albar, 1998). Rabbit does are particularly sensitive to vitamin A excess, with symptoms of toxicity similar to those observed for deficiency (Cheeke et al., 1984; Grobner et al., 1985; Moghaddam et al., 1987; Deeb et al., 1992). Therefore, high doses of vitamin A supplied continuously through feed or water to increase immune status and combat stress or other field problems should be avoided. The NRC (1987) recommends a maximum of 16,000 IU to be added to rabbit diets as an upper safe level.

Several authors have observed some benefits when the diets of sows and dairy cows are supplemented with β-carotene, irrespective of vitamin A status (Byers et al., 1956; Czarnecki et al., 1992; Chew, 1994a,b). Cows receiving extra β-carotene show more intense oestrus, increased conception rates and a reduced incidence of follicular cysts. The suggestion is that β-carotene has a specific function in reproduction, independent of its role as a precursor of vitamin A. The mechanism is not known. In the cow, β-carotene is absorbed intact through the intestinal wall and concentrates in the ovarian follicles, where it may exert a beneficial action on reproduction. However, other authors have not found any benefit of β-carotene supplementation other than as a source of vitamin A (Wang et al., 1982, 1988). In the rabbit, this theory has been tested by several authors (Parigi Bini et al., 1983; Elmarimi et al., 1989; Kormann et al., 1989; Besenfelder et al., 1996) with conflicting results. In some cases, the injection or addition through feed of 30–40 mg β-carotene kg−1 improved doe conception and the survival rate of lactating kids. In others, no benefits were noted. The DSM
(2006) recommends supplementing doe feeds with 10–20 mg β-carotene kg\(^{-1}\) in order to improve prolificacy. In contrast to cattle, horses and poultry, rabbits are ‘white fat’ animals and they are not capable of storing carotenoids. Therefore, it is unlikely that supplementation of β-carotene to diets rich in vitamin A through the feed can improve fertility. The β-carotene molecule will be split at the intestinal mucosa by a 15,15′- dioxygenase and converted into a single molecule of vitamin A. Kerti et al. (2005) showed that carotenoids are found in considerable amounts in the hard and soft faeces of adult female rabbits fed standard diets containing 10,000 IU vitamin A and 13.1 mg total carotenoids kg\(^{-1}\). However, no significant amounts were detected in tissues such as blood, liver and kidneys. Moreover, the ovarian follicles of rabbits fed β-carotene showed no detectable levels of β-carotene or other carotenoids (Kormann et al., 1989). Therefore, the only explanation could be that the mechanism by which β-carotene exerts its benefits in rabbits is different from that observed in the cow. Kormann et al. (1989) speculated that cleavage of β-carotene may yield a biologically active metabolite of an ‘as yet’ unknown nature. Based on the lack of agreement among authors on the influence of β-carotene on reproduction and the cost of supplementation, caution is needed. Therefore, it is advisable not to make any recommendation until additional research confirm the benefits of β-carotene supplementation of rabbit diets.

Table 7.7. Vitamin requirements of rabbits (mg kg\(^{-1}\), unless otherwise indicated).

<table>
<thead>
<tr>
<th></th>
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<th></th>
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<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Growing-fattening</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vitamin A (mIU)</td>
<td>0.58</td>
<td>6</td>
<td>10</td>
<td>6</td>
<td>6</td>
<td>10</td>
</tr>
<tr>
<td>Vitamin D (mIU)</td>
<td>–</td>
<td>0.9</td>
<td>1</td>
<td>0.8</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Vitamin E</td>
<td>40</td>
<td>50</td>
<td>20</td>
<td>30</td>
<td>30</td>
<td>50</td>
</tr>
<tr>
<td>Vitamin K(_3)</td>
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<td>0</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Niacin</td>
<td>180</td>
<td>50</td>
<td>31</td>
<td>50</td>
<td>50</td>
<td>50</td>
</tr>
<tr>
<td>Pyridoxine</td>
<td>39</td>
<td>2</td>
<td>0.5</td>
<td>2</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Thiamine</td>
<td>–</td>
<td>2</td>
<td>0.8</td>
<td>2</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Riboflavin</td>
<td>–</td>
<td>6</td>
<td>3</td>
<td>6</td>
<td>6</td>
<td>2</td>
</tr>
<tr>
<td>Folic acid</td>
<td>–</td>
<td>5</td>
<td>0.1</td>
<td>5</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>Pantothenic acid</td>
<td>–</td>
<td>20</td>
<td>10</td>
<td>20</td>
<td>20</td>
<td>20</td>
</tr>
<tr>
<td>Cyanocobalamin</td>
<td>–</td>
<td>0.01</td>
<td>0.01</td>
<td>0.01</td>
<td>0.01</td>
<td>0.01</td>
</tr>
<tr>
<td>Choline</td>
<td>1200</td>
<td>–</td>
<td>300</td>
<td>50(^g)</td>
<td>200</td>
<td>100</td>
</tr>
<tr>
<td>Biotin</td>
<td>–</td>
<td>0.2</td>
<td>10</td>
<td>0.2</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td><strong>Lactating does</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vitamin A (mIU)</td>
<td>–</td>
<td>12</td>
<td>0.01</td>
<td>10</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td>Vitamin D (mIU)</td>
<td>–</td>
<td>0.9</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Vitamin E</td>
<td>30</td>
<td>50</td>
<td>20(^a)</td>
<td>50</td>
<td>50</td>
<td>50</td>
</tr>
<tr>
<td>Vitamin K(_3)</td>
<td>–</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Niacin</td>
<td>–</td>
<td>–</td>
<td>31</td>
<td>–</td>
<td>40</td>
<td>50</td>
</tr>
<tr>
<td>Pyridoxine</td>
<td>–</td>
<td>–</td>
<td>0.5</td>
<td>–</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Thiamine</td>
<td>–</td>
<td>–</td>
<td>0.8</td>
<td>–</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Riboflavin</td>
<td>–</td>
<td>–</td>
<td>3</td>
<td>–</td>
<td>6</td>
<td>2</td>
</tr>
<tr>
<td>Folic acid</td>
<td>–</td>
<td>–</td>
<td>0.1</td>
<td>–</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>Pantothenic acid</td>
<td>–</td>
<td>–</td>
<td>10</td>
<td>–</td>
<td>20</td>
<td>20</td>
</tr>
<tr>
<td>Cyanocobalamin</td>
<td>–</td>
<td>0</td>
<td>0.01</td>
<td>–</td>
<td>0.01</td>
<td>0.01</td>
</tr>
<tr>
<td>Choline</td>
<td>–</td>
<td>–</td>
<td>300</td>
<td>100(^g)</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>Biotin</td>
<td>–</td>
<td>–</td>
<td>0.01</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

\(^a\)Common feed for does and fryers.  
\(^b\)Young does.  
\(^c\)As choline chloride.  
\(^d\)Increase to 50 mg kg\(^{-1}\) for high-producing does.
**Vitamin D**

Vitamin D is synthesized by the animal when exposed to sunlight. The two major natural sources are cholecalciferol (vitamin D$_3$ of animal origin) and ergocalciferol (vitamin D$_2$ of plant origin). Vitamin D$_3$ is preferred to vitamin D$_2$ by rabbit tissues.

Vitamin D, after dihydroxylation in the liver and kidney, acts as a hormone and plays a central role in the metabolism of calcium and phosphorus, as in other mammalian species, influencing bone mineralization and mobilization. The classic symptoms of deficiency are rickets in growing animals and osteomalacia in adults. Under normal circumstances (calcium levels in excess of requirements) rabbits are very efficient in absorbing calcium, a process that seems to be quite independent of vitamin D status. Bourdeau et al. (1986) showed that the net intestinal absorption of calcium and phosphorus in adult rabbits is similar for rabbits deficient in vitamin D and those with vitamin D-supplemented diets. Fébel and Huszar (2000) found that the injection of a large dose of 100,000IU cholecalciferol did not affect calcium and phosphorus excretion via the faeces. In addition, excess vitamin D$_3$ increased renal tubular reabsorption of calcium, but did not affect that of inorganic phosphorus. Levels of vitamin D$_3$ as low as 2300IU kg$^{-1}$ are detrimental to rabbit productivity, with increased fetal mortality, depressed appetite, diarrhoea, ataxia, paralysis and death (Ringler and Abrams, 1970; Kubota et al., 1982; Lebas, 1987; Zimmerman et al., 1990).

Excess vitamin D, rather than deficiency, is more likely to be a problem under practical conditions. The excess causes resorption of bones and calcification of soft tissues such as the arteries, liver and kidneys (Löliger and Vogt, 1980; Kamphues, 1991). The incidence of problems because of excess dietary vitamin D$_3$ is more acute when calcium is fed in excess of requirements. Consequently, the recommended level of vitamin D$_3$ for rabbits is low and should not, under practical conditions, exceed 1000–1300IU (Table 7.7). Most of the commercial premixes surveyed (Table 7.8) were within this range, but >0.3 (ten out of 29) appeared to have an excess of this vitamin.

**Vitamin E**

Vitamin E activity is found in a series of eight compounds of plant origin: four tocopherols and four tocotrienols that occur as α, β, γ and Δ forms. The various forms of vitamin E existing in nature have different biological activity, with the natural source isomer, called RRR-α-tocopherol or d-α toco-

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**Table 7.8. Premix composition and practical vitamin recommendations for commercial rabbit feeds (mg kg$^{-1}$ diet as-fed basis, unless otherwise indicated).**

<table>
<thead>
<tr>
<th>Vitamin</th>
<th>Mean ± SD</th>
<th>Range</th>
<th>Does</th>
<th>Fatteners</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vitamin A (mIU)</td>
<td>9.2 ± 1.3</td>
<td>6–12.5</td>
<td>10</td>
<td>6</td>
</tr>
<tr>
<td>Vitamin D (mIU)</td>
<td>1.2 ± 0.4</td>
<td>0.6–2</td>
<td>0.9</td>
<td>0.9</td>
</tr>
<tr>
<td>Vitamin E</td>
<td>24.9 ± 10.3</td>
<td>10–50</td>
<td>50</td>
<td>15</td>
</tr>
<tr>
<td>Vitamin K$_3$</td>
<td>1.16 ± 0.6</td>
<td>0–3.3</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Niacin</td>
<td>28.1 ± 11.1</td>
<td>11–50</td>
<td>35</td>
<td>15</td>
</tr>
<tr>
<td>Pyridoxine</td>
<td>1.32 ± 0.9</td>
<td>0–4</td>
<td>1.5</td>
<td>0.5</td>
</tr>
<tr>
<td>Thiamine</td>
<td>1.11 ± 0.6</td>
<td>0–2</td>
<td>1</td>
<td>0.8</td>
</tr>
<tr>
<td>Riboflavin</td>
<td>3.65 ± 1.6</td>
<td>0.5–8</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td>Folic acid</td>
<td>0.23 ± 0.3</td>
<td>0–1</td>
<td>1.5</td>
<td>0.1</td>
</tr>
<tr>
<td>Pantothenic acid</td>
<td>10.1 ± 5.8</td>
<td>0–22</td>
<td>13</td>
<td>10</td>
</tr>
<tr>
<td>Cyanocobalamin</td>
<td>0.013 ± 0.01</td>
<td>0–0.1</td>
<td>0.012</td>
<td>0.01</td>
</tr>
<tr>
<td>Choline</td>
<td>251 ± 92</td>
<td>0–450</td>
<td>200</td>
<td>100</td>
</tr>
<tr>
<td>Biotin</td>
<td>0.014 ± 0.03</td>
<td>0–0.1</td>
<td>0.08</td>
<td>0.01</td>
</tr>
</tbody>
</table>

*Vitamin premix composition (n = 29).*
pherol, the most active. Synthetic forms of \( \alpha \)-tocopherol are known as all-rac-\( \alpha \)-tocopherol or dl-\( \alpha \)-tocopherol, and include an eight-isomer equimolar mix of which only one isomer is identical to the \( d \)-\( \alpha \) tocopherol found in nature. Current evidence in pigs and poultry indicates that natural sources have approximately twice as much bioactivity than synthetic sources of vitamin E (Lauridsen et al., 2002; Wilburn et al., 2008; Boler et al., 2009). Major functions of vitamin E are the synthesis of prostaglandins, blood clotting, stability of membrane structure and modulation of the immune response. As discussed previously, the functions of vitamin E are closely related to those of selenium for most species, but the role of selenium in rabbit tissues is less important than that of vitamin E. In fact, selenium does not seem to have a sparing effect on vitamin E requirements in the rabbit.

The main signs of vitamin E deficiency are muscular dystrophy in the growing rabbit and poor reproductive performance, with increased abortion rates and stillbirths in the pregnant doe (Yamini and Stein, 1989). Furthermore, problems related to myocardial damage, exudative diathesis, hepatitis, oedema, ulcerations and an increased incidence of mastitis, mammitis and agalaxia have been reported in rabbits fed vitamin E-deficient diets. No recent experiments are available on the vitamin E requirements of rabbits under intensive production systems. Recommended levels in the literature and practical supplementation values are based either on old data (Ringler and Abrams, 1971) or on extrapolation from other species. Until more information is available, it seems advisable to recommend 15 and 50 mg vitamin E kg\(^{-1}\) for fatteners and does, respectively. However, vitamin E recommendations might depend on the amount and fatty acid profile of the fat source used, because the fatty acid composition of cell membranes is modified as well as their susceptibility to oxidation. In cases of impaired immunity (Fortun-Lamothe and Drouet-Viard, 2002), high incidence of infections and inflammation of the reproductive organs (Castellini et al., 2007) and in the presence of coccidiosis (Diehl and Distler, 1961) it might be advisable to increase these levels. In addition, Castellini et al. (2007) reported that vitamin E-enriched diets (200 mg vitamin E kg\(^{-1}\) diet) reduce the production of free radicals and improve semen quality (viability, membrane integrity and motility of spermatozoa), particularly after storage. The inclusion of 200 mg vitamin E kg\(^{-1}\) in diets supplemented with unsaturated fat sources (30 g kg\(^{-1}\)) has been found to reduce oxidative damage of the jejunum mucosa and lipid oxidation of the liver (Rey et al., 1997) and muscle tissues in rabbits (López-Bote et al., 1997).

Unlike other fat-soluble vitamins, vitamin E does not accumulate to toxic levels in the liver and the excess is excreted via bile and urine. The absorption of dietary vitamin E varies with rabbit age and the duration of the supplementation period. In adult rabbits the absorption seems to be a saturable process (Castellini et al., 2000), whereas in young rabbits the continuous administration of a dose seven to ten times higher than required increases the concentration of vitamin E in plasma and muscle tissue (Oriani et al., 2001). The concentration of the degradation product of \( \alpha \)-tocopherol (\( \alpha \)-CEHC) in urine may serve as indicator of adequate \( \alpha \)-tocopherol supply in rabbit bucks. On the other hand, meat cuts from rabbits fed diets supplemented with high levels of vitamin E (>200 mg kg\(^{-1}\) diet) have been found to have greater stability, better colour, lower dripping losses and longer shelf-life than cuts from control animals (Bernardini et al., 1996; Castellini et al., 1998, 2001; Corino et al., 1999; Dal Bosco et al., 2004; Lo Fiego et al., 2004).

**Vitamin K**

As indicated for other fat-soluble vitamins, the term ‘vitamin K’ is used to describe a group of compounds that share the common characteristic of antihaemorrhagic effects. These compounds can be of vegetable (phyloquinone or K\(_{1}\)), microbial or animal (menaquinones or K\(_{2}\)) origin. Vitamin K is involved in the mechanism of blood coagulation. It is required for the synthesis of prothrombin and other plasma-clotting factors.
Deficiency may result in haemorrhagic conditions and lameness in growing rabbits and in placental haemorrhage and abortion of kits in pregnant does (NRC, 1977). Other vitamin K-dependent enzymes have now been discovered, indicating that this vitamin has more roles than previously thought. For example, osteocalcin, a metabolite involved in the mineralization and formation of bone, has a vitamin K-dependent calcium-binding amino acid that facilitates the binding of osteocalcin to hydroxyapatite in bone (McDowell, 2000).

Most ingredients used in feeds are poor sources of vitamin K; the exception is lucerne meal, which may contain up to 20–25 mg vitamin K kg\(^{-1}\). However, a considerable number of microorganisms present in the rumen and hindgut synthesize large amounts of vitamin K and, consequently, the faeces contain substantial amounts of the vitamin even if none is present in the feed. Therefore, the requirement of rabbits for this vitamin is partly satisfied through coprophagy.

Rabbit requirements for vitamin K are difficult to evaluate. In fact, no studies have been conducted in this respect. Most commercial feeds include levels of vitamin K close to 1 mg kg\(^{-1}\) (Table 7.8), an amount that should suffice in most situations. However, in cases of subclinical coccidiosis, the use of sulpha or other drugs, or the inclusion of antimetabolites in the feed (i.e. mouldy ingredients, amprolium), an increase in vitamin K supplementation is advisable, especially in diets for pregnant does.

### 7.2.2 Water-soluble vitamins

**Vitamin C**

Vitamin C (ascorbic acid) plays an important role in many biochemical reactions in which oxygen is incorporated into the substrate. It is involved in the biosynthesis of collagen (hydroxylation of lysine and proline) and carnitine, and stimulates phagocytic activity of leukocytes. Vitamin C is synthesized from D-glucose in the liver by most mammals, including the rabbit. Therefore, it is not strictly considered a vitamin for these species (Jennes et al., 1978). In the body, ascorbic acid is found mainly in aqueous compartments such as plasma and seminal fluid. However, extra supplementation with vitamin C does not reduce the number of tocopherol radicals within the membranes of spermatozoa (Castellini et al., 2007). Vitamin C has been shown to act as a pro-oxidant or as an antioxidant depending on the vitamin E status of the tissue (Chen, 1989). More recent studies (Castellini et al., 2003; Lo Fiego et al., 2004) have shown that when vitamins C and E are supplemented simultaneously, the deposition of vitamin E in the muscles and organs of the rabbit increases, indicating that vitamin E is protected from oxidation by the presence of vitamin C.

It has been reported that vitamin C reduces the effects of stress in many species. Under adverse conditions, such as hot weather, intensive production, high stocking density, poor transport and weaning and in the presence of subclinical diseases, the synthesis of ascorbic acid from glucose might be inadequate; consequently, the concentration of vitamin C in the plasma is reduced. Under these circumstances exogenous supplementation with ascorbic acid may be useful (Mahan et al., 1994; Zakaria and Al-Anes, 1996). No direct confirmation of these effects has been reported in the rabbit, although rabbits under heat stress show a reduced vitamin C concentration in plasma (Verde and Piquer, 1986). In fact, Ismail et al. (1992a,b) found a reproductive response in rabbits fed vitamins C and E when subjected to high ambient temperature, but, because of the experimental design used, the effects of vitamin E and C were confounded. In stressful situations, Xiccato (1996) recommended supplementing the diet with 50–100 mg vitamin C kg\(^{-1}\). In all cases, any supplement of this vitamin must be added to the premix in a protected form, because ascorbic acid is easily oxidized, especially under moist conditions and when exposed to contact with copper, iron and other oligoelements.
B vitamins

Appreciable amounts of water-soluble vitamins are supplied to the rabbit through caecotrophy. In fact, caecotrophy meets rabbit requirements for maintenance and average levels of production (NRC, 1977; Harris et al., 1983). However, fast-growing fryers and high-producing does may respond to additional supplementation of B vitamins, namely thiamine (B₁), riboflavin (B₂), pyridoxine (B₆) and niacin (Maertens, 1996; Xiccato, 1996; Lebas, 2004).

Few recent detailed studies have been conducted on the requirements of rabbits for B vitamins. Dietary ingredients used in rabbit diets, such as lucerne meal, wheat middlings and soybean meal, are excellent sources of most B vitamins (Cheeke, 1987). Even when semi-purified diets are used, the classic symptoms of deficiency are seldom observed; no reports are available using high-producing rabbits as experimental animals. Therefore, most of the recommendations for intensive production have been extrapolated from other species or are based on field observations.

Choline is utilized by the organism as a building unit and as an essential component of other molecules involved in the regulation of many metabolic processes. Choline is essential for: (i) building and maintenance of cell structure as a component of phospholipids; (ii) fat metabolism in the liver, preventing abnormal lipid accumulation; (iii) formation of acetylcholine, which allows the transmission of nerve impulses; and (iv) donation of labile methyl groups for the formation of methionine, betaine and other metabolites. Unlike all other vitamins of the B group, choline is synthesized in the liver and acts more as a structural constituent than as a coenzyme. As in other species, betaine is used in practice to replace part of the choline requirements (methyl donor).

In the rabbit, choline deficiency results in retarded growth, fatty liver and necrosis of the kidney tubules (McDowell, 2000). In addition, progressive muscular dystrophy has been reported in fryers fed diets deficient in choline (NRC, 1977). Recommendations for supplementation vary widely (Table 7.7), but unfortunately no recent reports have been published on the requirements of rabbits for this vitamin. Under practical conditions, choline is supplemented through the premix at levels between 0 and 450 mg kg⁻¹ (Table 7.8). Based on this information, and taking into account data from other species, a choline supplement of 200 mg kg⁻¹ diet should suffice for most situations.

Folic acid is necessary for the transfer of single-carbon units, a role analogous to that of pantothenic acid in the transfer of two-carbon units. Therefore, folic acid is important for the biosynthesis of nucleic acids and for cell division. Folic acid has attracted the attention of scientists because of studies showing an improvement in number of piglets born alive when gestating sows are fed a diet supplemented with choline (Lindemann, 1993; Matte and Giard, 1996). In pigs, the response in litter size with folic acid supplementation seems to be a result of improved embryo and fetal survival. However, no information is available on the folic acid requirements for reproduction in does. In fact, the NRC (1977) does not add any information on the requirements for this vitamin in rabbits. The study of El-Masry and Nasr (1996) indicated that additional supplementation of doe diets with 5 mg of folic acid may improve performance and prolificacy. However, as mentioned before, the experimental conditions used in this research were not representative of modern rabbit production (poor productivity, high mortality at weaning, small number of replicates, high variability and inappropriate composition of the premix used for the control diet). Consequently, this information has to be viewed cautiously.

Values recommended in the literature vary from 0.1 to 5 mg kg⁻¹ (Table 7.7). This wide variability indicates the lack of information on the vitamin requirement for rabbits. Commercial premixes used in Spain have a folic acid content varying from 0 to 1 mg kg⁻¹, without any evidence of deficiency even at the lowest level (Table 7.8). Based on the available information, and until further information becomes available, 0.1 and 1.5 mg kg⁻¹ are recommended for growing-fattening and does, respectively.
Biotin (vitamin H) is involved in many metabolic reactions, including the interconversions of protein to carbohydrate and carbohydrate to fat. It plays a role in maintaining normal blood glucose when carbohydrate intake is low. Deficiency is detected by abnormal function of the thyroid and adrenal glands, reproductive tract and nervous system (McDowell, 2000). The more obvious clinical signs are dermatitis and secondary lameness. In the rabbit, no deficiency signs have been reported even in the absence of exogenous supplementary biotin. Only when raw egg white, which contains avidin (an antivitamin H), has been fed have a loss of hair and dermatitis been noted (NRC, 1977). In any case, there is no information on the requirements for reproduction and growth under intensive rearing conditions. Recommended values in the literature vary from 0 to 0.2 mg kg\(^{-1}\) diet, with greater values for young rabbits. Commercial premixes used in Spain vary in biotin content from 0 to 0.1 mg kg\(^{-1}\), although most do not include any supplement at all (Table 7.8). Data available for pigs indicate a benefit from biotin supplementation on hoof cracks, growth and reproduction (Kornegay, 1986; Lewis et al., 1991). Therefore, until more information is available, 0.01 and 0.08 mg kg\(^{-1}\) are recommended for fatteners and does and rearing kits, respectively.

Thiamine is a coenzyme of certain reactions of the citric acid cycle. The classic symptoms of deficiency are neurological disorders, cardiovascular damage and lack of appetite. In the rabbit, a mild ataxia and flaccid paralysis have been reported when extremely low thiamine diets are used (NRC, 1977). Recommended values in the literature vary from 0 to 2 mg kg\(^{-1}\) diet. Until more information is available, 0.01 and 0.08 mg kg\(^{-1}\) are recommended for fatteners and does and rearing kits, respectively.

Riboflavin is required as a coenzyme in many metabolic processes. Most flavoproteins (flavin adenine dinucleotide, flavin mononucleotide) contain vitamin B\(_2\) and, therefore, this vitamin is involved in the release of food energy and the assimilation of nutrients. Typical symptoms of deficiency involve the eyes, skin and nervous system. Milk is rich in riboflavin and deficiency should not therefore be expected in suckling rabbits. Diets deficient in riboflavin have more negative effects on early embryonic mortality than on fertility. Riboflavin concentrates in the uterus in the early pregnancy of sows, and a massive increase in dietary riboflavin may improve embryo survival and litter size (Bazer and Zavy, 1988). Moreover, Pettigrew et al. (1996) observed an increase in farrowing in early pregnant sows that were extra-supplemented with riboflavin, but no increases in litter size were detected. No reports are available on the requirements of highly productive rabbits for this vitamin. Values recommended in the literature vary between 2 and 6 mg kg\(^{-1}\) (Table 7.7). Spanish and Portuguese premixes provide between 0.5 and 8 mg kg\(^{-1}\) (Table 7.8). Based on the few available data, 3 and 5 mg kg\(^{-1}\) is recommended for fryers and does, respectively.

Niacin is involved in many metabolic reactions such as electron transport, which yields energy to the animal. It plays a role in tissue integrity, especially of the skin, gastrointestinal tract and nervous systems. Deficiency is characterized by hair loss, dermatitis, diarrhoea, lack of appetite and ulcerative lesions. Therefore, in cases of deficiency, bacterial infection and enteric conditions are likely to develop. In the rabbit, substantial amounts of niacin are synthesized by the hindgut microorganisms, which add to satisfy requirements. In addition, a small amount of this vitamin can be derived from dietary tryptophan, although the process is very inefficient. In all cases, rabbits seem to respond to extra niacin supplementation (NRC, 1977). Recommended values in the literature vary between 31 (Mateos and Piquer, 1994) and 180 mg kg\(^{-1}\) (NRC, 1977). These large discrepancies are inexplicable, even in the absence of experimental information. Practical observations indicate that the NRC (1977) recommendations grossly overestimate rabbit requirements. In fact, no symptoms of deficiency have been reported when rabbit does are
supplemented with as low as 10–15 mg niacin kg\(^{-1}\) diet.

Pyridoxine refers to a group of three related compounds: pyridoxine, pyridoxal and pyridoxamine, with equivalent activity in mammals. This vitamin plays a role in the Krebs cycle and in amino acid, carbohydrate and fatty acid metabolism. Synthesis of niacin from tryptophan, conversion of linoleic to arachidonic acid, formation of adrenalin from phenylalanine and tyrosine, incorporation of iron into haemoglobin and antibody formation are some of the reactions in which pyridoxine is involved. Pyridoxine deficiency produces retarded growth, dermatitis, convulsions, anaemia, scaly skin, alopecia, diarrhoea and a fatty liver, among other symptoms.

In the rabbit, pyridoxine deficiency causes inflammation around the eyes and nose, scaly thickening of the skin around the ears, alopecia in the forelegs and skin desquamation (Bräunlich, 1974). Supplemental values recommended in the literature vary from 0.5 mg kg\(^{-1}\) for lactating does and growing rabbits (Mateos and Piquer, 1994), 39 mg kg\(^{-1}\) for growing-fattening (NRC, 1977) and up to 400 mg kg\(^{-1}\) for growing angora rabbits (Schlolaut, 1987). Again, this extreme range of recommendations is equivocal and is partly due to a lack of experimental data. Spanish and Portuguese premixes included in the survey contained between 0 and 4 mg pyridoxine kg\(^{-1}\). Most of the commercial premixes (25 out of 29) contained between 1 and 2 mg pyridoxine kg\(^{-1}\) and no clinical symptoms have ever been detected in the field using these low levels (Mateos and Piquer, 1994). Based on current field observations, 0.5 and 1.5 mg kg\(^{-1}\) are recommended for fatteners and does, respectively.

Pantothenic acid is a constituent of coenzyme A and acyl carrier proteins, key metabolites in tissue metabolism. Pantothenic acid deficiency reduces growth and produces symptoms such as skin lesions, nervous disorders, gastrointestinal disturbances, impairment of adrenal function and decreased resistance to infection. No deficiency symptoms have ever been described in the rabbit (McDowell, 2000) because of deficiency in this vitamin. Kulwich et al. (1953) observed that caecotrophs have up to six times more pantothenic acid than hard faeces. Literature requirements vary from 10 to 20 mg kg\(^{-1}\) (Table 7.7). Contents of Spanish and Portuguese premixes vary from 0 to 22 mg kg\(^{-1}\) diet. Until new data are available, 10 and 13 mg kg\(^{-1}\) are recommended for growers and does, respectively (Table 7.8).

Vitamin B\(_{12}\) (cyanocobalamin) was the last but the most potent vitamin to be discovered. It is synthesized in nature only by microorganisms and is not found in feeds of plant origin. As mentioned before, cobalt is the prosthetic group of this molecule (being the only role known for this micromineral). Vitamin B\(_{12}\) is involved as a coenzyme in reactions such as the formation of one-carbon units (methyl group synthesis). Therefore, vitamin B\(_{12}\) is metabolically related to choline, methionine and folacin, among other essential nutrients. Symptoms of deficiency include anaemia, loss of appetite, rough skin, diarrhoea and reduced litter size. Rabbits are capable of producing substantial amounts of vitamin B\(_{12}\) through coprophagy, provided that cobalt is available, and no deficiency symptoms have ever been described when commercial diets are used. Values recommended in the literature vary from 0 to 0.01 mg kg\(^{-1}\). Commercial premixes contain between 0 and 0.1 mg kg\(^{-1}\) (Table 7.8). On the basis of current knowledge, 0.01 to 0.012 mg kg\(^{-1}\) is recommended for growers and does, respectively.

The vitamin composition of 29 premixes marketed in Spain and Portugal that correspond to more than 0.90 of the total feed compound produced in these two countries is presented in Table 7.8. Furthermore, the recommended levels of vitamins of premixes intended for commercial rabbit diets are included in this table.

### 7.3 Additives

A large number of feed additives are used in rabbit feeding worldwide to improve certain characteristics of the feed or to enhance...
animal performance. The list is very broad and includes anticoccidial drugs, growth promoters, preservative agents, enzymes, flavours, prebiotics, probiotics, acidifiers and pellet binders. Some (i.e. antibiotics) are not legally permitted in many countries, including the EU-27, and some (i.e. enzymes, probiotics) may need to pass through a registration process prior to commercialization. A selection of additives authorized by EU legislation and more likely to be used in conventional rabbit feeds is now presented.

### 7.3.1 Anticoccidial drugs

Coccidiosis is one of the most important diseases affecting rabbitries. Intestinal and liver coccidiosis may cause diarrhoea and death. In most commercial situations the disease occurs subclinically, with growth retardation and impairment of feed conversion. Consequently, anticoccidial drugs are frequently used in intensive production systems as a prophylactic therapy to reduce losses caused by coccidiosis. The production of rabbits in wire cages together with the use of preventive medication reduces the incidence of the disease to manageable levels in modern rabbitries.

Several products are available to control coccidiosis. Those used in the EU include robenidine (Licois and Coudert, 1980), salinomycin (Gaca-Lagodzinska et al., 1994; Paefgen et al., 1996) and diclazuril (Table 7.9) (Vanparis et al., 1989; Van Meirhaeghe et al., 1996). Other products that have been shown to be effective but that are not registered in the EU are metichlorpindol and the combination of metichlorpindol and methylbenzoquate. Some ionophores, successfully used in poultry, are toxic for rabbits (e.g. narasin, monensin) and cross-contamination with feeds from other species may cause problems (Salles et al., 1994).

Most of the available coccidiostats to control the disease have some side effects, especially when the recommended doses are not followed. For example, robenidine can taint the muscles and, more specifically, the liver of the rabbits, and might not be as effective as other drugs in controlling hepatic coccidiosis. Furthermore, if cross-contamination occurs with layer feeds, a taint may appear in egg yolks. Salinomycin, in excess of recommended levels, decreases feed intake, which is a quite common side effect for most ionophore drugs and also for other therapeutic drugs (Okerman and Moermans, 1980; Peeters et al., 1980; Morisse et al., 1989).

In addition, ionophore cross-contamination may be responsible for toxicity in animals other than the target species. Horses, turkeys, guinea fowls and broiler breeders are the species more greatly affected by toxicity of ionophores when cross-contamination occurs.

### 7.3.2 Antibiotics and growth promoters

Currently, bacitracin, colistin, apramycin and tiamulin are registered as therapeutic drugs in most European countries. All of them require veterinary prescription for use in rabbit feeds. Several antibiotics, most of them effective against Gram-positive microorganisms, have been shown to improve rabbit growth and feed efficiency at low levels of inclusion. Flavophospholipol (2–4 mg kg⁻¹), avoparcin (10–20 mg kg⁻¹), bacitracin (50–100 mg kg⁻¹) and virginiamycin (30 mg kg⁻¹) are some of the antibiotics effective in improving rabbit productivity.

<table>
<thead>
<tr>
<th>Name</th>
<th>Amount (mg kg⁻¹ diet)</th>
<th>EU registration status (Annex 1)</th>
<th>Withdrawal period (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Robenidine</td>
<td>50–66</td>
<td>All types</td>
<td>5</td>
</tr>
<tr>
<td>Salinomycin</td>
<td>20–25</td>
<td>Growing-fattening</td>
<td>5</td>
</tr>
<tr>
<td>Diclazuril</td>
<td>1</td>
<td>All types</td>
<td>1</td>
</tr>
</tbody>
</table>
performance (Escribano et al., 1982; Mateos, 1989; Maertens et al., 1992; Abecia et al., 2005; Ayed and Saïd, 2008). However, the use of any antibiotic as a growth promoter is forbidden in the EU.

Many antibiotics used as therapeutic drugs in other species have side effects on rabbit performance (Licois, 1980; Thilsted et al., 1981). Ampicillin, lincomycin and other drugs disturb the normal microflora of the intestines, increasing mortality and depressing growth (Mateos, 1989; Morisse et al., 1992; Lafargue-Hauret et al., 1994; Licois, 1996).

7.3.3 Probiotics and prebiotics

Because of uncertainty regarding the use of antibiotics and growth promoters in animal feeds, new lines of products, more acceptable to the consumer, are appearing in the market. These are used to reduce the incidence of enteric diseases and to improve feed intake and digestibility. Probiotics, such as yeasts (Maertens and De Groote, 1992) and Bacillus (Maertens et al., 1994), and prebiotics, such as oligosaccharides (Morisse et al., 1992; Lebas, 1993) and yeast cell walls, are finding a place in rabbit feeding. A review by Falçao-e-Cunha et al. (2007) reported the results published in the literature on the use of these additives in rabbits.

Probiotics are supplements that contain beneficial live or revivable microorganisms. It is thought that these supplements colonize the gut, contributing to the maintenance of the flora equilibrium (Maertens and De Groote, 1992). The objective is to create a gut barrier against pathogens. The mechanism of action of probiotics has not been elucidated, but might include: (i) reduction of toxin production; (ii) stimulation of enzyme production by the host; (iii) production of some vitamins or antimicrobial substances; (iv) competition for adhesion to epithelial cells and increased resistance to colonization; and (v) stimulation of the immune system of the host (Simon et al., 2003; Falçao-e-Cunha et al., 2007). A summary of 13 trials conducted with probiotics in fattening rabbits and four trials in does from 1991 to 2006 has been published (Falçao-e-Cunha et al., 2007). At this moment, Bacillus cereus var. toyoi and Saccharomyces cerevisiae NCYC Sc 47 are registered for rabbits in the EU (Falçao-e-Cunha et al., 2007). Some probiotics have been shown to benefit rabbit performance (de Blas et al., 1991; Onifade et al., 1999; Trocino et al., 2005; Pinheiro et al., 2007), but none works under all systems of production (Aoun et al., 1994; Maertens et al., 1994; Michelan et al., 2002).

Prebiotics are non-digestible food ingredients that can selectively stimulate certain intestinal bacteria with potential benefits for the health of the rabbit. The main commercial oligosaccharides available on the market are fructo-, α-galacto-, transgalacto-, mannan- and xylo-oligosaccharides (Falçao-e-Cunha et al., 2007). The main advantages of prebiotics over probiotics are the lack of problems when heat is applied during feed processing or with the acidity of the stomach. In addition, prebiotics are not live organisms, which facilitates the legal registration process. Prebiotics selectively stimulate the beneficial bacteria of the caecum microflora. Supplementation of rabbit feeds with certain oligosaccharides increases volatile fatty acids in the caeca of weanling rabbits, decreasing the caecal ammonia concentration. In addition, to stimulate the beneficial microflora of the gut, prebiotics may prevent the adhesion of pathogens to the mucosa and stimulate the immune response (Forchielli and Walker, 2005; Falçao-e-Cunha et al., 2007). Several authors (Aguilar et al., 1996; Lebas, 1996) have observed a decrease in mortality and an improvement in performance when oligosaccharides are added to rabbit feeds. The beneficial effects of these additives are more evident when rabbits are reared under poor commercial conditions than under clean experimental conditions (Mourao et al., 2006). The changes in the intestinal environment produced by the inclusion of prebiotics in the diet may prevent or reduce
the incidence of colibacillosis (Peeters et al., 1992). However, beneficial effects are not always observed with the use of these additives (Guidenne, 1995; Pinheiro et al., 2009). Thus, more research and information are needed prior to recommending their inclusion in rabbit diets.

7.3.4 Enzymes

Extensive research conducted in poultry throughout the world has clearly demonstrated that adding exogenous enzymes to diets rich in cereals such as wheat and barley improves bird performance (Bedford and Morgan, 1996; Gracia et al., 2003; García et al., 2008). The mode of action of enzymes has not been fully elucidated, but might be related to modifications of the intestinal environment, including changes in the viscosity of the digesta (Bedford, 1995; Lázaro et al., 2003). This may allow a better contact between nutrients, endogenous enzymes and the absorptive mucosa, and therefore a better use of the diet. In addition, non-starch polysaccharides may coat the nutrients contained in the grain and the addition of cell-wall-degrading enzymes (e.g. xylanases, β-glucanases) may release nutrients facilitating their digestion (Classen, 1996; Cowan et al., 1996). Furthermore, enzyme supplementation increases the rate of passage in poultry, which may improve feed intake (Lázaro et al., 2003) and reduce the growth of Clostridium species and other anaerobes in the gut.

The use of enzymes as feed additives has not been extensively studied in the rabbit (Falçao-e-Cunha et al., 2007). Rabbits are very efficient in the utilization of nutrients (except for fibre), probably because of coprophagy (Marounek et al., 1995; Guidenne and Lacois, 2005). Makkar and Singh (1987) found that the activity of proteases and amylases was higher in the caecum of rabbits than in the rumen. Marounek et al. (1995) reported that the caecal contents of 4-week old rabbits contained most of the total activity of pectinase (0.43), amylase (0.45), lactase (0.57), xylanase (0.65), cellulase (0.69), β-glucosidase (0.70) and urease (0.80) present in the rabbit digestive tract, and that these values increased with age. Consequently, the beneficial effects of carbohydrase supplementation are expected to be very limited. In fact, most published results with exogenous enzymes in rabbit diets have not found any improvement in performance (Tor-Aghydye et al., 1992; Fernández et al., 1996; Remois et al., 1996; Pinheiro and Almeida, 2000; Falçao-e-Cunha et al., 2004, 2007). Moreover, Bolis et al. (1996) found a negative effect on nutrient digestibility when a commercial protease was added to the diet. Others, however, have found benefits when an enzyme cocktail is added to diets for rabbits under extensive (Bhatt et al., 1996) and intensive production (García-Ruiz et al., 2006) systems, especially in young animals. The inclusion of proteases in the diet reduced rabbit mortality during the first 14 days of the fattening period (García-Palomares et al., 2006a, b). García-Palomares et al. (2006a) and Chamorro et al. (2005) found that nitrogen flow reaching the terminal ileum decreased with enzyme inclusion, reducing the colony counts of highly pathogenic Clostridium perfringens in the caecum. García-Palomares et al. (2006b) supplemented a starter diet for early weaned rabbits (25 days old) with a carbohydrase cocktail (β-glucanase, β-xylanase, α-amylase and pectinase) and found a significant improvement in digestibility, growth rate and feed efficiency from 25 to 39 days of age and decreased mortality for the entire fattening period.

Therefore, at present, the addition of exogenous carbohydrase and protease enzymes to rabbit feeds should be limited to diets for the first 14 days after weaning. Similarly, the use of phytases may have some merits in rabbit feeds (Gutierrez et al., 2000), although the benefits are probably less than those observed for other non-ruminant species.
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8 Feed Evaluation

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8.1 Units for Feed Evaluation

8.1.1 Energy

The most commonly used unit for expressing energy value in rabbit diets is digestible energy (DE). However, the use of DE leads to some systematic errors when used for raw materials in diet formulation, especially for certain groups of ingredients.

For instance, DE overestimates the energy content of protein concentrates, as it does not take into account either the higher energy losses in urine or the energy cost of urea synthesis in the liver associated with the use of an excess of this type of ingredient in the diet. Similarly, the DE content of feedstuffs containing significant amounts of digestible fibre (e.g. sugarbeet/citrus pulps or soybean hulls) also overvalues their relative energy concentration, as the use of DE does not consider energy losses (methane and heat of fermentation) linked to the microbial digestion of fibre in the caecum. On the other hand, the relative energy content of fats and feeds with a high fat content is underestimated by DE, because dietary fatty acids are retained in the body more efficiently than other dietary components.

These disadvantages explain the current interest in replacing DE with metabolizable energy (ME) or net energy (NE). However, most of the information available at present has been obtained as DE. As a consequence, DE is still used as the unit of expression of the energy value of diets in rabbits. However, some important points should be taken into account to improve the expression of the energy value of raw materials.

To prevent the use of protein concentrates as energy sources, a maximum protein content of compound feeds should be established. This restriction is also required to control the incidence of diarrhoea (de Blas et al., 1981; Gidenne and García, 2006) and to reduce environmental pollution by animal excreta (Maertens et al., 1997). An alternative is to use ME corrected to zero nitrogen equilibrium (MEn), as in poultry nutrition, instead of DE. Values of MEn can be derived for each ingredient by subtracting 4.8 kJ g⁻¹ digestible protein from its DE content (Maertens, 1992). For these reasons, MEn values are introduced in the final feedstuff table of this chapter. A better hierarchy between protein- and carbohydrate-rich feedstuffs is obtained using the MEn system. Consequently, raw materials are more optimally chosen for their nutritional characteristics when using the MEn system in the formulation of compound diets for rabbits (Maertens et al., 2002).

Digestible fibre and the fat content of compound feeds should also be limited to...
allow for maximal energy intake (García et al., 1993) and for technological reasons (rabbit feed must be pelleted), respectively. These restrictions limit the errors associated with the use of DE to <5% in extreme practical diets (de Blas et al., 1985; Ortiz et al., 1989; de Blas and Carabaño, 1996; Fernández and Fraga, 1996). In any case, the use of correction factors (−2.51 and +5.85 kJ DE kg⁻¹) for ingredients or diets containing a high proportion of digestible neutral detergent fibre (NDF) and ether extract (EE), respectively, might be envisaged.

8.1.2 Protein and amino acids

Total crude protein (CP) and amino acids are still the most common units used to formulate diets for rabbits. However, the ileal digestibility of nitrogen is increasingly used mainly for early weaned rabbits and for preventing intestinal problems or epizootic rabbit enteropathy. Large variations in essential amino acid digestibilities have been found for lucerne hays harvested at different stages of maturity (García et al., 1995) and between average lysine, methionine or threonine digestibility in a basal diet compared to synthetic forms of these amino acids (Taboada et al., 1994, 1996; de Blas et al., 1998). These results have been confirmed by work on protein evaluation (Llorente et al., 2006, 2007a, b; Carabaño et al., 2009). Furthermore, as ileal and faecal digesta contains important amounts of protein of endogenous origin (3.8 and 2.5 g 100 g⁻¹ dry matter (DM) intake, respectively; García et al., 2004; Llorente et al., 2006) the use of true instead of apparent units is advisable (Carabaño et al., 2009). These results indicate that the use of digestible, instead of crude, protein and amino acid units would considerably improve the accuracy of feed evaluation and decrease nitrogen excretion. However, more information is needed on animal requirements and amino acid digestibility prediction for the most commonly used ingredients.

8.1.3 Fibre

Fibre is one of the main components of rabbit diets and NDF accounts for about one-third of matter. In a recent paper on compound feeds, hemicelluloses, cellulose and soluble fibre plus sugars were at similar levels (172, 140 and 164 g kg⁻¹ DM, respectively; Villamide et al., 2009), but with high variation (about 20% coefficient of variation (CV)) and negative correlation between them. Units used to express the fibre content of feed ingredients include NDF, acid detergent fibre (ADF), acid detergent lignin (ADL), crude fibre (CF) and soluble fibre estimated by difference from the organic matter, CP, EE, NDF, starch and sugars. These are described and discussed in detail in Chapter 5.

8.2 Methodology of Feed Evaluation

8.2.1 Complete diets

The evaluation of complete diets is usually undertaken by digestibility assays. The standardization of the procedures used in these assays is the first step in reducing the variability of the results. In this way, a European reference method for the in vivo determination of diet digestibility in rabbits has been proposed by the European Group on Rabbit Nutrition (EGRAN) (Pérez et al., 1995a). The most relevant variables to control in a digestibility assay are the length of the experimental period and the number of animals used. The recommended values are at least 7 days of adaptation period and 4 days of collection period (which implies 5 days of control) using ten rabbits per treatment. No advantage in accuracy was found by Pérez et al. (1996a) when increasing the adaptation period from 7 to 14 days. The number of replicates can be decreased when the length of the collection period increases. Thus, Villamide and Ramos (1994) found the same variability for DM digestibility using ten rabbits and 4 days, eight rabbits and 7 days and seven rabbits and 10 days of collection period. When using growing rabbits, however, a longer collection period is
necessary because of greater differences between intake at the beginning and at the end. Lebas et al. (1994) obtained the same accuracy in digestibility determinations with ten cages of one rabbit and four cages of four rabbits each, although in the latter case there is a greater risk of missing data if any of the animals in the group have health problems.

Other sources of variation in digestibility assays are rabbit breed, sex, litter, age and physiological state. No differences have been found for meat breeds of rabbit of the same size (Maertens and De Groote, 1982; Dessimoni, 1984). However, Pascual et al. (2008) found greater DM and organic matter digestibility values (about 0.01 point) and ADF digestibility (+0.03 points) in growing rabbits from a genetic line selected for litter size compared to another selected for reproductive longevity. Because of the low sexual dimorphism of this species, the effect of sex is not relevant (Xiccato et al., 1992; Pérez et al., 1995b). Litter has shown an effect on DM intake and excretion in rabbits from 25 to 40 days of age, but does not affect DM digestibility (Gómez-Conde et al., 2004). In any case, to eliminate a possible effect of litter, rabbits of the same litter should be distributed evenly across the treatments.

Digestibility is usually measured in growing rabbits (from 42 days onwards) when their digestive system is fully adapted to non-maternal feed. However, the effects of age during this period and the validity of extrapolation of the results obtained with young animals to reproductive females is not clear. It seems that the effect of age on energy and protein digestibility from 7 weeks to slaughter is limited (Maertens and De Groote, 1982; Xiccato and Cinetto, 1988). In work on nitrogen contamination, a decrease in CP digestibility from 0.790 to 0.703 has been observed with age (Calvet et al., 2008). However, as the caecal content weight increases during the first weeks after weaning (by 70% from 30 to 40 days of age; Peeters et al., 1992) a significant part of the ingested feed remains in the digestive tract, leading to an overestimation of digestibility in young rabbits (Blas et al., 1991; Fernández et al., 1994). Thus, Gómez-Conde et al. (2004) obtained a linear decrease of DM digestibility from weaning (25 days) to 32 days of age (0.0217 points each day), whereas digestibility remained constant from 32 to 40 days of age. Comparisons between the digestibility of growing rabbits and breeding does are contradictory. Maertens and De Groote (1982) and Pérez et al. (1996b) found higher digestibility values in growing rabbits, whereas de Blas et al. (1998) found higher digestibility in breeding does, especially for NDF.

Digestibility determinations in rabbits have a high variability. This is shown in Table 8.1, for which 23 papers on digestibility assays were reviewed (García et al., 2001). The mean standard deviation varied from 0.026 to 0.076 for DM and CF digestibility, respectively (which means a CV of about 3.8% and 40%). When the digestibility and analytical methodology is harmonized, however, the variability decreases. Thus, in a ring-test study on the chemical analysis of feed and faeces and its influence on the calculation of digestibility, Xiccato et al. (1996) obtained CVs within laboratories (repeatability) of 0.96%, 1.1% and 6.2% for energy, CP and NDF digestibility, respectively. Furthermore the reproducibility (CV among laboratories) was improved when all of the laboratories used not only the same reference method for digestibility assays, but also harmonized analysis (from 1.6% to 1.0%, from 2.7% to 1.5% and from 21.3% to 7.4%, for gross energy, CP and NDF digestibility, respectively, Pérez et al., 1995b; Xiccato et al., 1996). Therefore, the expected variability in digestibility assays has to be taken into account in the experiment design for calculating the minimum number of rabbits (replicates) to obtain significant differences among treatments (Table 8.1).

8.2.2 Feedstuffs

The nutritive value of feedstuffs can be directly determined (fed as the sole feed) when they are relatively balanced and palatable. Feedstuffs such as lucerne hay and other hays, wheat bran or sunflower meal can be used as sole feeds in a digestibility assay and evaluated directly. Thus, Maertens and De Groote (1981) did not find
differences between lucerne hay evaluated by substitution or directly, and nor did Villamide et al. (2003) comparing direct determination with multiple regression. Similarly, García et al. (1995) determined the energy, NDF, CP and amino acid digestibility of five samples of lucerne hay by using the direct method and obtained good accuracy.

Most feedstuffs are not nutritionally balanced in relation to the requirements of rabbits. When they are fed as a sole diet, the digestive transit time and intake can be changed, which, as a consequence, can alter the nutritive value (Fernández-Carmona et al., 1996). Thus, these authors observed an inverse relationship between feed intake and the nutritive value of feedstuffs, as determined directly. For the majority of feedstuffs, therefore, nutritive value is estimated by difference or regression if more than one substitution rate is used. Figure 8.1 shows the DE of grape pulp determined directly or by difference from a basal diet or a reference feedstuff at an inclusion rate of 300 g kg\(^{-1}\), or by extrapolation using four substitution rates (Villamide et al., 2003).

No differences were observed among the values obtained by difference or extrapolation, but an overestimated energy value was shown when DE was determined directly.

The use of substitution methods implies that there is no interaction between the basal diet (or the reference ingredient) and the test ingredient. However, an effect of basal diet concentration has been detected for citrus and sugarbeet pulp evaluation (Table 8.2). The nutritive value of both feedstuffs was significantly lower when estimated from the lowest-energy basal diet, probably because the high levels of indigestible fibre in this diet produced a lower entry rate of the potentially digestible fibre of pulps into the caecum (de Blas and Villamide, 1990). The opposite effect occurs with basal diets with a high proportion of wheat straw or when feedstuffs with high levels of indigestible fibre are evaluated at high substitution rates (>200 g kg\(^{-1}\)). Thus, Villamide et al. (1991) observed an underestimation of soybean meal when evaluated at a low substitution rate (150 g kg\(^{-1}\)) with a basal diet that included 580 g wheat straw kg\(^{-1}\).

Table 8.1. Number of rabbits required to detect a significant difference (P = 0.05) between two means for digestibility traits varying in standard deviation (SD) (García et al., 2001).

<table>
<thead>
<tr>
<th>Difference in digestibility</th>
<th>SD</th>
<th>0.02</th>
<th>0.03</th>
<th>0.04</th>
<th>0.05</th>
<th>0.06</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dry matter digestibility (20)(^a)</td>
<td>0.0258</td>
<td>16</td>
<td>9</td>
<td>7</td>
<td>5</td>
<td>4</td>
</tr>
<tr>
<td>Gross energy digestibility (20)</td>
<td>0.0273</td>
<td>17</td>
<td>9</td>
<td>6</td>
<td>5</td>
<td>4</td>
</tr>
<tr>
<td>Crude protein digestibility (23)</td>
<td>0.0332</td>
<td>24</td>
<td>13</td>
<td>8</td>
<td>6</td>
<td>5</td>
</tr>
<tr>
<td>Neutral detergent fibre digestibility (15)</td>
<td>0.0467</td>
<td>45</td>
<td>22</td>
<td>13</td>
<td>10</td>
<td>8</td>
</tr>
<tr>
<td>Acid detergent fibre digestibility (12)</td>
<td>0.0608</td>
<td>71</td>
<td>35</td>
<td>21</td>
<td>15</td>
<td>11</td>
</tr>
<tr>
<td>Crude fibre digestibility (7)</td>
<td>0.0763</td>
<td>112</td>
<td>50</td>
<td>31</td>
<td>21</td>
<td>5</td>
</tr>
</tbody>
</table>

\(^a\)The numbers in parentheses indicate the number of trials considered for each trait.
at a 6 g kg\(^{-1}\) than at a 12 g kg\(^{-1}\) rate of inclusion (Maertens et al., 1986). Similarly, Santomá et al. (1987) and Fraga et al. (1989) found an increase in the digestibility coefficient of 0.058 of all nutrients when 30–60 g fat kg\(^{-1}\) was added to the diets.

Therefore, both the substitution rate of the test ingredient and the basal diet should be designed to prevent interactions and to obtain accurate estimates of the test ingredient’s nutritive value, taking into account that the higher the substitution rate the lower the error, but also the greater the probability of interaction between the test ingredient and the basal diet.

When interactions between feedstuffs are expected, or lower rates of inclusion (<200 g kg\(^{-1}\)) have to be used (because of technological or nutritional problems), substitution of the basal diet at several rates is recommended (Villamide, 1996). The linearity between the dietary nutritive value and the substitution rate is analysed and, if it is established, estimation of the nutritive value is undertaken by regression and extrapolation to total substitution. When the relationship between the dietary nutritive value and the substitution rate is non-linear, a nutritive value of the test feedstuff can be assigned for a recommended range of inclusion. Outside this range the nutritive value should be calculated from second- or third-degree equations.

No differences between the energy value estimations of grape pulp have been obtained using the substitution or extrapolation methods (Fig. 8.1) and the standard error of estimation only decreased by 0.1 MJ kg\(^{-1}\) DM (Villamide et al., 2003). Similarly, no advantage has been observed by using...
lucerne as a reference feedstuff instead of a basal diet in the evaluation of grape pulp despite the highly lignified fibre of this feedstuff, and therefore the lower imbalance among extreme diets (Villamide et al., 2003).

The multiple regression equation method involves a simultaneous evaluation of several diets containing test ingredients in varying proportions. Table 8.3 shows the nutritive value (energy and CP digestibility) of six common ingredients in rabbit diets by the substitution or multiple regression equation method using two data sets. There are no significant differences among the different methodologies in their estimations of nutritive value, except for the CP digestibility of grape pulp. This was overestimated in multiple regression equations with independent data with respect to those obtained with all data or by difference. Nevertheless, the multiple regression method implies a diet design with no correlation among ingredients. This is very difficult to fulfil taking account of rabbit requirements, not only in energy, protein and amino acids, but also in the different components of fibrous content.

The above methodology has been extensively applied to DE and protein determinations; however, its use for amino acids evaluation or fibre digestibility is not recommended because of its high variability. The differences in amino acid content among balanced diets are very low, and therefore attributing a digestibility value to a test ingredient by the differences observed among diets is not accurate. A possible method for overcoming these problems is the use of semi-purified diets, where all the protein comes from the test ingredient or from casein, assuming its complete digestibility (García et al., 2005). In this case, the amino acids found in excreta or ileal digesta can come only from the indigestible test ingredient or from endogenous protein (including caecotrophs). A more detailed description is found in Chapter 3. The question now is whether amino acid digestibility obtained this way can be extrapolated to practical diets. In an assay carried out in our laboratory (Llorente et al., unpublished data), trying to test the additivity of the apparent faecal and ileal and true ileal digestible amino acid of four ingredients (sunflower meal, wheat, wheat bran and lucerne hay), much lower amino

### Table 8.3. Comparison of nutritive value (means ± standard error) of ingredients by substitution or multiple regression method (Villamide et al., 2003).

<table>
<thead>
<tr>
<th>Ingredient</th>
<th>Measure</th>
<th>Substitution</th>
<th>Multiple regression&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Multiple regression&lt;sup&gt;b&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>All diets (n = 179)</td>
<td>Independent data (n = 86–169)</td>
</tr>
<tr>
<td>Grape pulp</td>
<td>DE, MJ kg⁻¹</td>
<td>6 ± 0.6</td>
<td>5.7 ± 0.33</td>
<td>6.4 ± 0.70</td>
</tr>
<tr>
<td></td>
<td>CPd</td>
<td>0.4 ± 0.60&lt;sup&gt;c&lt;/sup&gt;</td>
<td>−0.8 ± 0.57&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0.6 ± 0.10</td>
</tr>
<tr>
<td>Lucerne meal</td>
<td>DE, MJ kg⁻¹</td>
<td>7 ± 0.1</td>
<td>8.4 ± 0.35</td>
<td>7.4 ± 0.64</td>
</tr>
<tr>
<td></td>
<td>CPd</td>
<td>0.5 ± 0.04</td>
<td>0.7 ± 0.04</td>
<td>0.55 ± 0.06</td>
</tr>
<tr>
<td>Wheat bran</td>
<td>DE, MJ kg⁻¹</td>
<td>12.20 ± 0.61</td>
<td>12.6 ± 0.42</td>
<td>12.8 ± 0.44</td>
</tr>
<tr>
<td></td>
<td>CPd</td>
<td>0.778 ± 0.07</td>
<td>0.7 ± 0.05</td>
<td>0.7 ± 0.05</td>
</tr>
<tr>
<td>Wheat</td>
<td>DE, MJ kg⁻¹</td>
<td>16.1 ± 0.33</td>
<td>15.6 ± 0.36</td>
<td>14.8 ± 0.47</td>
</tr>
<tr>
<td></td>
<td>CPd</td>
<td>0.71 ± 0.064</td>
<td>0.64 ± 0.067</td>
<td>0.46 ± 0.086</td>
</tr>
<tr>
<td>Full-fat soya meal</td>
<td>DE, MJ kg⁻¹</td>
<td>18.7 ± 0.32</td>
<td>18.6 ± 0.65</td>
<td>18.6 ± 0.92</td>
</tr>
<tr>
<td></td>
<td>CPd</td>
<td>0.80 ± 0.015</td>
<td>0.84 ± 0.031</td>
<td>0.80 ± 0.043</td>
</tr>
<tr>
<td>Sunflower seed</td>
<td>DE, MJ kg⁻¹</td>
<td>10.0 ± 0.73</td>
<td>10.0 ± 0.70</td>
<td>8.4 ± 1.11</td>
</tr>
<tr>
<td>meal</td>
<td>CPd</td>
<td>0.82 ± 0.041</td>
<td>0.81 ± 0.041</td>
<td>0.6 ± 0.06</td>
</tr>
</tbody>
</table>

CPd, crude protein digestibility; DE, digestible energy.
<sup>a</sup>Including diets that determine the nutritive value by difference.
<sup>b</sup>Independent diets.
<sup>c</sup>Not significant.
acid digestibility was observed in the mixed diet (with a lower proportion of purified components) than in the purified one.

In the case of fibre, there are two problems: (i) the high variability in its digestion (reproducibility from 7% to 34% for NDF, ADF or CF digestibility, whereas that of energy is from 1% to 1.6%; Xiccato et al., 1996); and (ii) the influence of the different fibrous components on transit time and therefore on the digestibility of fibre of the ingredient and of the other components of the basal diet, which implies nutritive interactions. The use of semi-purified diets where all the fibre comes from the test feedstuff increases the precision of estimates, although sometimes the results differ from those obtained by substitution (García et al., 1996). The question is whether these fibrous sources maintain their value when they are combined with another kind of fibre or when they are included at lower levels in commercial diets.

The effect of errors in DE determination of experimental diets on the DE estimate of ingredients is shown in Table 8.4. Small differences in the nutritive value of experimental diets result in large differences (proportionally to substitution rate) in the nutritive value of test feedstuffs, so very careful determinations (large numbers of animals and replicates in the chemical analyses of diets) of the nutritive value of diets must be performed.

8.3 Composition and Nutritive Value of Feedstuffs for Rabbits

Table 8.5 shows the chemical composition and nutritive value of 55 feedstuffs commonly used in rabbit nutrition. Data are expressed on an as-feed basis, with a common DM content for each group of feedstuffs, in view of practical utilization. Chemical composition includes DM, ash, CP, EE, CF, NDF, ADF, ADL, soluble fibre, starch, lysine, methionine, methionine plus cystine, threonine, calcium, phosphorus, sodium, chlorine, magnesium and potassium. The chemical composition is based on the tables from the first edition of this book and partly modified according to data from FEDNA (2003), INRA tables (Sauvant et al., 2004) and CVB (2007).

The nutritive value is based on a literature compilation. The tables from the first edition of this book have been revised, taking into account feedstuffs tables published in 2002 (Maertens et al., 2002) and some more recent experimental data (Falcão e Cunha et al., 2004; Martínez et al., 2006; Gidenne et al., 2007; Michelan et al., 2007). The values proposed in Table 8.5 were retained after assessing the methodology used and were considered as the most accurate at practical levels of dietary inclusion. Amino acid digestibility has been estimated from the data of García et al. (2005) and Llorente et al. (2006, 2007a,b) and corrected according to CP digestibility.

| Table 8.4. Error in the estimation of mean digestible energy (DE) of an ingredient (12.55 MJ kg\(^{-1}\) dry matter (DM), DE of basal diet 11.3 MJ kg\(^{-1}\)) when the variables were measured with ±1% error using substitution rates of 200 and 400 g kg\(^{-1}\). Figures express the percentage of error and the difference between the actual and measured DE of ingredients (kJ kg\(^{-1}\) DM) (Villamide, 1996). |
|-----------------------------------------------|-----------------|-----------------|-----------------|
| Error in basal diet                           | 200 g kg\(^{-1}\) | 400 g kg\(^{-1}\) |
| DM intake or excreted, GE faeces              | 2.25%           | 0.85%           | 284             | 109             |
| GE basal diet                                 | 5.85%           | 2.20%           | 736             | 276             |
| Error in substituted diets                    | 2.73%           | 1.35%           | 343             | 171             |
| DM intake or excreted, GE faeces              | 7.33%           | 3.67%           | 920             | 460             |

GE, gross energy.
158

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Table 8.5. Composition and nutritional value of raw materials commonly used for rabbits
(data in g kg−1, as-fed basis).
DM

Ash

Cereals
Barley
880 22
Maize
880 12
Oats
880 26
Triticale
880 18
Wheat
880 16
Cereal by-products
Maize gluten feed
900 67
DDGS
900 60
Malt sprouts
900 61
Rice bran
900 90
Wheat bran
880 50
Wheat feed
880 40
Wheat shorts
880 36
Other energy concentrates
Beet molasses
750 86
Cane molasses
750 98
Cassava 60
880 57
Cassava 65
880 57
Cassava 70
880 35
Glycerine
900 45
Legume and oil seeds
Faba bean
880 33
Lupin
880 35
Peas
880 30
Rapeseed
900 41
Soybean
900 47
Oil meals
Coconut cake
900 60
Palm cake
900 40
Rapeseed meal
900 68
Soybean meal 44
900 68
Soybean meal 46
900 63
Soybean meal 48
900 61
Sunflower meal 28
900 68
Sunflower meal 32
900 68
Sunflower meal 36
900 68
Oils and fats
Animal fat
995
–
Olein
995
–
Rapeseed oil
995
–
Soybean oil
995
–
Sunflower oil
995
–
Fibrous feedstuffs
Lucerne meal 12
900 90
Lucerne meal 15
900 99
Lucerne meal 18
900 99
Beet pulp
900 72
Cacao hulls
900 80
Carob meal
900 32
Citus pulp
900 67
Flax chaff
900 76
Grape pomace
900 81
Grape seed meal
900 36
Grass meal
900 80
Olive leaves
900 72
Rice straw
900 162
Soybean hulls
900 46
Sunflower hulls
900 34
Wheat straw
900 61
Wheat straw treated 900 73
Whole maize plant
900 36
(dehydrated)

CF

NDF

ADF

ADL

Soluble
fibre

ST

20 46
35 19
51 111
16 23
18 22

175
95
280
125
110

55
25
135
31
31

9
5
22
9
9

25
1
32
11
3

510
640
370
570
600

25
15
15
30
25

215
43 78
253
90 81
232
19 126
135 153 81
150
34 95
140
40 50
158
36 70

312
316
378
211
405
271
326

94
89
139
101
118
77
100

12
12
18
36
35
24
27

63
66
30
11
1
29
34

180
105
110
270
190
270
240

105
45
26
26
26
–

–
–
124
95
80
–

–
–
77
68
50
–

–
–
21
20
14
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109
137
48
24
7
–

257
13 77
326
70 128
220
12 57
189 396 81
369 193 56

123
210
120
181
117

89
155
70
124
73

8
15
4
49
8

202
147
361
432
450
468
279
306
342

74
84
25
18
18
18
27
23
19

125
178
121
77
63
50
252
225
180

447
605
277
161
132
124
428
383
306

235
372
189
100
82
65
302
270
216

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153
180
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164
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59
102
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122
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32
72

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20
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12
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25

297
261
216
180
183
78
133
315
280
441
225
200
295
355
468
395
365
126

475
418
346
428
390
289
220
455
560
730
460
455
585
588
693
750
694
360

CP

103
82
106
110
108

EE

–
–
7
7
7
4

–
–
48
44
31
–

Met SAA

Thr

Ca

3.9
2.3
4.4
3.9
3.3

1.7
1.7
1.9
1.9
1.8

4.2
3.5
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5.1
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2.4
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1.4

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650
700
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470
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853

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1
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0.3
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1
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0.7
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4.2 9.2
5.2 11.4

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80
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10

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168
209
240
216
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21
100
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114
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30
60
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424
230
–
20
–
80
90
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20

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6.6
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The continued demand for high standards of quality in meat production call for the development of new tools capable of meeting such demands. The quality of rabbit meat largely depends upon the rabbit’s nutrition. Most research conducted in recent years on rabbit meat quality has focused on incorporating bioactive compounds in meat using different feeding strategies. The influence of different dietary factors on meat quality and safety are discussed in this chapter.

9.1 Rabbit Meat Quality

9.1.1 Definition of meat quality

Meat quality consists of: (i) nutritional properties, such as appropriate proportions of bioactive compounds, proteins, lipids and their essential sub-constituents; (ii) sensory characteristics, such as appearance, texture and flavour; (iii) health, which depends on fat and saturated fatty acid (SFA) content; and (iv) technological factors, such as processing. It also includes the consumer’s perception of animal rearing conditions in relation to animal welfare, the impact of animal production on the environment and food safety.

Rabbit meat consumption depends heavily on cultural, traditional and religious beliefs. Rabbit meat production is strongly developed in Mediterranean countries of the European Union. Meat sensory properties are crucial in the consumer’s choice. Traditional consumers consider rabbit meat to have positive sensory properties, being tender, lean and with a delicate flavour (Dalle Zotte, 2002). Hedonistic quality differs from standard aspects and depends on the various types of meat presentation. In traditional markets rabbits are sold as a whole carcass and retail cuts. The current market, however, and younger consumers in particular, is more concerned with the way a product is presented. Rabbit meat could gain commercial acceptance if sold fresh and in ready-to-cook- and-serve retail packs, and if packaging systems were competitive.

Consumer demand is now more influenced by growing concerns with the healthiness of the meat. Other issues more widespread in the developed world include residues and contaminants. Because the wholesomeness of rabbit meat is becoming an indispensable requirement for consumers, rabbit meat quality chain managers must become more willing to certify their product and guarantee traceability ‘from farm to fork’.

Although all of the above factors are very important for the consumer, cost is perhaps the most critical. The lack of
increased meat consumption in developed countries now creates fierce competition between several meats. In this sense, because rabbit meat is more expensive than other ‘white meats’, its consumption may increase if efforts are made to inform the public of its high nutritional and dietetic properties while increasing its serviceability and preservability.

### 9.1.2 Nutritive value

Rabbit meat offers excellent nutritive and dietetic properties (see reviews by Combes, 2004; Dalle Zotte, 2004; Combes and Dalle Zotte, 2005; Hernández and Gondret, 2006). It is a lean meat that is rich in protein. The leanest portion is the loin and the fattest is the foreleg, with average lipid contents of 1.8 and 8.8 g 100g⁻¹, respectively. Rabbit meat offers a moderately high energy value, even if this depends primarily on its high protein content, which accounts for 0.80 of the energy value (Table 9.1).

Along with high protein content, rabbit meat also contains high levels of essential amino acids (EAAs). Compared to other meats, it is richer in lysine (2.12 g 100g⁻¹), sulphur-containing amino acids (1.10g 100g⁻¹), threonine (2.01g 100g⁻¹), leucine (1.73g 100g⁻¹) and phenylalanine (1.04g 100g⁻¹). This elevated and balanced EAA content together with easy digestibility give rabbit meat proteins a high biological value. Furthermore, rabbit meat does not contain uric acid and has a low purine content (Hernández, 2007).

The meat is an important source of B vitamins. The consumption of 100g of rabbit meat provides around 0.21 of vitamin B₆ and 0.77 of daily vitamin B₁ requirements. With respect to vitamin B₁₂, ruminants and rabbits are a much richer source than other meats, and the consumption of 100g of rabbit meat provides three times the daily recommendation of vitamin B₁₂ (Combes and Dalle Zotte, 2005). The vitamin E content of rabbit meat depends on the rabbit’s diet; it can be increased by >50% with extra dietary supplements (Castellini et al., 2000).

Like other white meats, rabbit meat contains low levels of iron (1.3 and 1.1mg 100g⁻¹ for the hind leg and loin, respectively; Dalle Zotte, 2004) and zinc (0.55 and 1.1mg 100g⁻¹ in the carcass and hind leg, respectively; Lombardi-Boccia et al., 2005; Hermida et al., 2006). Because the haem iron in meat is easily absorbed, rabbit meat can also contribute to meeting human requirements.

Rabbit meat is characterized by its low sodium content (37 and 49.5mg 100g⁻¹ for the loin and hind leg, respectively), which makes it particularly appropriate for those with hypertension. Conversely, rabbit meat is rather rich in phosphorus (222 and 234mg 100g⁻¹ for the loin and hind leg, respectively; Dalle Zotte, 2004). Poultry, pig and lamb meat have lower phosphorus contents, at

| Table 9.1 - Chemical composition and energy value of rabbit meat portions (g 100g⁻¹, unless otherwise stated) (adapted from Combes and Dalle Zotte, 2005). |
|---|---|---|---|---|
| Fore leg | Loin (m. longissimus dorsi) | Hind leg | Carcass |
| Average ± SD | Average ± SD | Average ± SD | Average ± SD |
| Water | 70 ± 1.3 4 | 75 ± 1.4 24 | 74 ± 0.8 33 | 70 ± 2.6 6 |
| Protein | 19 ± 0.4 3 | 22 ± 1.3 21 | 22 ± 0.7 31 | 20 ± 1.6 6 |
| Lipid | 9 ± 2.5 4 | 2 ± 1.5 24 | 3 ± 1.1 36 | 8 ± 2.3 6 |
| Ash | -- -- | 1 ± 0.1 14 | 1 ± 0.5 20 | 2 ± 1.3 4 |
| Energy (kJ 100g⁻¹) | 899 ± 47 2 | 603 1 | 658 ± 17 7 | 789 ± 106 3 |

SD, standard deviation.

*a Number of studies considered.
200, 174 and 147–194 mg 100 g−1, respectively (Williams, 2007). The selenium levels of rabbit meat vary widely according to dietary selenium supplementation, ranging from 9.6 µg 100 g−1 in non-supplemented diets to about 39.5 µg 100 g−1 with a supplementation of 0.50 mg kg−1 feed (Dokoupilová et al., 2007). According to Rayman (2004), 140 g of meat of selenium-fed rabbits would meet the recommended selenium daily intake for adults.

Meat is a major source of SFAs and cholesterol and its consumption can have a negative influence on health (Valsta et al., 2005). Nutritionists recommend not only limiting fat intake, but also consuming large amounts of polyunsaturated fatty acids (PUFA), especially n-3 rather than n-6 PUFA. Current recommendations state that the n-6:n-3 ratio in human diets should be <4.0. Rabbit meat has a higher PUFA content (0.27–0.33 of total fatty acid) than other meats (Table 9.2). C18:2 n-6 is a major fatty acid in rabbit meat, derived entirely from the diet. It represents 0.22 of total fatty acids. C18:3 n-3 is also an essential fatty acid and it is very abundant in rabbit meat, accounting for 0.03 ± 0.015 total fatty acids (this compares with 0.014 in lamb, 0.010 in pork and 0.001–0.023 in beef; Enser et al., 1996). Rabbit meat contains significant proportions of long-chain (C20–22) PUFA. Important PUFA are C20:4 n-6, C20:5 n-3 (eicosapentaenoic acid, EPA) and C22:6 n-3 (docosahexaenoic acid, DHA), which all play various metabolic roles. Rabbit meat possesses a fairly high n-6:n-3 ratio, at 5.1, 10 and 6.6 for the loin, hind leg and carcass, respectively.

Rabbit meat contains the lowest cholesterol levels (47.0 and 61.2 mg 100 g−1, for the loin and hind leg, respectively; Table 9.2) of all the most popular meats (60, 74 and 81 mg 100 g−1 in beef, turkey and chicken, respectively; Dalle Zotte 2004).

### 9.1.3 Sensory properties and processing characteristics

In the sensory map made by Rødbotten et al. (2004) comparing meat from 15 commercial animal species, rabbit meat was ranked among the most tender, together with lamb, roe deer, moose, hare and chicken. The sensory map assigned rabbit meat coarseness similar to that of the hare, lamb and roe deer. Rabbit meat was considered the meat with the least colour, odour intensity and odour attributes (sweet, metallic, liver, gamy), flavour intensity and flavour attributes such as sweet, liver and gamy (just after chicken, turkey and pork). Rabbit meat was also ranked with the lowest fatty feeling in the mouth and its juiciness was ranked medium-low as a result.

In addition to the general descriptors listed above, the sensory analysis of rabbit meat considers other specific descriptors.

| Table 9.2. Relative proportions of different types of fatty acids (proportion of total fatty acid) and cholesterol content (mg 100 g−1) of rabbit meat portions (adapted from Combes and Dalle Zotte, 2005). |
|-----------------|-----------------|-----------------|-----------------|
| **Loin (m. longissimus dorsi)** | **Hind leg** | **Carcass** |
| **Average ± SD** | **No. a** | **Average ± SD** | **No. a** | **Average ± SD** | **No. a** |
| SFA | 0.39 ± 0.048 | 17 | 0.39 ± 0.055 | 18 | 0.41 ± 0.016 | 4 |
| MUFA | 0.28 ± 0.044 | 17 | 0.28 ± 0.036 | 17 | 0.32 ± 0.24 | 4 |
| PUFA | 0.33 ± 0.067 | 17 | 0.32 ± 0.084 | 17 | 0.27 ± 0.020 | 5 |
| EPA | 0.002 ± 0.0013 | 10 | 0.001 ± 0.0002 | 11 | 0.0001 ± 0.00003 | 2 |
| DHA | 0.004 ± 0.0034 | 10 | 0.002 ± 0.0027 | 10 | 0.0001 ± 0.00001 | 2 |
| n-6:n-3 | 5 ± 2.2 | 10 | 10 ± 3.7 | 13 | 7 ± 1.3 | 4 |
| Cholesterol | 47.0 ± 7.9 | 5 | 61 ± 5.2 | 17 | 55 ± 18.5 | 3 |

DHA, docosahexaenoic acid; EPA, eicosapentaenoic acid; MUFA, monounsaturated fatty acid; PUFA, polyunsaturated fatty acid; SFA, saturated fatty acid.

aNumber of studies considered.
such as fibrousness, sticky, intensity of rabbit odour and flavour, aniseed odour and flavour, intensity of grass odour, overall appraisal (Carrilho et al., 2009) and off-flavour perception (rancid, freeze-burned) (Dalle Zotte et al., 2008). The latter study showed that the high intensity of rabbit flavour was considered positive by 0.72 of the panellists, and the off-flavour evaluation did not affect the rabbit flavour judgment.

The main sensory properties of meat are colour, juiciness, tenderness and flavour. Muscle pH and water-holding capacity (WHC) exert a high influence on the technological and eating quality of meat. The post-mortem evolution of pH and the pHu (pH measured at 24 h post-mortem) affects the brightness of meat, its WHC and toughness (Lawrie, 1998). In rabbits, the important factors affecting muscle pHu are identified as muscle type, age, slaughter method and carcass treatment post-mortem whereas, animal diet has a small effect (Dalle Zotte, 2002). In rabbits, pHu ranges between 5.4 and 6.4 depending on muscle location (Hulot and Ouhayoun, 1999). To date, the literature has not reported any abnormal post-mortem acidification kinetics characteristic of pale, soft and exudative or acidic meat in the rabbit. However, dark, firm, dry meat has been reported (Rodríguez-Calleja et al., 2005).

Meat colour is the most important factor affecting consumer acceptance and purchasing decisions. Rabbit meat colour has primarily been instrumentally measured using the CIE colour system (CIE, 1976). The three fundamental colour coordinates are L* (lightness), a* (redness) and b* (yellowness). Mean L*a*b* colour values of the rabbit longissimus dorsi (LD) muscle are L*= 56–60, a* = 2.6–3.4 and b* = 4.0–5.0 (Dalle Zotte, 2004). The main colour variability factors are the type of muscle (muscle energy metabolism and contractile properties), muscle pHu and myoglobin content (Ouhayoun and Dalle Zotte, 1993), age and diet of the rabbits (Dalle Zotte et al., 1996) and even the activity undertaken by the animal (Gondret et al., 2009). Compared to white meat species (pork, turkey and chicken) and when evaluating similar muscles (breast white muscle in poultry), rabbit meat rates first in lightness and third in redness after pork and turkey (Dalle Zotte, 2004; Molette et al., 2005).

The WHC determines the juiciness of meat, and is defined as the ability of meat to retain its water during the application of external forces such as cutting, heating, grinding or pressing. As previously mentioned, meat WHC is greatly affected by pH. Drip loss is defined as the loss of fluid from meat cuts by the shrinkage of contractile muscle proteins in the form of drip. A rapid pH fall or a lower pHu tends to cause protein denaturation and greater drip loss. Karakaya et al. (2006) compared the WHC and the cook loss of mutton, goat, beef and rabbit ground meat, and observed a lower WHC in rabbit and beef meat (about 0.22) than in mutton and goat meat (0.41–0.46). Cook loss, however, did not vary much among the four species compared (around 0.34). Several other studies on rabbit LD muscle have indicated a higher WHC (0.33) (Pla and Cervera, 1997; Martinez et al., 2005) than that found by Karakaya et al. This is still lower, however, than that of chicken meat fillet (about 0.44). Cook loss is the most widely used variable for estimating WHC in rabbit meat. According to the meat cuts considered, cook loss varies from 0.205 in the hind leg to 0.271 in the loin (Dalle Zotte, 2007; Combes et al., 2008; Dalle Zotte et al., 2009).

Tenderness can be measured instrumentally by Warner-Bratzler shear force testing (WBSF) and texture profile analysis testing. Meat tenderness depends mainly on the post-mortem changes affecting myofibrillar proteins and the connective tissue (collagen content and solubility), which represents the ‘background’ toughness. Although information on collagen content and its solubility in rabbit meat is scarce, high collagen solubility has in any case been documented (0.75 ± 0.081 as a proportion; Combes, 2004) because of the young slaughter age of rabbits (10–11 weeks). Therefore, the myofibrillar component represents a more important factor than connective tissue characteristics in influencing rabbit meat tenderness. WBSF
values of rabbit meat are quite low at 2.4 ± 1.6 kg cm\(^{-2}\), and the meat of the loin (2.9 kg cm\(^{-2}\)) is tougher than that of the hind leg (0.94 kg cm\(^{-2}\)) (Dalle Zotte, 2007; Dalle Zotte et al., 2009). In addition, an improvement in meat tenderness in rabbit loins after 7 days of aging has been observed by several authors (Gil et al., 2006; Hernández and Pla, 2008).

### 9.1.4 Rabbit meat and its role as a functional food

In recent years, much attention has been paid to the influence of diet on human health and well-being. The principal function of the diet is to provide the nutrients required to satisfy the nutritional needs of an individual. Some food and food components have physiological and psychological effects beyond the contribution of basic nutrients (Jones and Jew, 2007). These are called functional foods.

In the case of meat, the object of including functional ingredients is not only concerned with providing meat with certain desirable properties, but also attempts to change its image in these health-conscious days. Indeed, meat is a major source of SFAs and cholesterol and its consumption could be related to cardiovascular disease, hypertension, obesity and diabetes (Valsta et al., 2005). However, different strategies can be effectively used to increase or reduce bioactive compounds in order to produce functional meat and meat products (for a review, see Jiménez-Colmenero et al., 2006).

Rabbit meat, as has been previously discussed, is a lean meat rich in proteins of high biological values, with highly unsaturated lipids and low cholesterol content. Moreover, rabbit meat consumption could become a good way to provide these bioactive compounds to human consumers, since manipulation of the rabbit diet is very effective in increasing the levels of n-3 PUFA (Kouba et al., 2008; Tres et al., 2008), conjugated linoleic acid (CLA) (Corino et al., 2002, 2003), or vitamin E (Castellini et al., 1999) as will be discussed later.

### 9.2 Influence of Dietary Factors on Meat Quality

#### 9.2.1 Effect of dietary energy and feed restriction

When feeding modifies growth potential it also modifies carcass and meat quality. An efficient chemostatic appetite regulation mechanism makes daily energy intake constant, but this only occurs at >9.2 MJ digestible energy (DE) kg\(^{-1}\). The best meat production performance is obtained by feeding rabbits ad libitum with a DE concentration >10.45 MJ kg\(^{-1}\). Rabbits also require a certain fibre quantity, however, and this limits high DE intake.

Nutrient requirements change as rabbits age, and feeding plans have been developed accordingly. The influence of feeding plans on carcass and meat quality has not, however, been shown to have a great effect. Diets with a high energy content from post-weaning to slaughter have been found to lower the feed conversion ratio (FCR) significantly, enhance dissectible fat content and decrease pHu in the LD muscle, without noticeable variations in meat proximate composition or lightness (Dalle Zotte et al., 1996; Xiccato, 1999). Furthermore, muscle fibre type distribution and fibre cross-sectional area were not affected by the dietary energy level.

Although starch is the main dietary energy source in rabbit feed, it is hard to separate its effect on carcass and meat quality from that of other dietary components, particularly fibre. Increased starch levels usually decrease crude fibre and fibre fraction concentration. Dietary starch levels alone do not appear to affect rabbit carcass and meat quality significantly, apart from their role in increasing the diet’s energy concentration and thereby improving FCR. However, Xiccato et al. (2002) found that a starch level of 206 g kg\(^{-1}\) dry matter (DM) resulted in a higher slaughter yield, but also increased meat cook loss and WBSF. More recently, Carraro et al. (2007) did not observe any differences in carcass and meat quality after raising the starch level from 120 to 180 g kg\(^{-1}\).
Sartori et al. (2003) found that phase feeding programmes with an increasing dietary starch to acid detergent fibre (ADF) ratio from 0.8 in the post-weaning period to ≥1 during the fattening period, implemented for the purpose of reducing post-weaning digestive disorders, did not affect slaughter yield, carcass adiposity, meatiness or m. biceps femoris lightness. For the same purpose, two digestible fibre to ADF ratios were tested (1.0 and 1.3). Once again, growth performance and slaughter traits were unaffected (Carraro et al., 2007).

Feed restriction is becoming a common practice on rabbit farms, and is performed to reduce post-weaning digestive disorders and improve the FCR. Feed restriction can be quantitative in terms of level (proportion of restriction of the ad libitum intake) and length or qualitative (DE concentration <9.2 MJ DE kg⁻¹).

Regarding restriction levels, some studies have shown that when rabbits ingest <0.85 of the ad libitum diet, growth, feed efficiency, slaughter yield, carcass adiposity and lipid content can be seriously compromised. This intake level is therefore unsuitable for meat production (Dalle Zotte, 2002). Moreover, an 0.85–0.90 feed restriction from 4 weeks to slaughter increases lightness and cook loss and reduces redness in LD muscle (Metzger et al., 2008).

Feed restriction affects live performance, carcass yield and muscle to bone ratio variously according to restriction plans. When moderately feed-rationed post weaning, for example, rabbits show a large compensatory growth rate during the following more-liberal fattening period correlated with good global feed efficiency (Xiccato, 1999; Dalle Zotte, 2002). Moreover, the lowering of the pHu of the hind leg muscles of re-fed rabbits suggests an enhancement of the muscular glycolytic metabolic pathway. This feature was confirmed in a study by Dalle Zotte et al. (2005). Specifically, muscular glycolytic metabolism, slowed by feed rationing of 0.70 ad libitum from 5 to 8 weeks of age, was compensated for by subsequent re-feeding (0.90 ad libitum) from 8 to 11 weeks of age. Tůmová et al. (2006) tested different restriction plans from weaning to 3 weeks before slaughtering. Although restriction plans did not affect slaughter yield or meat pHu, late restriction (after 56 days of age) reduced rabbit loin and perirenal fat incidence. Not even 0.80 feed restriction from weaning to 60 days of age and 0.90 up to slaughter during the summer had a negative effect on carcass traits, meat pHu, WHC or proximate composition (Bovera et al., 2008). Together, these results show that the best performance is achieved by early feed restriction followed by ad libitum feed intake.

With current attempts to produce certified quality label rabbits characterized by slow growth and higher slaughter age, some producers feed rabbits with moderate restriction. Poorer live performance, carcass weight, yield and adiposity and less intramuscular fat content and proportion of oxidative fibres in LD muscle have been observed when food intake is restricted, even if these rabbits were 3 weeks older than the ad libitum rabbits when slaughtered (see the review of Dalle Zotte, 2002). A study by Larzul et al. (2004) showed that although carcass traits and meat composition are largely compromised by feed restriction, the sensory quality of the rabbit meat remains unaffected.

### 9.2.2 Effect of dietary fibre content

The relationship between energy content and digestible protein (DP) to DE ratios makes the fibre level a fundamental variable in rabbit diets. Because the rabbit’s feed intake capacity is a limiting factor, increasing dietary fibre content may lead to energy deficiency. The dilution of DE and feed restriction have common effects on both overall body growth rate and the relative growth of tissues and organs and body composition. Diets with high fibre levels invariably decrease growth rates, but when such a rate is unimpaired by fibre increase, the slaughter yield remains the same (Ouhayoun, 1989). When a high dietary fibre level decreases the growth rate, slaughter yield falls due to increased digestive tract
proportions. Carcass adiposity and meat lipid content decrease, but water and protein contents rise. Comparing three diets with increasing crude fibre content (138, 163 and 198 g kg\(^{-1}\)) and decreasing energy level (10.2, 9.3 and 8.6 MJ DE kg\(^{-1}\)), Parigi Bini et al. (1994) observed no differences in slaughter yield, carcass meatiness or fatness; only the hind leg meat from rabbits fed a more fibrous diet was leaner and richer in water. Carrilho et al. (2009) performed a similar study, using three increasing levels of dietary crude fibre (143, 180 and 205 g kg\(^{-1}\) DM) with decreasing energy levels (9.3, 9.1 and 8.0 MJ DE kg\(^{-1}\) DM). These three diets were fed to rabbits from 5 to 8 weeks of age, followed by a finishing diet until slaughter. No significant differences ascribed to diet were observed in instrumental (pHu, L\(^*\)a\(^*\)b\(^*\) colour, WHC, toughness) or sensory meat traits. Neither crude fibre dietary content nor the digestible fibre to ADF ratio appear to directly compromise carcass or meat quality. Even increasing dietary fibre levels during the last week of the fattening period does not seem to significantly impair slaughter traits or meat pHu (Margüenda et al., 2008; Villena et al., 2008).

9.2.3 Effect of dietary protein

The effects of dietary protein content on live performance, carcass and meat quality have been studied by modifying dietary protein concentrations (iso-energetic diets) or simultaneously varying protein and energy content. The former complicates extrapolating the real protein effect because changes in the DP to DE ratio reveal different protein intakes. Because the optimum level of protein with balanced EAAs increases with the dietary energy level, the latter simplifies the dietary protein effect calculation.

DP to DE ratios below optimum values of 10.5–11.0 g MJ\(^{-1}\) are insufficient to cover the daily protein requirements, and might therefore compromise the growth rate because muscular protein accretion is suboptimal. Animals might show low dissectible fat deposits due to delays in tissue development or elevated intracellular lipid accumulation caused by high energy levels. The decreased growth rate obtained in this way seems to enhance meat quality by limiting muscle glycolytic metabolism, and produces less lean meat with better WHC (see the reviews of Xiccato, 1999; Dalle Zotte, 2002).

Effects on carcass and meat quality with DP to DE ratios above the optimum value of 10.5–11.0 g MJ\(^{-1}\) have not been precisely established. Some authors have observed no variation in live performance or carcass and meat quality; others, however, have observed significant reductions in dissectible fat deposit only at very high DP to DE ratios (>12 g MJ\(^{-1}\)), together with worse live performance and meatiness with ratios >14 g MJ\(^{-1}\). In a 10.5–11.0 g MJ\(^{-1}\) DP to DE range, growth performance is high and remains in the range because protein intake permits the maximum expression of muscular protein synthesis. Meat water and nitrogen content tend to increase at the expense of fat content. Other meat qualities are unaffected at higher dietary DP to DE ratios (see reviews of Xiccato, 1999; Dalle Zotte, 2002).

The effect of lower DP to DE ratios (11.5 versus 12.5) on nitrogen output has been demonstrated by Maertens et al. (1998). In this DP to DE ratio range, whenever EAAs (lysine, sulphur amino acids and threonine) cover daily requirements, decreasing dietary protein content appears possible without compromising the zootechnical performance or carcass and meat quality. Reviewing protein-amino acid nutrition in rabbits, Carabaño et al. (2008) found that crude protein levels in commercial feeds currently exceed recommendations, especially in final growth phases. The authors suggested adopting protein levels of 140 g kg\(^{-1}\) from weaning to slaughter. If the DP to DE ratio is around 9.5 and the amino acid supply is correct, this level does not appear to impair growth performance.

Protein requirements change during growth, and growth can be compromised by an unbalanced dietary protein supply. Low-protein diets in early post weaning can, in
fact, cause low slaughter yield as a consequence of impaired growth. Compensative growth may produce leaner carcasses, however. In contrast, a high DP to DE ratio during early post weaning and onwards may increase carcass fat deposition and lipid content (see the review of Xiccato, 1999). The effects of dietary protein levels or specific dietary EAAs on the rheological and sensory properties and fatty acid profiles of rabbit meat have not yet been assessed.

9.2.4 Effect of dietary fat

Increasing the fat content of the diet improves its energy level and results in a higher DE intake and improved growth and feed efficiency (Maertens, 1998; Xiccato, 1999; Dalle Zotte, 2002). The level and source of fat in the diet can have different impacts on carcass and meat quality. A low or moderate addition of fat (20–60 g kg\(^{-1}\)) increases carcass yield (Castellini and Battaglini, 1992) and the amount of dissectible fat (Fernández and Fraga, 1996). An increase in dietary fat over these values (>90 g kg\(^{-1}\)) may impair carcass quality due to an excess of carcass adiposity (Pla and Cervera, 1997). However, higher dietary fat inclusion may also increase the meat lipid content (Pla and Cervera, 1997), increasing meat quality as a consequence of the influence of muscular fat content on sensory characteristics such as juiciness and tenderness.

The composition of dietary fat, as a result of the use of various fat sources, can modify the fatty acid composition of different rabbit tissues. It is well known that rabbits, and other non-ruminants, are able to incorporate dietary fatty acids into adipose and muscle tissue lipids. The effect of various dietary fat sources has been the subject of many experiments, which are discussed in this review.

Changes in the n-3 and n-6 fatty acid profile

The lipid fraction has considerable implications on health. The recommendation to increase consumption of PUFA, particularly n-3 PUFA, is based on its role on the development and prevention of cardiovascular disease, atherosclerosis and other diseases (Goodnight, 1993; Simopoulos, 2002). Much research has been carried out on modifying the nutritional value of meat through animal diets.

The addition of vegetable fat compared to animal fat sources in the diet leads to differences in rabbit meat quality, especially regarding the fatty acid composition of the tissues and meat flavour. For instance, sensory test panels attribute a higher ‘liver’ taste to animals fed with an animal fat diet, while meats of animals fed with a vegetable diet have a higher ‘aniseed’ or ‘grass’ flavour. However, no differences between groups have been found for texture parameters (Oliver et al., 1997; Hernández et al., 2000).

The dietary use of linseed in its different forms (oil, extruded, whole) has been proposed by many authors as a way to raise the content of n-3 PUFA and reduce the ratio n-6 to n-3 PUFA. Dal Bosco et al. (2004) studied the synergistic effect of dietary α-linolenic acid and vitamin E on the oxidative stability and nutritional and eating characteristics of fresh and stored rabbit meat. The ability of rabbits to synthesize long-chain PUFA (EPA and DHA) from the dietary precursor, leading to an increase in the n-3 PUFA content of the meat of rabbits consuming the n-3 diet, without any alteration of oxidative stability and sensory quality of the meat was confirmed. Tres et al. (2008) evaluated the effects of replacing beef tallow added to rabbit feeds with different levels (0, 15 and 30 g kg\(^{-1}\)) of n-6- or n-3-rich vegetable sources (sunflower and linseed oil, respectively). The level and source of the fat added influenced meat fatty acid composition, modifying the n-6 to n-3 PUFA ratio, which was more nutritionally favourable when linseed oil was used (Table 9.3). However, carcass and meat quality may be affected as a consequence of the PUFA increase, although diets enriched with 30 g kg\(^{-1}\) of sunflower or linseed oil and 100 ppm of
α-tocopherol acetate have been found to have small effects on rabbit carcass characteristics. Retail cuts, lightness and yellowness were the most affected traits (Pla et al., 2008). A small effect on instrumental texture properties was also found, but there was no negative effect on sensory characteristics (Hernández and Pla, 2008).

Extruded linseed has also been used to improve the nutritional value of rabbit meat (Gigaud and Combes, 2008; Kouba et al., 2008; Maertens et al., 2008), leading to a decrease in the n-6 to n-3 ratio. Bianchi et al. (2006) studied the influence of dietary use of whole linseed at different proportions (from 0 to 80 g kg⁻¹) and supplemented with α-tocopherol acetate (200 mg kg⁻¹ feed) on rabbit meat quality, also finding a decrease in the n-6 to n-3 PUFA ratio with the linseed diet supplementation. The increase of the PUFA content produced by the dietary use of linseed could lead to oxidation and a reduction in the shelf life of the meat (Monahan, 2000). Therefore, supplementation with antioxidants such as α-tocopherol acetate is required in these experiments.

Alternative dietary sources of n-3 PUFA for rabbit production have been studied. Supplementation of rabbit diets with false flax (*Camelina sativa* L.) seeds (Peiretti et al., 2007) or chia (*Salvia hispanica* L.) (Peiretti and Meineri, 2008) has been successful in increasing PUFA content and reducing the n-6 to n-3 PUFA ratio, without significant adverse effects on growth performance and carcass characteristics. Grass-based diets can also modify the fatty acid composition of rabbit meat, enhancing the n-3 fatty acid content (Forrester-Anderson et al., 2006).

Other strategies for specifically increasing long-chain fatty acids such as EPA and DHA are based on the dietary use of fish oils or algae. A high increase of specifically long-chain PUFA can be achieved by feeding rabbits diets enriched with fish sources, such as herring meal (Castellini and Dal Bosco, 1997) or fish oil (Bernardini et al., 1999; Kowalska, 2008). However, high levels of lipid oxidation, lower growth and impaired carcass and meat quality may result, depending on the fish oil used (Navarrete et al., 2007).

**Conjugated linoleic fatty acid**

CLA has also received a great deal of attention as a supplement in rabbit feed. CLA is a mixture of positional and geometric isomers of linoleic acid (18:2, n-6) with conjugated double bonds. It has been reported to have a wide range of beneficial effects, including anticarcinogenic (Kelley et al., 2007), antithrombogenic (McLeod et al., 2004) and antiobesity (Whigham et al., 2007) activities.

Food sources that originate from ruminants are known to have markedly higher CLA concentrations than those from monogastric animals (Schmid et al., 2006). Non-ruminants are unable to synthesize CLA, and the CLA present in their meat therefore comes from the diet. In addition, rabbits are able to recycle part of their end microbial fermentation products through caecotrophy, so that the amount of CLA retained in their meat might be higher than in other non-ruminant species (Gómez-Conde et al., 2006).

Dietary CLA inclusion is an effective tool for increasing, in a dose-dependent manner, the amount of CLA in the intramuscular lipids of rabbits, with cis-9, trans-11 being the predominant isomer (Lo Fiego et al., 2005; Petacchi et al., 2005). It is

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**Table 9.3.** Effect of the source and dose of unsaturated fat used to replace beef tallow in feeds on the content of n-6 and n-3 fatty acids in raw meat (adapted from Tres et al., 2008).

<table>
<thead>
<tr>
<th></th>
<th>30 g BT kg⁻¹</th>
<th>15 g SO + 15 g BT kg⁻¹</th>
<th>30 g SO kg⁻¹ BT kg⁻¹</th>
<th>15 g LO + 15 g BT kg⁻¹</th>
<th>30 g LO kg⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ratio PUFA:SFA</td>
<td>0.6</td>
<td>1</td>
<td>1.5</td>
<td>1</td>
<td>1.5</td>
</tr>
<tr>
<td>Ratio n-6:n-3</td>
<td>7.4</td>
<td>12.0</td>
<td>16.9</td>
<td>1.8</td>
<td>1.1</td>
</tr>
</tbody>
</table>

BT: beef tallow; LO: linseed oil; PUFA: polyunsaturated fatty acid; SFA: saturated fatty acid; SO: sunflower oil.
possible to increase the CLA content in rabbit loin from 1.3 to 10.4 mg 100 g−1 meat with a 5 g kg−1 supplementation of CLA in the diet (Corino et al., 2007).

In addition to the beneficial effects of CLA on human health, CLA can favourably modify the rabbit’s body composition (Corino et al., 2002, 2003) due to its potential to increase lean tissue deposition. The effect of dietary CLA inclusion depends not only on the extent and dose of CLA supplementation, but also on the animal’s age (Corino et al., 2002, 2003). Rabbit growth performance and carcass characteristics at standard slaughter weight (2.5 kg, 76 days) were not affected by diets supplemented with 2.5 or 5 g CLA kg−1. However, CLA supplementation reduced perirenal fat weight at a heavy slaughter weight (3.1 kg) and lowered the concentration of serum triglycerides and total cholesterol (Corino et al., 2002). Regarding the chemical composition of rabbit meat, a significant decrease in meat lipid content was evident only when rabbits were fed with a high supplementation level of CLA (5 g kg−1) and at heavy slaughter weight (3.1 kg; Corino et al., 2003).

9.2.5 Antioxidants

Rabbit meat has a high content of PUFA, which may lead to oxidation problems. In addition, there has been increasing interest in the use of antioxidants in rabbit feed formulae because the dietary manipulation of tissue lipid composition to produce meat with a high PUFA content may decrease meat oxidative stability. Lipid oxidation is a major non-microbial factor responsible for the quality deterioration of muscle foods. It leads to discoloration, higher drip loss, the development of off-odours and off-flavours and loss of nutritional value (Monahan, 2000).

Vitamin E is commonly used in animal feed for their antioxidant activity. Hernández and Gondret (2006) reviewed the use of vitamin E in the rabbit diet. In recent years various studies have examined the influence of the addition of α-tocopherol acetate to the diet on the deposition of α-tocopherol in tissues, meat quality characteristics, oxidative stability and the shelf life of rabbit meat. Several authors have shown that the deposition of α-tocopherol in rabbit muscle is very efficient and has a strong relationship with the dose supplemented in the diet (Dal Bosco et al., 2001; Lo Fiego et al., 2004). For instance, the addition of 100 mg α-tocopherol acetate kg−1 of feed increases the content of α-tocopherol in rabbit meat by threefold (Tres et al., 2008). These authors also found that cooking reduces α-tocopherol in rabbit meat by 9%. However, the α-tocopherol level of cooked meat depends on the cooking method, with the resistance of vitamin E higher for fried and roasted meat than for boiled meat (Dal Bosco et al., 2001).

Vitamin E is effective in reducing lipid oxidation of rabbit meat during refrigerated or frozen storage (Castellini et al., 1999; Lo Fiego et al., 2004) and also after cooking (Castellini et al., 1999; Tres et al., 2008). Dietary α-tocopherol acetate supplementation has been found to stabilize the colour of raw meat (Corino et al., 1999). In addition, a high α-tocopherol level improves some physical traits of meat, reducing shear values and increasing WHC (Castellini et al., 1998). The effect of synergetic supplementation of the diet with vitamins C and E has been found to increase vitamin content and reduce lipid oxidation (Castellini et al., 2000; Dalle Zotte et al., 2000; Lo Fiego et al., 2004).

Various natural ways of improving the oxidative stability of rabbit meat have also been studied. For example, lipid oxidative stability has been improved by increasing the level of oats in the rabbit diet (López-Bote et al., 1998). Coni et al. (2000) verified the antioxidant efficiency of extra-virgin olive oil and oleuropein, an olive oil biphenol, in rabbit plasma and isolated low-density lipoproteins. However, oleuropein does not appear to reduce meat susceptibility to oxidation (Paci et al., 2001). Supplementation of the rabbit diet with essential oil of oregano has been found to
improve the oxidative stability of muscle tissues (Botsoglou et al., 2004).

9.3 Influence of Diet on Rabbit Meat Safety

Food safety is an important issue for consumers, especially in the meat sector. Major meat safety issues and related challenges include microbial pathogens, food additives and chemical residues.

Safety and the shelf life of meat are limited by microbial growth. Dominant contaminants on carcasses and packed rabbit meat are Pseudomonas, lactic acid bacteria, yeasts and Brochothrix thermosphacta (Rodríguez-Calleja et al., 2004) with total bacteria counts between 4.01 and 4.96 log cfu g⁻¹. However, components of the feed may play a specific role in the growth rate of some microbial groups, affecting the microbiological characteristics of carcass and rabbit meat. Vannini et al. (2003) showed that a dietary supplementation of whole linseeds limited the growth rate of several microbial groups (except psychrotrophic bacteria), with a consequent increase in meat shelf life. In addition, high percentages of dehydrated lucerne meal in the diet seem to have an inhibiting effect on microbial growth in rabbit meat products (Vannini et al., 2002). Dietary fibre can affect the microbial ecology of rabbit meat. The source and level of dietary fibre has a major impact in controlling the digestive content. The rabbit gastrointestinal content represents a main concern at the slaughterhouse because of its impact on carcass yield, potential microbial contamination of meat and the cost of offal withdrawal (Villena et al., 2008). Margüenda et al. (2008) studied the effect of dietary type and level of fibre on carcass yield and its microbiological quality. They showed that a decrease in dietary fibre (from 350 to 320 g neutral detergent fibre kg⁻¹), when sources of insoluble fibre are included, enhances carcass yield and improves microbiological quality. For the same level of fibre, including 100 g beet pulp kg⁻¹, there was an improvement in the microbiological characteristics of the rabbit carcass without affecting the carcass yield. In addition, an increased level of dietary fibre may reduce muscle glycogen content in rabbits by increasing the pH of the meat, which could have an impact on the meat shelf life (Gierus and Teixeira, 1997). However, Villena et al. (2008) found no relationship between the level of fibre in the diet and the final pH of the meat.

The effect of dietary oregano essential oil supplementation on microbial growth of rabbit carcasses has now been studied (Soultos et al., 2009). The incorporation of oregano essential oil in the diet at the level of 100–200 mg kg⁻¹ had no detrimental effects on rabbit performance and had an inhibitory effect on the microbial growth of carcasses during refrigerated storage.

The composition, quality and contamination of fat materials used in animal feed are of considerable importance in assessing the quality and safety of meat production. The level of polycyclic aromatic hydrocarbons (PAHs) in rabbit tissues and their rate of transfer from feed have been studied by Devier and Budzinski (2007). PAHs were not detected in meat or liver, even when extremely high total concentrations, from 1 to 4 mg g⁻¹, were present in the feeds, confirming the high capacity of animals to rapidly metabolize these contaminants. However, PAH metabolites are more toxic than the corresponding PAH. When the contents of PAH corresponding to those usually found in fat by- and co-products were assayed, no PAH metabolites were found.

Ábalos et al. (2007) studied the presence of dioxins (polychlorodibenzo-p-dioxins and dibenzofurans, PCDD/Fs) and ‘dioxin-like’ polychlorinated biphenyls (DL-PCBs) in rabbit and chicken meat samples from animals fed with fish oil spiked with different levels of contaminants. Three different levels of contaminants under the maximum quantity allowed by the European Union Directive (Commission Directive 2006/13/EC of 3 February, 2006) were tested. The profile of PCDD/Fs in chicken samples from the three different treatments resembled the profile previously observed in the
corresponding feeds. Generally, the levels of the different compounds increased when increasing their amount in the feed. In rabbit meat samples, however, different bioaccumulation behaviour was observed. The profile of PCDD/Fs in rabbit meat did not correspond to that present in feeds. In fact, there were no significant differences in PCDD/F toxicity among rabbit samples from the three different treatments. For DL-PCBs, the profile was similar between feeds and meat samples, both in chickens and rabbits.

References


10 Nutrition and Feeding Strategy: Interactions with Pathology

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10.1 Introduction

Nutrition and feeding strategies play a key role in rabbit breeding, not only to optimize production itself (e.g. meat, milk, fur), but also to prevent various pathologies through: (i) the presence of toxic compounds in the feeds or utilization of unbalanced diets; and (ii) the presence of pathogenic agents (viruses, bacteria, parasites) in feeds or drinking water. This last aspect is not considered in this chapter since it does not cover nutrition directly, but is rather a question of feeding management and hygiene. Similarly, the presence of undesirable pesticides in feed ingredients can impair rabbit health. Very few specific data are available for rabbits in production conditions, and so this aspect is also not considered here; readers can consult more specialized books devoted to this aspect of animal feeding.

In this chapter, it is assumed that some effort has been made to provide the daily minimum requirements for the main individual components such as energy, protein and amino acids, minerals and vitamins, as recommended in other chapters. Nevertheless it is generally difficult to provide all nutrients and energy exactly at the optimum level and, as a consequence of the composition of available raw materials, it is necessary to accept an excess or imbalance in some components to ensure that the minimum of other nutrients is met.

By itself, an imbalance should only be responsible for low performance, not for health troubles if the breeding conditions are good. For example, in controlled experimental conditions, a diet containing only 60 g fibre kg\(^{-1}\) dry matter (DM, as acid detergent fibre, ADF) does not induce digestive trouble (Davidson and Spreadbury, 1975). A similar situation has been observed with diets containing up to 280–300 g crude protein (CP) kg\(^{-1}\) (Lebas, 1973). Such imbalances only induce a higher susceptibility of rabbits to problems, mainly digestive disorders, and the above extreme levels must never be recommended for practical feeding. One of the objectives of this chapter is to indicate the rules, when known, that are able to minimize the risk of disorders and some give ideas on ‘acceptable’ imbalances in everyday feeding practice.

In addition to imbalance problems, absolute excess of ingredients such as some minerals (e.g. phosphorus) or vitamins (e.g. vitamin D), can be toxic independently of the health status of rabbits. The only question is – when does a nutrient supplied above the recommended minimum or optimum become toxic?

The present chapter therefore considers health troubles (mainly digestive) linked to the balance of dietary components and the presence of nutrients in excess, mainly in relation to the initial composition of feed.
ingredients. The first part will consider feeding strategies, particularly the control of feed intake for the young rabbit to reduce post-weaning digestive troubles. The second part will cover the health consequences of non-nutritional components that are frequently associated with feed ingredients, such as mycotoxins. And the final part will be devoted to water quality, since water is also able to induce nutritional disorders when certain soluble components are too concentrated.

10.2 Methods to Estimate Health Status and Measure the Risk of Digestive Troubles

A common indicator used to evaluate the impact of a disease in breeding is the mortality rate. More recently, a morbidity indicator has been developed for the growing rabbit to more precisely assess the incidence of clinical symptoms (Gidenne, 1995), and it may be combined with mortality to obtain the health risk index (HRi = morbidity + mortality rate). This approach allows a more precise assessment of health status. However, these traits show large variations according to many factors. For instance, the mortality rate of rabbits fed the same diet may range from 0% up to 70% according to various factors, such as litter effect, preventive medication, age at weaning and the sanitary and immune status of the animals. This means that a large number of animals is required to detect a significant difference in mortality between two treatments. For instance, to detect a difference between two mortality rates of 5%, >300 animals are required in each group (Table 10.1).

When the clinical symptoms (e.g. diarrhoea, caecal impaction, borborygmus), are clear, the morbidity rate is relatively easy to measure. However, when only a reduction in growth rate is detectable, a threshold must be defined to class the animal as morbid or not, such as the average −2 × standard deviation (SD, signifying the 2.5% of the animals with a lower growth rate) or up to 3 SDs. However, a large set of rabbits within a group is required to precisely define the mean and its range of variation. Moreover, adequate statistical methods are necessary to treat discrete data (such as mortality or morbidity). For instance, when analysing models with more than one factor or including more than two levels (within a factor) or to test interaction among two factors, a specific categorical analysis based on a weighted least-square analysis must be used instead of a simple chi-squared test.

10.3 Problems Related to Major Nutrient Imbalances

Among the various health problems related to feeding, intestinal pathology and respiratory diseases are the predominant causes of morbidity and mortality in commercial rabbit husbandry. The first mainly occurs in young rabbits, after weaning (4–10 weeks of age), while the second preferentially affects adults. In France, enteritis in growing rabbits induced a mortality rate of 11–12% before the appearance of epizootic rabbit enteropathy (ERE) (Koehl, 1997). However, with general production cycles, mortality is currently around 8.5% (Lebas, 2008), but with frequent use of preventive antibiotherapy. Nevertheless, it may frequently exceed 15% and even reach up to 50%. Moreover, digestive disorders are responsible for important morbidity characterized by growth depression and poor feed conversion. These economic losses, less obvious than mortality, are often underestimated by rabbit breeders.

Table 10.1. Number of rabbits required per treatment to detect a significant difference \((P = 0.05)\) in the mortality rate between two treatments.

<table>
<thead>
<tr>
<th>Difference to be detected (%)</th>
<th>Number of rabbits required</th>
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<tbody>
<tr>
<td>5</td>
<td>338</td>
</tr>
<tr>
<td>10</td>
<td>87</td>
</tr>
<tr>
<td>15</td>
<td>40</td>
</tr>
<tr>
<td>20</td>
<td>23</td>
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Diagnosis of intestinal diseases is difficult because, whatever the cause (nutritional problems or a true specific illness), symptoms and lesions are generally similar. The difficulty in recognizing the aetiology for rabbit intestinal disorders is reinforced by the fact that, as for most diseases in humans or animals, several factors are involved in the development of enteritis and must be considered. The first is the status of the animal itself (age, genetics, immunity). The second concerns the pathogenic agents involved (parasites, bacteria, viruses). The third is represented by environmental factors, including nutritional factors and breeding conditions such as hygiene, stress and so on. Although many factors are able to provoke enteritis, the main and constant clinical sign observed is the diarrhoea that occurs in about 0.90 of enteritis cases (Licois et al., 1992). This may be related to the characteristics of the rabbit intestinal tract and its complex physiology.

The composition of caecal contents as well as caecal function and caecal bacterial community and activity (see Chapter 1) are significantly affected in cases of enteritis (Figs 10.1 and 10.2). The motility of the caecum is stimulated whereas that of the ileum and jejunum is inhibited in experimentally induced diarrhoea with Coccidia (Fioramonti et al., 1981). Furthermore, Hodgson (1974) observed increased motility of the proximal colon, which appeared contracted and thickened, in rabbits fed a low-fibre diet, and a higher retention of digesta in the total tract that should be related to lower feed intake. This probably reflects a higher antiperistaltic activity of the proximal colon (see Chapter 1) induced by the high proportion of fine particles in a low-fibre diet. It is thus difficult to postulate that rabbit diarrhoea is characterized by hypomotility of the caeco-colic segment. In parallel, caecal fermentative activity is upset (Fig. 10.2): for a 6-week-old rabbit, the caecal volatile fatty acid (VFA) concentration falls to <50 mM, butyrate is particularly affected (leading to a C3:C4 ratio in the range of 1.5–8 instead of 0.5–0.8) and larger inter-individual variations in the fermentation pattern are observed. Higher pH (+0.5) and ammonia levels may also be observed. The composition of the caeco-colic microbiota might also be affected, but the few results available are inconsistent, with some showing a decrease and others an increase in Escherichia coli and/or clostridia.

10.3.1 Fibre and starch intake

Fibre intake should be expressed in terms of quantity or quality (type) of cell wall constituents (see definition in Chapter 5). Similarly, the effect of starch intake may

![Fig. 10.1. Changes in the caecocolic ecosystem occurring in cases of digestive troubles (diarrhoea) in the growing rabbit. ?, further studies recommended; ±, inconsistent results; VFA, volatile fatty acid.](image-url)
differ according to the origin of the starch (see definition in Chapter 2).

Consequences of a reduction in fibre intake

An increased dietary starch to fibre ratio (associated with <300 g neutral detergent fibre (NDF), <150 g ADF and >200 g starch kg⁻¹), without major changes in the proportions of the cell wall constituents (e.g. hemicelluloses, lignins), could lead both to a lower ileal flow of DM and bacterial biomass production in the caecum of the young rabbit (Figs 10.1 and 10.2). In healthy growing animals, when the fibre intake is too low (<8–11 g ADF kg⁻¹ live weight day⁻¹), the caecal fibre level decreases while the starch concentration remains low (around 15–40 g kg⁻¹), and there are no consistent changes in the concentration of the fermentation end products (ammonia, VFA) and caecal pH (Fig. 10.3). Some authors have described lower fermentative activity (Bellier and Gidenne, 1996; Gidenne et al., 2000, 2002, 2004a; Nicodemus et al., 2003a, 2004), but most have not. However, the VFA molar proportion is affected by the fibre level, since the proportion of butyrate generally rises significantly when the fibre to starch ratio decreases.

It remains difficult to explain how these changes in the caecal ecosystem determine the greater incidence of digestive troubles (mainly diarrhoea, but also caecal impaction, mucus excretion and low feed intake) observed with low-fibre diets. It is probable that the microbial community is largely affected; for example, the caecal archaea has been seen to be double with a standard diet compared to a fibre-deficient diet (Bennegadi et al., 2003). Furthermore, when dietary NDF is reduced from 300 to 250 g kg⁻¹ microbiota biodiversity increases in the ileum but is reduced in the caecum (Nicodemus et al., 2004). Moreover, the favourable effect of a high fibre intake on rabbit digestive health has been shown using an experimental infection model reproducing colibacillosis (Gidenne and Licois, 2005) or ERE (Gidenne et al., 2001b).

Several hypotheses have been suggested to explain how the dietary supply of starch and fibre affects digestive physiology, but none has been completely validated by experimental results. Prohaszka (1980) put forward the antibacterial effect of caecal VFA originating from fibre fermentation, particularly in the case of *in vitro* *E. coli* assays. However, numerous studies have not observed a close relationship between the concentration of caecal VFA and pH or between *E. coli* flora and caecal pH. In addition, Padilha et al. (1995) showed that, between 29 and 49 days of age, caecal pH decreases while *E. coli* flora remains steady.

### Table 10.2

<table>
<thead>
<tr>
<th>Condition</th>
<th>Caecal VFA level (mM)</th>
<th>pH</th>
</tr>
</thead>
<tbody>
<tr>
<td>Healthy:</td>
<td>(41) 58 ± 9 (77)</td>
<td>(5.71) 6.45 ± 0.3 (7.03)</td>
</tr>
<tr>
<td>Sick:</td>
<td>(14) 48 ± 17 (103)</td>
<td>(5.65) 6.73 ± 0.59 (7.89)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Condition</th>
<th>Butyrate level (mM)</th>
<th>NH₃ (mM)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Healthy:</td>
<td>(2.6) 5.0 ± 1.7 (9.7)</td>
<td>(1.4) 5.6 ± 3.0 (11.0)</td>
</tr>
<tr>
<td>Sick:</td>
<td>(0.3) 2.2 ± 1.1 (4.2)</td>
<td>(1.7) 8.3 ± 4.4 (15.2)</td>
</tr>
</tbody>
</table>

Fig. 10.2. The *in vivo* caecal fermentation pattern (mean ± standard deviation) of healthya and sickb growing rabbits. Figures in parentheses are the minimum and maximum values observed from a set of 80 and 21 rabbits, respectively, for healthy and sick animals (data from Bellier, 1994). aCannulated rabbits, 7–11 weeks old. bRabbits having acute digestive troubles or abnormally low intake.
The favourable effect on health of a high level of low-digestible fibre (lignocellulose or ADF) could correspond to control of the rate of passage of digesta, particularly in the caeco-colic segment. Moreover, most results indicate that all of the factors contributing to an increase in retention time (lowering the fibre level, reducing the particle size of the feed, feed restriction) contribute to destabilizing the caecal microbial activity and favour enteritis. It could be speculated that a low caecal turnover of digesta leads to an insufficient supply of substrates available for the fibrolytic flora (Fig. 10.4).

Many experiments have been performed to evaluate the respective effects of fibre and starch on the incidence of diarrhoea in the growing rabbit, particularly just after weaning (Colin et al., 1976; de Blas et al., 1986; Blas et al., 1994; Bennegadi et al., 2001). This period is critical because it is associated with a large incidence of digestive problems, and also because overall digestive physiology actively matures and feed intake rapidly increases. Experiments that have dealt with this question compared diets with varying levels of fibre and simultaneously an inverse variation in the level of starch (since rabbits

Fig. 10.3. Effect of fibre deficiency on several parameters of the caecal ecosystem in the growing healthy rabbit. *Lower than 8–11 g acid detergent fibre (ADF) kg⁻¹ live weight day⁻¹, compared with the required >15 g ADF kg⁻¹ day⁻¹ for a diet balanced in fibre quantity. ?, Further studies needed; =, not a significant effect. ADC, apparent digestibility coefficient.

Fig. 10.4. Relationships between feeding the growing rabbit with low-fibre, high-starch diets and the incidence of digestive troubles.
are fed with complete feeds). Consequently, when a study has reported a positive effect of increased dietary fibre intake on digestive health, it has been difficult to exclude the possibility of an effect of reduced starch intake. Thus, two opposing hypotheses can be constructed: are digestive troubles linked to carbohydrate overload in the caecum or to fibre deficiency (or both)? This question has been approached by studying the ileal flow of starch and fibre in the growing rabbit (5–9 weeks old). With high-starch diets (≥300 g starch kg⁻¹, mainly from wheat), ileal starch digestibility was very high (>0.97) and the flow of starch remained <2 g day⁻¹ (intake around 30 g day⁻¹) at the ileum, while that of fibre was at least ten times higher (around 20 g NDF day⁻¹) (Gidenne et al., 2000; García et al., 2004; Nicodemus et al., 2004). An overload of starch therefore appears very unlikely, since starch digestion is very efficient already at 5 weeks old. Moreover, a large-scale study using a network of six experimental breeding units (GEC French group) demonstrated through a 2×2 factorial design (two levels of starch: 120 versus 190 g kg⁻¹, combined with two ADF levels: 150 versus 190 g kg⁻¹) that only the fibre level played a role in the occurrence of digestive problems, and not the starch level (Gidenne et al., 2004b).

Furthermore, by comparing iso-fibre diets, but with several starch sources (maize, wheat, barley) varying in their intestinal digestion, Gidenne et al. (2005a,b) observed no effect of starch ileal flow on the incidence of diarrhoea in the weaned rabbit. These results support the minor influence of starch on the health status of the animal when fibre requirements are covered. The positive effect of enzyme supplementation (a mixture of β-glucanases, β-xylanases, α-amylases and pectinases) on mortality (Gutiérrez et al., 2002b; Cachaldora et al., 2004) might thus be related to the partial hydrolysis of non-starch polysaccharides that produce complex oligomers, which may modulate the gut microbiota and lead to better digestive health. Moreover, since starch digestion is incomplete in the young rabbit, replacement of some starch by lactose has been studied, as occurs in piglets’ diets. However, lactose ileal digestibility was much lower than that recorded for starch (0.74 versus 0.92), which might be due to the severe reduction in lactase activity after weaning. This result led to a higher ileal flux of lactose and higher mortality (Gutiérrez et al., 2002a), possibly explained by a microbiota imbalance in the caecum.

Fibre intake thus plays a major role in the development of digestive problems in the classically weaned rabbit (28–35 days old). With rabbits weaned earlier (at 25 days of age), Gutiérrez et al. (2002a) observed that mortality remained low and similar with diets having 360 versus 300 g NDF kg⁻¹, but that the mortality rate tended to increase ($P = 0.06$) after a change of diet at 39 days of age, from experimental to commercial, for those previously fed with a diet containing 360 g NDF kg⁻¹.

Accordingly, several large-scale studies have aimed to clearly validate the relationship between dietary fibre and starch levels and diarrhoea incidence for the classically weaned rabbit, using an experimental design with a high number of animals per treatment. The relationship between low-fibre diets (<140 g ADF kg⁻¹) and a higher incidence of diarrhoea was clearly established in two studies where the quality of the fibre (e.g., the proportions of fibre fraction as analysed through the Van Soest procedure) was estimated (Blas et al., 1994; Bennegadi et al., 2001). In France, the GEC group has performed several large-scale studies (using at least 300 animals per treatment and five sites) to establish fibre recommendations for the prevention of digestive problems in the growing rabbit (weaned). The relevance of the Van Soest criteria was studied, since the crude fibre method was too imprecise for this purpose. A review of these studies and of new fibre recommendations has been published (Gidenne, 2003). A summary of the fibre requirements for post-weaned and growing rabbits from French (INRA) and Spanish (Technical University of Madrid) research groups is presented in Table 10.2.

The favourable effect of dietary fibre has also been analysed in the young rabbit during the weaning period (3–5 weeks old) in a large-scale study (six sites and three repro-
Table 10.2. Fibre and starch requirements (g kg\(^{-1}\))\(^a\) for the young weaned rabbit to prevent digestive troubles.

<table>
<thead>
<tr>
<th></th>
<th>INRA</th>
<th>Technical University of Madrid</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>Post weaning (28–42 days)</td>
<td>Growing (42–70 days)</td>
</tr>
<tr>
<td>Neutral detergent fibre (NDF)</td>
<td>≥310</td>
<td>≥270</td>
</tr>
<tr>
<td>Lignocellulose (ADF)</td>
<td>≥190</td>
<td>≥170</td>
</tr>
<tr>
<td>Lignin (ADL)</td>
<td>≥55</td>
<td>≥50</td>
</tr>
<tr>
<td>Cellulose (ADF – ADL)</td>
<td>≥130</td>
<td>≥110</td>
</tr>
<tr>
<td>Ratio lignins/cellulose</td>
<td>&gt;0.40</td>
<td>&gt;0.40</td>
</tr>
<tr>
<td>Hemicelluloses</td>
<td>&gt;120</td>
<td>&gt;100</td>
</tr>
<tr>
<td>(NDF – ADF)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>DgF(^b)/ADF</td>
<td>≤1.3</td>
<td>≤1.3</td>
</tr>
<tr>
<td>Neutral detergent soluble fibre(^c)</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Particles &gt;0.3 mm</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Starch</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

ADF, acid detergent fibre; ADL, acid detergent lignin; DgF, digestible fibre; NDF, neutral detergent fibre.

\(^a\)As fed basis, corrected to a dry matter content of 900 g kg\(^{-1}\).

\(^b\)Hemicelluloses (NDF – ADF) + water-insoluble pectins.

\(^c\)According to Hall et al. (1997).

ductive cycles) by Fortun-Lamothe et al. (2005). A lower mortality rate was reported for litters fed on a diet rich in fibre or when fibre and lipid replaced starch. However, in the suckling rabbit (or <5 weeks old) it can be speculated that feed intake regulation is not completely established and neither is pancreatic enzymatic activity (see Chapter 1). The combination of these two factors would lead to a high flow of starch into the caecum (Gidenne et al., 2005a), which may then favour digestive disturbances.

The substitution of starch for fibre has also been studied for rabbit doe diets, using five iso-energetic diets (10.6 MJ digestible energy (DE) kg\(^{-1}\)) with increasing levels of NDF (from 278 to 371 g kg\(^{-1}\)) and fat (from 20 to 51 g kg\(^{-1}\)) at the expense of starch (decreasing from 237 to 117 g kg\(^{-1}\)) (de Blas et al., 1995). Some impairment in the performances of does was observed in those fed the highest levels of fibre. This might be explained by higher fermentation losses in the caecum, together with an insufficient uptake of glucose from the gut to meet the requirements for pregnancy and milk lactose synthesis. Conversely, negative effects of high dietary starch concentrations were also mentioned and were related to an increase in diarrhoea mortality for the does.

**Effect of the type of cell wall constituents**

Apart from the important role of fibre intake, the quality of fibre (see Chapter 5) also interferes with diarrhoea incidence in the growing rabbit (30–70 days old). The favourable effect of lignocellulose on digestive disorders and mortality in fattening rabbits has been established in several studies. For example, the HRI has been found to decrease from 28% to 18% when the dietary ADF content increases from 150 to 190 g kg\(^{-1}\) (Gidenne et al., 2004b). But, within lignocellulosic components, the favourable effect of the lignin (acid detergent lignin, ADL) has also been demonstrated, and a strong negative relationship was found with the HRI (Fig. 10.5) (Perez et al., 1994, 1996; Nicodemus et al., 1999; Gidenne et al., 2001a). As discussed previously, these studies confirm that the effects of lignin and cellulose are confounded with NDF level. Increasing the cellulose fraction (ADF – ADL) also favours digestive health (Perez et al., 1996). However, lignin plays a specific role since an increase in the ratio of lignin to cellulose is associated with a lower HRI (Gidenne et al., 2001a). In summary, the lignin requirement (ADL) for the growing rabbit can be assumed to be 5–7 g day\(^{-1}\) and the cellulose requirement 11–12 g day\(^{-1}\). Moreover,
Although the digestive health of the classically weaned rabbit depends on the level and quality of lignocellulose, it also varies greatly for the same ADF level (Fig. 10.6) because the level of more digestible fibre (DgF) fractions (i.e. hemicelluloses (NDF – ADF) + water-insoluble pectins) could also vary independently of lignin and cellulose levels. Thus, a dietary recommendation for lignocellulose alone appears to be insufficient to prevent digestive disturbances in the rabbit. For instance the ratio of DgF to ADF ranges from 0.9 to 1.7 in Fig. 10.6. The DgF fraction may play a key role in digestive efficiency and digestive health, since it is more rapidly fermented compared to ADF and compatible with the retention time of the caeco-colic segment (9–13 h, see Chapter 1). Without changes in ADF dietary levels, the frequency of digestive problems decrease when DgF replaces starch (Perez et al., 2000) or protein (Gidenne et al., 2001b). This could originate from the favourable effect of DgF (compared to starch or protein) on caecal fermentative activity (Jehl and Gidenne, 1996; García et al., 2002) and possibly from its moderate effect on rate of passage (Gidenne et al., 2004b). However, too high an incorporation of DgF with respect to lignin and cellulose should be avoided to minimize the HRi (morbidity + mortality) during fattening. It is thus recommended that the ratio DgF to

Fig. 10.5. Increasing the dietary lignin concentration reduces the risk of digestive troubles (health risk index, HRi) in the growing rabbit. ADL, acid detergent lignin (Van-Soest sequential procedure; EGRAN, 2001). *HRi from digestive trouble = mortality + morbidity rate by diarrhoea, measured from 28 to 70 days of age, on at least 40 rabbits per diet (data for ten diets ranging from 14% to 20% acid detergent fibre level; Gidenne, 2003).

Nicodemus et al. (2006) reported better performance (e.g. milk production) for does fed a high-lignin diet (59 g ADL kg\(^{-1}\)). To date, however, no accurate and quick analytical method for determining lignin levels is available. Consequently, estimating the amount of lignin in a raw material remains difficult, particularly in tannin-rich ingredients (e.g. grape marc), and caution must be taken in establishing requirements.

Although the digestive health of the classically weaned rabbit depends on the level and quality of lignocellulose, it also varies greatly for the same ADF level (Fig. 10.6) because the level of more digestible fibre (DgF) fractions (i.e. hemicelluloses (NDF – ADF) + water-insoluble pectins) could also vary independently of lignin and cellulose levels. Thus, a dietary recommendation for lignocellulose alone appears to be insufficient to prevent digestive disturbances in the rabbit. For instance the ratio of DgF to ADF ranges from 0.9 to 1.7 in Fig. 10.6. The DgF fraction may play a key role in digestive efficiency and digestive health, since it is more rapidly fermented compared to ADF and compatible with the retention time of the caeco-colic segment (9–13 h, see Chapter 1). Without changes in ADF dietary levels, the frequency of digestive problems decrease when DgF replaces starch (Perez et al., 2000) or protein (Gidenne et al., 2001b). This could originate from the favourable effect of DgF (compared to starch or protein) on caecal fermentative activity (Jehl and Gidenne, 1996; García et al., 2002) and possibly from its moderate effect on rate of passage (Gidenne et al., 2004b). However, too high an incorporation of DgF with respect to lignin and cellulose should be avoided to minimize the HRi (morbidity + mortality) during fattening. It is thus recommended that the ratio DgF to

Fig. 10.6. The risk of digestive problems (health risk index, HRi) in the growing rabbit is jointly dependent of low-digested acid detergent fibre (ADF) and digestible fibre (DgF). *HRi from digestive trouble = mortality + morbidity rate by diarrhoea, measured from 28 to 70 days of age, on at least 40 rabbits per diet (one point = one diet, n = 13; Gidenne, 2003). *Lignocellulose (Van-Soest sequential procedure; EGRAN, 2001). *Water-insoluble pectins plus hemicelluloses (NDF – ADF).
ADF remains <1.3 (when the dietary ADF level is >150 g kg\(^{-1}\), see Table 10.2).

Another way to analyse the role of cell wall polysaccharides that are rapidly fermented is to determine the neutral detergent soluble fibre (NDSF) residue (Hall et al., 1997). This corresponds to the cell wall polysaccharides soluble in neutral detergent solution (= sum of water-soluble and -insoluble pectins + β-glucans + fructans + oligosaccharides (degree of polymerization >15)). Although the NDSF level is moderate in rabbit feeds, a reduction in its level (from 120 to 80 g kg\(^{-1}\)) may be detrimental to the digestive health of the early-weaned rabbit. Conversely, a higher level of NDSF improves mucosal morphology, functionality and immune response. Moreover, NDSF reduces the proportion of animals with *Clostridium perfringens* in the caecum and other pathogens such as *Campylobacter* both in the ileum and caecum. Accordingly, mortality due to ERE is reduced with a diet containing 120g soluble fibre kg\(^{-1}\) (Table 10.3) (Gómez-Conde et al., 2007, 2009).

The quality of dietary fibre might also be improved by determining the particle size distribution. It is acknowledged that the particle size distribution of a feed can affect digesta motility and, more importantly, the caeco-colic rate of passage. Fibrous raw materials with a small proportion of large particles (>0.3 mm) due to grinding (screen size 0.5–1 mm) or previous processing are retained for longer (Laplace and Lebas, 1977; Gidenne et al., 1991; García et al., 1999), but are not associated with a negative effect on the digestive health status (Lebas et al., 1986; Gidenne et al., 1991; Nicodemus et al., 2006). Only a very low content of large particles (<0.21 particles of <0.3 mm) would have a negative impact on performance. Nevertheless, a content of coarse particles <0.25 is unusual in practice; in a series of 77 commercial French feeds, the average proportion of coarse particles was 0.388 (minimum 0.227, mean –2 SDS 0.27; Lebas and Lamboley, 1999).

In conclusion, one criterion is not sufficient for fibre recommendation, because the risk of digestive problems in the growing rabbit is jointly dependent on low-digested ADF and the DgF fraction. As for other dietary fibre components, there is a minimum below which a ‘fibre deficiency’ may occur (see Table 10.2). In summary, it is important to establish the precise role of fibre in the young rabbit, and particularly the effects of the NDSF fraction.

### 10.3.2 Protein level and quality

Protein requirements are high in the young animal (see Chapters 12 and 3), not only for

<table>
<thead>
<tr>
<th>Dietary NDSF(^a) level (g kg(^{-1}) as fed)</th>
<th>120</th>
<th>90</th>
<th>70</th>
<th>(P)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jejunum morphology and functionality (35 days)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Villi length (µm)</td>
<td>722(^c)</td>
<td>567(^d)</td>
<td>493(^a)</td>
<td>0.001</td>
</tr>
<tr>
<td>Crypt depth (µm)</td>
<td>89(^c)</td>
<td>115(^d)</td>
<td>113(^d)</td>
<td>0.001</td>
</tr>
<tr>
<td>Sucrase specific activity (µmol glucose g(^{-1}) protein)</td>
<td>8671(^c)</td>
<td>6495(^d)</td>
<td>5202(^a)</td>
<td>0.019</td>
</tr>
<tr>
<td>Immune response in lamina propria (35 days)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CD4(^+) (%)</td>
<td>35.1</td>
<td>33.9</td>
<td>26.2</td>
<td>NS</td>
</tr>
<tr>
<td>CD8(^+) (%)</td>
<td>21.3</td>
<td>26.9</td>
<td>30.3</td>
<td>0.074</td>
</tr>
<tr>
<td>Frequency of detection <em>C. perfringens</em> (%)(^b)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ileum</td>
<td>0</td>
<td>22.2</td>
<td>9.1</td>
<td>0.062</td>
</tr>
<tr>
<td>Caecum</td>
<td>5.7(^c)</td>
<td>2.9(^d)</td>
<td>17.6(^d)</td>
<td>0.047</td>
</tr>
<tr>
<td>Mortality, 25–60 days (%)</td>
<td>5.3(^c)</td>
<td>8.5(^c,d)</td>
<td>14.4(^d)</td>
<td>0.016</td>
</tr>
</tbody>
</table>

NS, not significant.

\(^a\)According to Hall et al. (1997).

\(^b\)Terminal restriction fragment length polymorphism approach.

\(^c,d,e\)Means having the same superscript letter are not different (\(P<0.05\)).
body growth but also for intestinal mucosa development and renewal. Conversely, an excessive protein supply does not affect growth itself, but will promote the incidence of diarrhoea. For instance, de Blas et al. (1981) observed increased mortality during the fattening period with high-protein diets. A level of 1.8–1.9 g CP MJ⁻¹ DE seems optimum; even if with an increase of up to 2.6 g, Kjaer and Jensen (1997) observed only a slight non-significant increase in mortality. Similarly, Catala and Bonnafous (1979) showed that a higher ileal flow of protein (obtained through reduced protein digestion by a ligature of the pancreatic duct) leads to increased microbial proliferation in the hindgut. An excess of dietary protein could also favour the proliferation of *clostridia* in the rabbit and slightly increase the prevalence of *E. coli* (Haffar et al., 1988; Cortez et al., 1992), and thus could lead to an increase of enteric mortality. For instance, in a large-scale study, Gidenne et al. (2001b) showed that the replacement of protein by digestible fibre reduced the health risk for diarrhoea (Fig. 10.7). A hypothesis to explain this is a higher availability of substrates for microbial growth, with an increased prevalence of pathogenic species, when animals are fed with high-protein diets. A higher ileal flow of protein is also associated with a lower caecal pH in the young rabbit (Gutiérrez et al., 2003; Nicodemus et al., 2003b, 2004), which may affect the commensal microbiota.

Weaning implies a change from milk to vegetable proteins. The digestion of the latter is worse, and raw materials occasionally contain antinutritive factors such as lectins, antitrypsin or antigenic compounds. This may impair apparent ileal digestion or induce changes in the morphology of the intestinal mucosa, as occurs in other species. In rabbits, Scheele and Bolder (1987) observed an increase in mortality before weaning (35 days old) in rabbits fed diets containing a high proportion of soybean meal (200 g kg⁻¹) in comparison with two diets based on animal protein (310 versus 100 g kg⁻¹, respectively). Gutiérrez et al. (2000) observed that the substitution of soybean meal with animal plasma had a positive effect on the morphology of intestinal mucosa, feed intake, growth and mortality. In another study, Gutiérrez et al. (2003) compared four protein concentrates (sunflower meal, soybean meal 48, soybean concentrate and potato protein) in iso-nutritive starter diets. Animals fed diets with the protein sources with a lower content of antinutritive factors (sunflower meal and soybean concentrate) showed higher apparent ileal protein digestibility and growth performance and a lower mortality rate than those on the other diets. However, the gastric acidity, villus morphology and faecal digestibility values were similar between diets, and

---

**Fig. 10.7.** Impact of crude protein (CP) replacement by digestible fibre (DgF), on the health risk index between weaning and slaughter (Gidenne et al., 2001b). a, b: within the same period (weaning-49 days or weaning-slaughter), means having a letter in common and do not differ at the level P = 0.05.
no differences in phenotypic distribution of lymphocytes in the duodenal lamina propria (which might be related to the development of a tolerance mechanism by the animal) were detected (Mézes and Balogh, 2009). The importance of the reduction of the ileal flow of protein (by using digestible sources or reducing the protein level) in reducing the mortality rate has been supported in other experiments (García-Ruiz et al., 2006; Chamorro et al., 2007).

Most feed manufacturers limit the dietary protein level in fattening diets because of the increased mortality rate observed on rabbit farms when protein levels exceed by 20 g kg$^{-1}$ or more the minimum levels recommended for the maximum growth rate. Moreover, an excessive protein supply will probably become increasingly unusual in Europe because of increased dietary cost and, most importantly, because the European animal management strategy favours a reduction in nitrogen excretion to the environment through the use of low-protein diets (Maertens, 1999).

### 10.3.3 Lipids

Few studies have dealt with the role of dietary lipids on the digestive health of growing rabbits, since dietary levels are usually <30 g kg$^{-1}$ and lipids are well digested in the small intestine. Furthermore, it is difficult to separate the effect of lipids from that of DE intake. However, it has been found that some medium-chain fatty acids (MCFA), such caprylic and capric acid (in triacylglycerol form), exhibit antimicrobial activity for some bacteria of the caecal digestive microbiota (Marounek et al., 2002). Moreover maternal milk, rich in MCFA, protects the young rabbit against colibacillosis (Gallois et al., 2007) and the addition of MCFA to the feed has a favourable impact on the digestive health of the growing rabbit (Skrivanova and Marounek, 2006). However, contrasting results are obtained when rabbits are experimentally infected with pathogenic E. coli (Gallois et al., 2008; Skrivanova et al., 2008).

Some fatty acids, such omega (n)-3, have been implicated in the development of an immune response. Fortun-Lamothe and Boulier (2007) and Maertens et al. (2005) reported a higher post-weaning viability for young rabbits fed a diet with a low n-6 to n-3 ratio (1.0 versus 4.4). Moreover, the addition of fat to starter diets increases the energy intake of kits and contributes to the maintenance of good body condition. Therefore, this favours harmonious digestive maturation and immune system development, thus reducing weaning risk and improving resistance to digestive problems.

Furthermore, the incorporation of fat in the diets of breeding does may be of interest in terms of increasing their DE intake. However, contradictory results have been obtained indicating either a higher (Lebas and Fortun-Lamothe, 1996) or lower kit mortality (Fraga et al., 1989; Fernandez-Carmona et al., 1996). Despite this, neither the average weight of breeding does nor their fertility or prolificacy were significantly affected by dietary fat incorporation (Fortun-Lamothe, 2006).

### 10.3.4 Feed intake strategy and digestive pathology of the growing rabbit

Studies on feed intake regulation usually aim to analyse the effects on the carcass quality of the growing rabbit or to analyse digestive efficiency. More recently, however, some studies have dealt with the relationship between intake level and the incidence of digestive problems, including a study with an experimental ERE infection. The effect of a quantitative linear reduction of feed intake level (ad libitum to 0.6 of ad libitum) on the digestive health and growth of the rabbit was measured in a large-scale study (six experimental units, 2000 rabbits per treatment; Gidenne et al., 2009a). During feed restriction, the mortality and morbidity rates were significantly reduced (from 12% to 3.5% and from 12% to 6% for ad libitum + 0.9 ad libitum feeding level versus 0.7 + 0.6 ad libitum). Feed restriction for 20 days after weaning proportionally reduced the growth rate. Thereafter, returning to ad libitum feed
intake led to compensatory growth and better feed efficiency. Over the whole fattening period, the live weight loss of the more restricted rabbits (0.6 ad libitum) was 7.7%, compared to the control rabbits fed ad libitum from weaning. The favourable effect of limiting intake on the digestive health of the young rabbit has been confirmed by another large-scale study (Gidenne et al., 2009b), where there was no major effect of the mode of feed distribution (one or two times a day). Moreover, Boisot et al. (2003) also demonstrated a similar positive effect of feed restriction when rabbits were challenged with ERE inoculum. Physiological mechanisms explaining such a favourable effect of reducing feed intake on diarrhoea incidence have yet to be elucidated.

Similar results have been obtained by reducing the intake level through a time restriction for water consumption (Boisot et al., 2004; Verdelhan et al., 2004). Consequently, strategies for controlling the intake of the young after weaning are now widespread in French professional breeders, in parallel with the development of automatic feeding equipment.

10.4 Problems Associated with Dietary Compounds Present at Toxic Levels

10.4.1 Minerals and vitamins

Although recommendations for optimum and maximum levels of mineral and vitamins are described in detail in Chapter 7, it is important for this chapter to consider maximum acceptable levels in diets. In effect it is important that, during diet formulation, there is control over nutrient levels such that, even if analysis is not available, they are well below toxic levels.

The main available information is summarized in Table 10.4. The values are those from Lebas et al. (1996), amended according to the most recent data obtained mainly during the last World Rabbit Congresses: Bernardini et al. (1996) and Virag et al. (2008) for vitamin E in the growing rabbit; Abdel-Khalek et al. (2008) for vitamins E and C in breeding does; Abd El-Rahim et al. (1996) for iron; and Guimaraes and Motta (2000) and Ayyat and Marai (2000) for zinc.

It must be pointed out that the maximum acceptable level is in general far higher than the recommended level, but with some noticeable exceptions such as potassium, phosphorus and vitamin D.

10.4.2 Mycotoxins

Mycotoxins are metabolites produced by certain fungi in the field on standing crops or during the harvesting of feedstuffs. Mould growth can also occur on stored grains or other raw materials because of non-hygienic storage conditions. These toxic substances may be contained within the spore or secreted into the substrate on which the fungi are growing. Most of these substances have a high degree of animal toxicity. Feeding rabbits on naturally moulded diets (mixed toxin contamination) is responsible for many problems such as decreased feed intake, functional alteration of the liver and genital tract and changes in blood constituents (Abdelhamid, 1990). Mycotoxicoses appear in chronic and acute forms. The acute form is caused by the rapid ingestion of large amounts of toxins over a short period. For more details, see the review of Mézes (2008).

Aflatoxins are naturally occurring toxins produced in grains and other feedstuffs both before and after harvest by toxigenic strains of the fungi Aspergillus flavus and Aspergillus parasiticus. Aflatoxin B1 (AFB1) is of primary concern because it is the most abundant and the most toxic. Acute or chronic aflatoxicosis may occur depending on the dietary concentration of toxins. Rabbits are extremely sensitive to aflatoxin. The acute, oral, single-dose median lethal dose is about 0.3 mg kg⁻¹ body weight (Newberne and Butler, 1969), among the lowest of any animal species. Moderate to severe death losses can be encountered with diets containing even low concentrations of toxin (<100 ppb) (Krishna et al., 1991). Signs of toxicity include hepatic lesions (Abdelhamid et al., 2002), anorexia,
weight loss and emaciation, followed by icterus in the terminal stages (Morisse et al., 1981). Acute aflatoxin poisoning (AFB1 daily doses >0.04 mg kg\(^{-1}\) body weight) causes a prolonged blood-clotting time, extensive liver damage and death from liver failure (Clark et al., 1980, 1982, 1986).

Zearalenone (F-2 toxin) is an oestrogenic substance that is frequently recovered from maize and other grains contaminated by Fusarium graminearum (Perez and Leuillet, 1986). Zearalenone causes hypertrophic development of the genital tract of the female rabbit (Pompa et al., 1986; Abdel hamid et al., 1992). It can also affect components of the uterine tubal fluid known to be of critical importance during the early preimplantation period (Osborn et al., 1988). Zearalenone induces changes in blood serum enzyme activities. Low doses (10 µg kg\(^{-1}\)) result in significant increases in alkaline phosphatase (ALP) activity, while higher doses (100 µg kg\(^{-1}\)) lead to significant increases in the activity of aspartate aminotransferase, alanine aminotransferase, ALP, \(\gamma\)-glutamyl transpeptidase and lactate dehydrogenase, indicating possible liver toxicity due to chronic effects of the toxin (Čonková et al., 2001). Levels of zearalenone in feed as low as 1–2 ppm can interfere with the normal reproductive activity of rabbits when fed for only a few days (1–2 weeks). This high sensitivity of rabbits to this mycotoxin could be related to the slow hepatic transformation of zearalenone mainly into \(\alpha\)-zearalenol, a more uterotrophic metabolite (Pompa et al., 1986).

Another group of toxins produced by Fusarium species is the trichothecenes: T-2 toxin and vomitoxin. T-2 toxin is produced by some strains of the fungus Fusarium tricinctum. It is relatively common in fibrous raw materials that have been harvested or

Table 10.4. Maximum levels of minerals or vitamins that can be given without problems and levels known to induce signs of toxicity in the rabbit.

<table>
<thead>
<tr>
<th>Minerals</th>
<th>Maximum level observed without problems</th>
<th>Concentration with signs of toxicity</th>
<th>Period of life</th>
</tr>
</thead>
<tbody>
<tr>
<td>Calcium (g kg(^{-1}))</td>
<td>25</td>
<td>40</td>
<td>Growth</td>
</tr>
<tr>
<td></td>
<td>19</td>
<td>25</td>
<td>Reproduction</td>
</tr>
<tr>
<td>Phosphorus (g kg(^{-1}))</td>
<td>8</td>
<td>–</td>
<td>Growth</td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>10</td>
<td>Reproduction</td>
</tr>
<tr>
<td>Magnesium (g kg(^{-1}))</td>
<td>3.5</td>
<td>4.2</td>
<td>Growth</td>
</tr>
<tr>
<td>Sodium (g kg(^{-1}))</td>
<td>6</td>
<td>7</td>
<td>Growth</td>
</tr>
<tr>
<td>Potassium (g kg(^{-1}))</td>
<td>16</td>
<td>15–20</td>
<td>Growth</td>
</tr>
<tr>
<td></td>
<td>16</td>
<td>20</td>
<td>Reproduction</td>
</tr>
<tr>
<td>Chlorine (g kg(^{-1}))</td>
<td>4.2</td>
<td>–</td>
<td>Growth</td>
</tr>
<tr>
<td>Copper (ppm)</td>
<td>150–200</td>
<td>200–300</td>
<td>Growth</td>
</tr>
<tr>
<td>Fluorine (ppm)</td>
<td>–</td>
<td>400</td>
<td>Growth</td>
</tr>
<tr>
<td>Iodine (ppm)</td>
<td>10,000</td>
<td>–</td>
<td>Growth</td>
</tr>
<tr>
<td>Iron (ppm)</td>
<td>400</td>
<td>500</td>
<td>Growth</td>
</tr>
<tr>
<td>Manganese (ppm)</td>
<td>–</td>
<td>50</td>
<td>Growth</td>
</tr>
<tr>
<td>Selenium (ppm)</td>
<td>0.32</td>
<td>–</td>
<td>Growth</td>
</tr>
<tr>
<td>Zinc (ppm)</td>
<td>200</td>
<td>400</td>
<td>Growth</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Vitamins</th>
<th>Maximum level observed without problems</th>
<th>Concentration with signs of toxicity</th>
<th>Period of life</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vitamin A (IU kg(^{-1}))</td>
<td>100,000</td>
<td>–</td>
<td>Growth</td>
</tr>
<tr>
<td></td>
<td>40,000</td>
<td>75,000</td>
<td>Reproduction</td>
</tr>
<tr>
<td>Vitamin D (IU kg(^{-1}))</td>
<td>2,000</td>
<td>3,000</td>
<td>Reproduction</td>
</tr>
<tr>
<td>Vitamin E (mg kg(^{-1}))</td>
<td>300</td>
<td>–</td>
<td>Growth</td>
</tr>
<tr>
<td></td>
<td>160</td>
<td>–</td>
<td>Reproduction</td>
</tr>
<tr>
<td>Vitamin C (g kg(^{-1}))</td>
<td>2</td>
<td>–</td>
<td>Growth</td>
</tr>
<tr>
<td>Vitamin C (mg kg(^{-1}))</td>
<td>400</td>
<td>–</td>
<td>Reproduction</td>
</tr>
</tbody>
</table>
stored in poor conditions. In affected rabbits, T-2 toxin causes marked feed refusal, lesions of the digestive tract and impairment of blood-clotting mechanisms (Gentry, 1982; Fekete et al., 1989). Long-term (4–7 weeks) feeding of sub-lethal quantities of T-2 toxin (0.19 ppm) have been found to alter the ovarian activity of sexually mature female rabbits (Fekete and Huszenicza, 1993). Administration per os of 4 mg kg⁻¹ body weight of T-2 toxin causes death within 24 h (Vanyi et al., 1989).

Vomitoxin (4-deoxynivalenol) may be found in cereal grains. Contamination of rabbit feeds with this toxin results in feed refusal and vomiting. Adverse effects on fetal development have also been encountered in does. Khera et al. (1986) observed that a level of 0.00024 mg vomitoxin g⁻¹ diet caused a 100% incidence of fetal resorption.

The nephrotoxins (ochratoxin and citrinin) have been also implicated in rabbit mycotoxicosis. Ochratoxin is produced by toxigenic strains of Aspergillus ochraceus. Galtier et al. (1977) examined the excretion of ochratoxin A in rabbit females after a single intravenous administration (1–4 mg kg⁻¹ body weight) and demonstrated transfer of the toxin into the milk: the level in milk reached 1 ppm for the highest dose of administration. The actual toxicity for rabbits is unknown, but it can be pointed out that, in the above-mentioned experiment, lactating does accommodated a single dose of 4 mg kg⁻¹ body weight.

Citrinin is found in mouldy cereals contaminated by various fungal species of Aspergillus and Penicillium. Ingestion of this toxin induces acute erosive gastritis and fluid diarrhoea, with some rabbits dying less than 24 h after oral administration of a single 100–130 mg kg⁻¹ body weight dose (Hanika et al., 1983). In the rabbit, citrinin also causes renal damage with tubular dysfunction and necrosis similar to that found in other animal species (Hanika et al., 1984).

10.5 Water Quality and Pathology

In most texts on animal nutrition, the part devoted to water quality is very short. A common comment is that ‘the water provided for animals must be drinkable’ and the recommended values given are those for human consumption, without further comment.

If these values are effectively obtained at the watering point available to the animals, there is effectively no health problem linked to water quality. Nevertheless, the bacterial and chemical composition of the water destined for animal drinking does not always respect all of the recommended criteria.

In no way should water polluted with bacteria be recommended for rabbits, even if it is known that animals are more tolerant than humans. As very simple low-cost systems are available, the solution is disinfection. The classic criteria for the bacterial quality of drinkable water are presented in Table 10.5.

For minerals, removing the excess is technically possible in most cases, but the cost is very high and the constant question is: is it necessary for the health of rabbits? Different experiments have been conducted to establish the real tolerance of rabbits to mineral concentrations in drinking water, mainly in hot sub-Saharan regions or in intensive animal production areas. The results are summarized in Table 10.6. Values are given for each mineral, but it does not mean that water with all of criteria at maximum will be accepted by rabbits.

It can be pointed out that, when known, the tolerance limits of rabbits are very wide compared to the maximum ‘officially’ acceptable values for human consumption. One of the most significant is the tolerance of rabbits to high levels of nitrates or nitrites

<table>
<thead>
<tr>
<th>Microorganisms</th>
<th>Maximum count</th>
</tr>
</thead>
<tbody>
<tr>
<td>Salmonella spp.</td>
<td>0 in 5,000 ml</td>
</tr>
<tr>
<td>Staphylococcus spp.</td>
<td>0 in 100 ml</td>
</tr>
<tr>
<td>Enteroviruses</td>
<td>0 in 10,000 ml</td>
</tr>
<tr>
<td>Faecal Streptococcus spp.</td>
<td>0 in 100 ml</td>
</tr>
<tr>
<td>Thermo-tolerant coliforms</td>
<td>0 in 100 ml</td>
</tr>
<tr>
<td>Clostridium spp.</td>
<td>1 in 20 ml</td>
</tr>
</tbody>
</table>

Nutrition and Feeding Strategy

(tenfold the maximum accepted for human consumption), which has led to considerable debate in intensive animal production regions such as the Netherlands or Brittany in France. None of the maxima for rabbits is lower than that recommended for human consumption. Therefore, no specific chemical control is necessary if the water provided for rabbits is the same as that provided for human consumption by a controlled public system. Conversely, alteration of water quality by increasing some minerals can be illegal for human consumption, but is not necessarily injurious to rabbit health (Table 10.6).

Table 10.6. Chemical composition of drinkable water for rabbits.

<table>
<thead>
<tr>
<th>Physical parameter (units)</th>
<th>Recommended maximum</th>
<th>Maximum tolerated</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>pH</td>
<td>7–8.5</td>
<td>6.5–9.2</td>
<td>3.5–9.0</td>
</tr>
<tr>
<td>Chemical parameters (in ppm)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total soluble salts</td>
<td>500</td>
<td>1500</td>
<td>3000</td>
</tr>
<tr>
<td>Sodium</td>
<td>100</td>
<td>150</td>
<td>900</td>
</tr>
<tr>
<td>Potassium</td>
<td>10</td>
<td>12</td>
<td>140</td>
</tr>
<tr>
<td>Phosphorus</td>
<td>2</td>
<td>5</td>
<td>–</td>
</tr>
<tr>
<td>Calcium</td>
<td>75</td>
<td>200</td>
<td>400</td>
</tr>
<tr>
<td>Magnesium</td>
<td>30</td>
<td>150</td>
<td>–</td>
</tr>
<tr>
<td>Iron</td>
<td>0.2</td>
<td>1.0</td>
<td>–</td>
</tr>
<tr>
<td>Copper</td>
<td>0.1</td>
<td>1.5</td>
<td>60</td>
</tr>
<tr>
<td>Manganese</td>
<td>0.05</td>
<td>0.5</td>
<td>12</td>
</tr>
<tr>
<td>Zinc</td>
<td>5</td>
<td>15</td>
<td>55</td>
</tr>
<tr>
<td>Aluminium</td>
<td>0.2</td>
<td>–</td>
<td>250</td>
</tr>
<tr>
<td>Antimony</td>
<td>0.01</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Arsenic</td>
<td>0.05</td>
<td>0.20</td>
<td>–</td>
</tr>
<tr>
<td>Cadmium</td>
<td>0.005</td>
<td>0.05</td>
<td>–</td>
</tr>
<tr>
<td>Chromium</td>
<td>0.05</td>
<td>1.0</td>
<td>–</td>
</tr>
<tr>
<td>Cobalt</td>
<td>–</td>
<td>1.0</td>
<td>–</td>
</tr>
<tr>
<td>Fluoride</td>
<td>1.5</td>
<td>2.0</td>
<td>–</td>
</tr>
<tr>
<td>Lead</td>
<td>0.05</td>
<td>0.10</td>
<td>0.40</td>
</tr>
<tr>
<td>Mercury</td>
<td>0.001</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Nickel</td>
<td>0.05</td>
<td>1.00</td>
<td>–</td>
</tr>
<tr>
<td>Selenium</td>
<td>0.01</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Silver</td>
<td>0.01</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Vanadium</td>
<td>–</td>
<td>0.10</td>
<td>–</td>
</tr>
<tr>
<td>Chloride (Cl)</td>
<td>250</td>
<td>600</td>
<td>1100</td>
</tr>
<tr>
<td>Sulfate (SO₄)</td>
<td>200</td>
<td>400</td>
<td>1340</td>
</tr>
<tr>
<td>Nitrate (NO₃)</td>
<td>45</td>
<td>50</td>
<td>600</td>
</tr>
<tr>
<td>Nitrite (NO₂)</td>
<td>0.05</td>
<td>0.10</td>
<td>11</td>
</tr>
<tr>
<td>Ammonium (NH₄)</td>
<td>0.05</td>
<td>0.50</td>
<td>–</td>
</tr>
<tr>
<td>H₂S</td>
<td>0.05</td>
<td>0.10</td>
<td>–</td>
</tr>
<tr>
<td>Bicarbonate</td>
<td>–</td>
<td>–</td>
<td>400</td>
</tr>
<tr>
<td>Nitrogen (N from NO₃ and NO₂ excluded)</td>
<td>2</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Cyanide (CN)</td>
<td>0.05</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

References


11 Feed Manufacturing

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1Acedo-Rico and Asociados, Burgos, Spain; 2Cooperativas Orensanas, Ourense, Spain; 3Agrovic-Nutreco, Barcelona, Spain

11.1 Introduction

Raw materials need to be processed by a combination of different treatments of individual processes to produce an acceptable final feed. This must satisfy all of the nutrient and physical presentation requirements of the animal, except for water.

Before feed manufacturing starts, logistics and nutrition play an important role. Choosing from all the raw materials available in the market suitable for rabbit feeding will be the first step. Feed formulation considering the nutrient requirements of rabbits and the nutritional value of raw materials will produce specific formulae that need to be properly manufactured. Quality control of raw materials is required for achieving good knowledge of their nutritive value. It will also allow checking their stability prior to arriving at the mill, as well as evaluating their organoleptic characteristics. Quality control during the process and on the manufactured feed must be undertaken and, in order to achieve that, hazard analysis and critical control points (HACCP) must be followed, including tracing and tracking.

Once the raw materials arrive at the feed mill and are accepted by the quality control system they will be discharged and placed into bins for further processing. Modern feed mills manufacture the feed in a sequence of processes that run on a batch-type system (Figs 11.1 and 11.2). Following the reception and storage of raw materials, the manufacturing process starts to produce a specific feed associated with a particular type of formulation, previously designed by the nutritionist.

The manufacturing of each feed will always be conditioned by raw material composition and the nutritionist should take into account both individual and collective effects in the feed process itself. The initial process is weighing out according to the formula, followed by grinding for particle size reduction. Following the addition of premixes, homogenization of all the raw materials included in the formula is undertaken. Following an adequate mixing time, manufactured feed is obtained as a mash. However, as will be discussed later, rabbits are not fed mash diets and the feed therefore needs to be further processed by pelleting. Obtaining good quality pellets is one of the main targets of rabbit feed manufacturing and quality control of this step is essential.

There are two main systems used for feed manufacturing. Both use the same individual processes, and the only difference is the sequence in which they are arranged. The pre-milling system is more commonly used in modern feed mills because of economic reasons (e.g. energy cost, investment). In this system, weighing out is done prior to
grading. The pre-grinding system was used more in the past when fewer raw materials were available and mash was the main means of feed presentation. The pre-milling system sequence will be considered in this chapter as it is more commonly used and better for rabbit feed manufacturing.

11.2 Raw Material Addition

Raw materials are extracted from silos according to their concentration in the formula and transferred to a weigh scale, which records individual data on each of them. Such extractions are done either with screws or slides. Good accuracy can be reached with both systems. Scales are constructed under a metallic bin placed over load cells linked by cable to the automation control of the scale. The design of the scale is important: it must permit appropriate conditions of filling and discharge of the raw materials once weighing is finished.

The standard error of weighing for each raw material is constantly corrected by the automation of the weighing system to minimize deviations between the formulation and the actual weight obtained on the scale. Different ranges of weigh scales are usually found in a modern feed mill in order to manage the weighing of raw materials according to the level of inclusion in the formulation. Weighing should be carried out with precise scales with an error <0.5% to prevent wide variations in the characteristics of the final product. For raw materials that are at high levels in the formulation, such as lucerne and wheat bran, the weighing mechanism and the corresponding scale should allow the weighing in a short period of time, with a final period for weight adjustment. On the other hand, the weighing of raw materials that are present at lower rates, such as limestone or dicalcium phosphate when they are stored as bulk in silos, the weighing system and scale should be more precise in order to avoid oversupply.

Equipment must include safety elements to stop the process whenever a deficiency or an excess during weighing occurs. A printed register on every formula of all individual weights should be kept for assuring control.
Fig. 11.2. Feed processing in a modern feed mill.
of the process and final product quality, as well as allowing traceability within the whole operation. Adequate software needs to be used for formulating feeds and limitations in terms of minimum amounts included, and rounding of each raw material should be adjusted according to the weighing system limitations of each feed mill.

11.2.1 Premix addition

Vitamins, minerals, amino acids, coccidiosis-tats and other micronutrients should be weighed on specific scales with greater accuracy than the general scales used for the major raw materials included in the feed. It is advisable to prepare a previous mixture with these products before adding them to the main mixer. Regulations on feed manufacturing in the European Union state that any raw material at a rate >2 kg t⁻¹ must be added to the main mixer, whereas those at a rate <2 kg t⁻¹ need to be premixed in advance to reach this inclusion rate.

All premix materials should be weighed on specific scales, with records of this operation kept, before being added to the main mixer.

11.3 Grinding

Grinding is a critical part of the feed manufacturing process because particle size reduction is a requirement for all types of domestic species and undoubtedly for the rabbit. Raw materials available for feed production vary greatly according to their original texture and particle size: for example, cereals and legumes arrive at the feed mill as whole grains, without any previous treatment, while lucerne, wheat bran, grain co-products and straw arrive as pellets after being ground at the processing plants from which they originate.

Grinding is needed to: (i) reduce particle size in order to increase digestibility in the rabbit; and (ii) obtain an optimum particle size that allows successful mixing of the raw materials and subsequent steam, thus assuring a good pelleting process to obtain pellets of acceptable quality.

As discussed earlier, there are two means of grinding the raw materials, dependent on the feed manufacturing system design: pre-milling, also called post-grinding (Fig. 11.3), and pre-grinding (Fig. 11.4). With pre-milling, the raw materials come to the grinder together, whereas in pre-grinding each ingredient is ground individually. Both systems have advantages and disadvantages.

11.3.1 Pre-grinding system

Each raw material is ground individually and weighing is later in the sequence, in which mash is used as the weighing component of the feed.
The advantages of this system are as follows:

- Particle size distribution for each ingredient can be modified on changing the grinder sieves.
- Advantage can be taken of the maximum grinding capacity because a homogeneous product is ground, so grinding yield is optimized.
- The mixing plant does not depend upon the grinding plant so grinding and mixing can be undertaken separately, while this cannot occur with the pre-milling system.

The disadvantages are as follows:

- There is a risk of final separation problems because of the different particle size distribution of the individual raw materials.
- Raw materials with a high oil content, such as oilseeds, are difficult to grind and cannot be ground individually.
- A larger number of silo-bins is required because the same raw material requires at least two bins, one for reception and another for the ground raw material.
- Materials with a high proportion of hulls, such as oats or barley, are ground more efficiently together with other ingredients such as maize or oilseed meals.
- The storage life of ground products is shorter than that of whole products.

11.3.2 Pre-milling system

When grinding is scheduled after weighing, the whole mix of raw materials travels through the grinding system. As stated before, this system has been more frequently used over the last decade in feed mill design, mainly because of lower production costs and investment for a similar feed manufacturing capacity to the pre-grinding system.

Hammer mill grinders are commonly used with both systems. Two different designs are available according to the shaft layout: vertical or horizontal. The main advantages of the vertical hammer mill are that it requires less space, consumes less energy per tonne ground, gives a lower dispersion of the particle size distribution and has lower maintenance costs (Acedo-Rico, 2006). Control of the hammer mill grinder by an automated system that controls the feeding of the grinder according to energy consumption is necessary. The feeding device should also include one separator of heavy particles and metals.

The use of a sieve before the grinder facilitates the grinding process and saves energy (because particles that are already small bypass the grinder), enlarges the productive life of the grinder (because materials such as minerals, which are very abrasive, can also bypass the grinder) and can increase the efficiency of grinding by decreasing plugging problems at the decompression hoses. A proper air intake will improve the grinding yield and reduce losses due to decreased moisture content.

11.3.3 Particle size

Particle size reduction enables the later pelleting process and consequently favours pellet quality. The finer the grind, the greater the particle size reduction, but the more energy will be expended on the process.

From a physiological standpoint, excessive grinding can increase the retention time of the feed in the intestine (Lang, 1981) and, as a result, nutrient digestibility may increase. In this way it has been found that neutral detergent fibre digestibility is positively correlated with the proportion of particles with a size <0.315 mm. However, an increase in the retention time of feed in the gut is apparently associated with digestive disturbances, which can predispose to diarrhoea (Lebas and Laplace, 1975; Laplace and Lebas, 1977). This increase in the retention time occurs mainly in the caecum, which enlarges, and undesirable fermentation patterns take place. In accordance with this, irregularities of ileo-caecal valve motility with very fine grinding (1 mm sieve) in comparison with coarser grinding (4 mm sieve) have been reported (Pairet et al., 1986).
In practice, fine grinding should be achieved with sieves with a diameter between 2.5 and 3.5 mm, because they permit a good balance between pellet quality and intestinal motility. It is important to take periodic assessments of the particle size distribution to ensure its suitability, because this is influenced by wearing of the parts of the hammer mill (sieves and hammers). Wear due to friction of raw material particles produces coarser mash feeds.

It has been suggested, without any strong experimental evidence, that using two kinds of grinding might be useful: a fine grind for low-fibre ingredients (e.g. cereals, soybean meal) and a coarse grind for fibrous ingredients (e.g. lucerne, straw). It is thought that the former ingredients have greater digestibility when finely ground, while the latter have a mechanical function as ballast when coarsely ground, thus influencing intestinal motility (Mateos and Rial, 1989).

Grinding throughput and particle size vary according to several parameters, as presented in Table 11.1.

In addition, the raw material itself will have a considerable influence on both factors. Identical conditions in a hammer mill will give different particle size distributions depending on the raw material being ground (Table 11.2).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Throughput</th>
<th>Particle size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hammer tip speed</td>
<td>Higher</td>
<td>Decrease</td>
</tr>
<tr>
<td></td>
<td>Lower</td>
<td>Increase</td>
</tr>
<tr>
<td>Number of hammers</td>
<td>Smaller</td>
<td>Increase</td>
</tr>
<tr>
<td></td>
<td>Greater</td>
<td>Decrease</td>
</tr>
<tr>
<td>Sieve hole diameter</td>
<td>Smaller</td>
<td>Decrease</td>
</tr>
<tr>
<td></td>
<td>Larger</td>
<td>Increase</td>
</tr>
</tbody>
</table>

### Table 11.2. General guidelines for particle size distribution for rabbit feeds.

<table>
<thead>
<tr>
<th>Particle size (mm)</th>
<th>Proportion</th>
</tr>
</thead>
<tbody>
<tr>
<td>&gt;1.5</td>
<td>0.15</td>
</tr>
<tr>
<td>1.0–1.5</td>
<td>0.20</td>
</tr>
<tr>
<td>0.5–1.0</td>
<td>0.40</td>
</tr>
<tr>
<td>&lt;0.5</td>
<td>0.25</td>
</tr>
</tbody>
</table>

11.4 Mixing

Mixing is the central process of feed manufacturing. The main objective of the mixing process is to homogenize the different raw materials that have been weighed and ground. Mixing is performed in the main mixer, and the aim is to mix as uniformly as possible particles of different size and density over a short period of time, called the mixing time. The main mixer is the machine in which feed is initially produced, and therefore it is very important to be sure about the mixing capability of the equipment and the uniformity of the complete batch.

It is also important to realize that the process will be mixing raw materials, which represent up to 400–500 kg t⁻¹ of the feed, with micro-ingredients that, in extreme cases such as biotin, vitamin B₁₂ or selenium, are included at levels of 10–100 mg t⁻¹.

Different types of mixing equipment are found in feed mills, but developments over the last decade have led to the use of horizontal batch-type mixers equipped with one or two axes and paddles (Fig. 11.5). These have the following characteristics:

- Adequate mixing capability (1:100,000).
- Low rotating cycle (33 rpm).
- Low mixing time (<180 s).
- Full discharge for minimal cross-contamination.
- Free inside access to enable cleaning and maintenance.
- Possibility of liquid addition (fats and oils, amino acids, organic acids).
- Stainless steel inside coating (desirable).

In order to check good operating function of the mixer, a homogeneity test must be conducted. Such a test consists of taking
10–20 samples from the mixer itself or at the outlet at regular time intervals. These samples are ground and divided in the laboratory into 10–20 g samples that are assessed for either a chemical component of the feed (e.g. salt, manganese) or a component that is specially added for this purpose. The latter components are special indicators (micro-tracers) added to the feed at a rate of around 10 g t⁻¹. Another alternative is to use a cobalt mix that can also replace the usual means of adding this mineral to a premix. Feed manufacturing standards consider a mixture to be of good quality when the coefficient of variation is <5% at a defined mixing time. The mixing time should be established for each item of equipment (Fig. 11.6).

Cross-contamination can occur on the main mixer if attention is not paid to details such as the sequence of feed going through the process, the cleaning programme of the mixer and the adequate full discharge of the whole batch. Cross-contamination is of particular concern in the case of some feed additives and pharmacological products, not only because of possible toxicity for the rabbit, but in terms of human health due to the residues that can accumulate in rabbit meat.

In most feed mills, the only way to minimize dangerous cross-contaminations is to have well-designed manufacturing sequence programmes. After mixing medicated feed in the central mixer, only feeds for animals that are not susceptible to the medicines or for animals whose products are not to be consumed by humans should be manufactured.

Rabbits are especially sensitive to some pharmacological medicines such as ampicillin or lincomycin, so special measures must be taken when planning manufacturing sequences with these antibiotics. Currently, it is possible to prevent these situations more easily through the use of software that includes all of the incompatibilities to be considered before manufacturing the feed. The best means of avoiding these situations is the use of an independent manufacturing line for medicated feeds. This strategy has been designed in modern feed mills with double processing lines, in which just one line is used for medicated feeds, while the other never allows drugs or additives with contamination potential to be added to the feeds being manufactured.
Some raw materials are available in liquid form and there are different places on the feed manufacturing process in which these liquids are included (Fig. 11.7). With rabbit feed production, the main raw materials used in liquid form are fats, oils and glycerol, molasses, amino acids, liquid flavours and enzymes.

11.5 Liquid Addition

11.5.1 Fats, oils and glycerol

Fats, oils and glycerol are added by spraying in the main mixer. It is important to wait for at least 30 seconds from the beginning of the process before starting fat injection into the mixer in order to ensure that the liquid is added to a more homogeneous environment. To facilitate distribution, liquids must
be injected from at least three different places in the mixer.

When the fat level in the diet is >20–30 kg t\(^{-1}\), it is advisable to use mechanical devices to add the extra fat after pelleting because high fat addition in the mixer impairs pellet quality. Because of its lubricating effect, it is convenient to distribute the fat supply at several places. Generally, fat is first added in the mixer. A second addition point can be at the pellet mill outlet to take advantage of the fact that the pellet is still hot and its absorption capacity is high. This addition system is known as ‘fat spray’, and 20 kg fat t\(^{-1}\) fat can be added at this level. Another possible fat addition stage is once the pellet is cool, but here a special mechanism based on a coater where the fat is sprayed onto the pellet is necessary. At this stage, the fat absorption capacity of the pellet is low because it is already cool; in order to increase this capacity, it is convenient to warm the equipment slightly. Therefore, a 3 mm pellet shows a specific surface that is double that of a 6 mm pellet, and its absorption capacity is 50–100% higher (Walter, 1990).

### 11.5.2 Molasses

Molasses is added after the main mixer. Small amounts of molasses (20–30 kg t\(^{-1}\)) can be added on a continuous mixer placed just after the main mixer, while another 20–30 kg t\(^{-1}\) can be added on the pellet conditioner just before pelleting. The inclusion of molasses must be automatically controlled because this is a continuous process and the mash flow through the machine determines the amount of molasses to be added. The longer the mixture remains in the machine and the more regular the advance of the product, the better the quality of the mixture. Because of a high level of sugars, molasses can be caramelized to a solid state. This process occurs when temperatures are >50–60\(^{\circ}\)C; therefore, these temperatures must not be exceeded when adding molasses.

### 11.5.3 Amino acids

Thermoresistant liquids that are added in small amounts, such as amino acids or choline, must be added in the mixer. Choline should be given special attention due to its aggressive action against other vitamins.

### 11.5.4 Liquid flavours

Liquid flavours are ideally added after pelleting, in order to keep their aromatic profile.

### 11.5.5 Enzymes

An important benefit for the poultry industry has been the introduction of enzymes designed to improve the digestibility of diets including barley or wheat. These benefits are not so clear in rabbits, but it is possible that new enzyme activities will be developed for this species. Enzymes can be added as a powder or liquid. As a powder, there is uncertainty about the stability of the product after thermal treatment (pelleting, expansion). To avoid this problem, apart from the technological improvements on the thermal stability of these additives, enzymes can be added as liquids at the cooler outlet, when commercial equipment is available.

### 11.5.6 Other considerations

Liquid addition is normally through volumetric devices, so some measures must be considered:

- To determine exactly and periodically the product density, because when formulating only weights are used, never volumes.
- To control the amounts added by weighing.
- To have the proper measuring equipment available for assessing flow.
11.6 Pelleting

Pelleting is not a single process; it is the combination of three independent processes that always operate in the following sequence: mash conditioning – pelleting – cooling.

The general objective of the process known as pelleting is to turn mash feed into compact pellets. Crumbling is a final process that is occasionally applied to pellets when the intention is to revert back to a mash-type feed presentation. Rabbit feed is always produced as pellets, with good-quality pellets (a low proportion of fines) and a 3–4 mm diameter.

11.6.1 Conditioning

Mash conditioning is achieved by the addition of steam to the conditioner placed on top of the pellet press. Conditioners are cylindrical containers placed horizontally on top of the press (Fig. 11.8).

There are different types of conditioners with varying parameters, including: (i) volume of the conditioner; (ii) number of conditioners; (iii) inside configuration; (iv) outside coating and heating devices; (v) long-term devices; and (vi) friction-type conditioners.

Conditioning of the mash feed is a consequence of steam addition at levels between 2% and 5%, depending on the type of raw materials used. Mash temperatures rise depending on the amount added. Retention time is the second factor influencing conditioning because it is the time in which mash feed remains heated by steam addition. Optimum conditioning of mash varies depending on the type of raw materials in the formulation: high-starch formulas are able to absorb higher amounts of steam than high-fibre formulas. Retention time is independent of temperature achieved and has more to do with the length of the conditioning period, which has a large influence on the mash.

The consequences of both parameters on mash feed are seen on the following:

- Physical properties: conditioned mash increases its plasticity, is less abrasive and tends to be stickier than non-conditioned mash. It should not get wet because this can cause problems later during pelleting. Fibre tends to become stickier than starch.
- Chemical properties: starch gelatinization can be partially caused by temperatures >60°C. Protein stability may be affected if high temperatures are achieved. Enzyme and vitamin stability can also be affected if over-processing occurs.
- Microbiological conditions: natural microbiological contamination of the raw materials will be lower after conditioning. Specific conditioning processes are used to substantially sterilize mash feed for other types of feed production.

![Fig. 11.8. Alternative conditioning systems before pelleting.]
As a rule of thumb, the higher the temperature and the longer the retention time, the more the mash feed will be conditioned and the subsequent pelleting process will be improved. Currently, a wide variety of conditioners are available to feed manufacturers and equipment should be installed in the feed mill depending on the specific targets and logistic situation of each manufacturer. Retention time can vary from 20 s on a single-type conventional conditioner to 240 s on a three-step-type long-term conditioner with an external heat coating.

Mash temperature increase will depend on the raw materials in the formulation. The amount of steam added will depend on its water absorption capability, which varies not only between different types of raw materials but also within raw materials of the same group. Grains absorb higher amounts of steam than fibre raw materials. Within grains, wheat can absorb a higher amount of steam than barley or maize.

Conditioners should always be constructed with stainless steel to maximize the hygiene of the feed, allow good cleaning conditions and increase the length of service of the equipment itself. Good inside access must be allowed for cleaning and maintenance, which should be undertaken on a regular basis. Besides steam addition, specific conditioners such as expanders or extruders input energy to the feed through friction. This allows not only increases in temperature but also increases in internal pressure. This will modify the physical structure of the feed due to an increase in specific weight because of the partial gelatinization of starch.

### 11.6.2 Pelleting

The aim of pelleting is to transform meal into compact pellets of cylindrical shape. As discussed earlier, after conditioning of meal with steam the conditioned product is pressed by rolls to pass through the holes of the pelleting die, which gives the meal the pellet shape.

When pelleting, different parameters associated with the mash, the pellet mill or the process itself will end up affecting final pellet quality. Researchers from Kansas State University, Feed Technology Department, have shown and quantified the main influencing factors (Fig. 11.9) (Behnke, 1996). Formulation is the main factor, but this includes not only the raw materials in the mash feed but also how these have been ground. The particle size of the mash arriving at the pellet mill has a definite influence and should be closely watched. Large particle size (>1.5 mm) hinders pelleting. On the other hand, very small particle size can promote digestive problems in the rabbit. As a consequence, a compromise between both extremes must be sought.

The physicochemical characteristics of the raw materials included in formulations influence the pelleting capacity of

![Fig. 11.9. Main influences on pellet quality (Behnke, 1996).](image)
the feed. Ingredients with a high fat level have a bad influence on pellet quality, because the lubricant effect increases the rate of mash flow through the die. The fibre content of ingredients also has to be watched, because the influence is greater according to the type of fibre rather than the rate of inclusion. Lignified fibre tends to impair pellet quality. Ingredients with high cellulose levels are more flexible on processing and the trend is towards a better pellet quality.

As far as starch is concerned, gelatinization starts at around 60°C, and this process favours pelleting. However, starch sources vary as far as their pelleting ability is concerned. Among grains, wheat gives the best pellet quality while maize gives the worst, with barley intermediate. Soybean meal is normally low in oil content; its variation can affect the pellet quality. Oil seeds such as soybean and sunflower have a high oil content, which impairs pellet quality. Among fibrous sources, straw promotes bad-quality pellets, while lucerne and beet pulp favour good-quality pellets. At low levels of inclusion and high temperatures, molasses improves pellet quality because of sugar caramelization.

Beside pellet quality, raw material inclusion on formulation has a big influence not only on pellet quality (Table 11.3) but also on throughput flow on the die (capacity) and abrasiveness effects on dies and rolls (wear). Minerals are abrasive, especially limestone, and therefore small particle-size limestone must be used. Because of their high fibre content, oats are also abrasive for the die. Manioc can contain significant amounts of silica, which is again very abrasive for the die and shortens its operating life.

Considering the influence of raw materials on pellet quality, modern feed mills use a larger number of raw materials than older mills. A wider range of ingredients creates a better opportunity to produce good-quality pellets. The mash density of raw materials has a considerable influence on compacting, as low-density materials tend to create more difficulties in pellet production.

<table>
<thead>
<tr>
<th>Raw material</th>
<th>Quality</th>
<th>Capacity</th>
<th>Abrasiveness</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wheat</td>
<td>7</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>Maize</td>
<td>5</td>
<td>7</td>
<td>4</td>
</tr>
<tr>
<td>Barley</td>
<td>6</td>
<td>7</td>
<td>5</td>
</tr>
<tr>
<td>Oats</td>
<td>3</td>
<td>4</td>
<td>7</td>
</tr>
<tr>
<td>Full-fat soybean meal</td>
<td>3</td>
<td>8</td>
<td>4</td>
</tr>
<tr>
<td>Soybean meal</td>
<td>6</td>
<td>6</td>
<td>5</td>
</tr>
<tr>
<td>Sunflower meal</td>
<td>6</td>
<td>6</td>
<td>5</td>
</tr>
<tr>
<td>Rapeseed meal</td>
<td>6</td>
<td>6</td>
<td>5</td>
</tr>
<tr>
<td>Palm kernel meal</td>
<td>6</td>
<td>4</td>
<td>6</td>
</tr>
<tr>
<td>Coconut meal</td>
<td>6</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>Groundnut meal</td>
<td>8</td>
<td>6</td>
<td>5</td>
</tr>
<tr>
<td>Cottonseed meal</td>
<td>6</td>
<td>6</td>
<td>5</td>
</tr>
<tr>
<td>Carob meal</td>
<td>5</td>
<td>2</td>
<td>9</td>
</tr>
<tr>
<td>Dried grains and solubles</td>
<td>3</td>
<td>4</td>
<td>5</td>
</tr>
<tr>
<td>Brewers’ by-products</td>
<td>7</td>
<td>6</td>
<td>5</td>
</tr>
<tr>
<td>Meat and bone meal</td>
<td>4</td>
<td>5</td>
<td>7</td>
</tr>
<tr>
<td>Citrus pulp</td>
<td>7</td>
<td>4</td>
<td>6</td>
</tr>
<tr>
<td>Beet pulp</td>
<td>8</td>
<td>3</td>
<td>6</td>
</tr>
<tr>
<td>Lucerne meal</td>
<td>7</td>
<td>3</td>
<td>7</td>
</tr>
<tr>
<td>Wheat bran</td>
<td>6</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>Minerals</td>
<td>2</td>
<td>4</td>
<td>10</td>
</tr>
</tbody>
</table>

As stated earlier, conditioning is very important and in general treatment with the highest temperature and retention time will give better pellet quality, not only with low fines but also with good flexibility. Pellet press equipment and spare parts (dies and rolls) obviously have the greatest influence on the quality of rabbit pellets. The die holes most frequently used for rabbit feed are between 3 and 4 mm.

In addition to diameter, the length of die holes (known as compression) should be well defined because both factors must be balanced in order to obtain good-quality pellets and adequate throughput in the press. For a given die hole diameter, more compacting will be achieved with longer
lengths and a lower press throughput will be obtained. Energy consumption at the pellet mill is directly related to the compacting capacity and therefore it is related to the die length and hole diameter.

Rolls are used to press mash through the die, and also have a big influence on pellet quality. It is advisable to use a set of rolls with the same die because they will fit better. Die roll distance must be between very narrow limits, around 0.2 mm, in order to reach a maximum pellet mill yield. If the gap is large, pressure on the mash decreases and the product remains inside the hole for longer. This results in lower pellet yields and a risk of excessively toasting the pellet. Dies and rolls will wear and good maintenance procedures should be used, changing both at a time in order to maximize pelleting efficiency. Figure 11.9 shows the influence of dies and rolls on final pellet quality.

11.6.3 Cooling

Since pellets obtained from the pellet mill are hot (50 – 65°C) and moist (140–160 g moisture kg⁻¹), they need to be dried and cooled down before they are stored in a silo. The target is to reduce the moisture content of the pellets to the same level as the mash before conditioning. Temperature should be reduced to ambient levels. Warm pellets are very fragile and deteriorate easily. It is therefore important to avoid deep falls and violent impacts in the pipes or in the subsequent management equipment, otherwise fines will increase.

Coolers are set usually just below the pellet press to avoid the shaking of pellets through pipes or mechanical transports. Counterflow-type coolers are mostly used because of their efficiency and good treatment of pellets. Other types such as belt coolers or the vertical type are still in operation, but are no longer recommended. External air is usually taken from inside the mill and passed through pellets placed inside the cooler. Warm air is extracted through large-diameter galvanized or stainless steel constructed pipes connected to a ventilator and taken outside the mill, usually via the roof. After cooling, good-quality pellets must be passed through a sieve to remove fines that will be directed to reprocessing at the conditioner. Cooling also has an influence on pellet quality (Fig. 11.9).

11.6.4 Pellet quality

Good pellet quality is a main target for feed mills producing this type of feed due to the large influence it has on rabbit production yields. Fines have been shown to have a negative effect on sanitary conditions and are frequently blamed for digestive or respiratory disturbances when present in the final feed. As discussed earlier, different factors affect pellet quality, but most must be considered before processing starts. Problems are usually seen once pelleting has started and there are few possibilities available to change pellet quality:

- Conditioning: the amount of steam can be increased and mash temperature will rise, but excess moisture can make rolls slip on the die and pellet yield will decrease.
- Pelleting: distances between rolls and the die can be adjusted, which can increase or reduce production at the press.

The use of binders such as lignosulphonates, vegetable gums, bentonites and sepiolites is sometimes used to improve pellet quality. When poor-quality pellets are obtained, the different process levels should all be analysed in order to improve quality. Consideration should be given to grinding, conditioning, pelleting, cooling and final feed delivery to the farms.

11.7 Other Processing Methods

11.7.1 Expansion

The expander is a thick-walled mixer pipe with an axle endowed with elements for mixing and kneading. The pipe has internal bolts and steam injector valves. The pres-
sure is maintained thanks to the final screw, which modifies the annular gap at the end of the pipe. The expander must be installed before the pellet mill with a bypass circuit to allow the double option of pelleting the product after the expander or transporting the product directly to the cooler.

Energy consumption is lower than for the extrusion process (see next section), but higher than for the pelleting process alone, although this extra energy consumption is partially compensated for by a higher throughput of the pellet mill after expansion. During expansion, mash supports a high temperature and pressure (Fig. 11.10), which greatly facilitates the following pelleting, even when including raw materials with low pelleting ability. The expansion process has an intermediate effect between extrusion and pelleting with regard to vitamin stability.

Expansion is not as severe a treatment as extrusion. Protein denaturation is very limited, so there is not a clear effect on the thermolabile antinutritional factors (ANFs) of legumes. In the same way, starch is only partially gelatinized.

11.7.2 Extrusion

Extrusion has been widely used in the food industry and pet food manufacturing for some considerable time. Application to the feed industry is more recent, and started with oilseed processing basically for denaturing ANFs. Subsequently, extrusion developed for the manufacture of starter-type diets for non-ruminant species. The mechanical process of the extruder combines energy input to mash feed by steam and shearing forces through friction of the mash feed against the inside walls and barrels of the extruder. At the end of the extruder barrel a die is located to allow pellet shape formation of the final extruded product.

Extrusion has three main effects on the nutritional value of the treated feed:

- Proteins are denatured, without affecting the amino acids. Proteins partially lose their tertiary and quaternary structure, but amino acid availability is not altered if the process is run properly.

![Fig. 11.10. Pressure and temperature curves during the expanding process (Pipa and Frank, 1989).](image-url)
The immediate consequence is a deactivation of thermally labile ANFs.

- Starch is gelatinized. This makes it more available, especially to young non-ruminants with immature endogenous enzyme production.
- Hygiene is improved. The temperature and pressure result in a low bacterial and mould count of the feed and can partially sterilize it.

However, rabbit feeds have a low starch content and usual protein sources such as soybean meal have been previously heat treated, so extrusion is inappropriate.

The effects on structural changes occurring during the extrusion process on the fermentation pattern in the rabbit hindgut have not been widely studied. Extrusion treatment implies high temperature and the thermal stability of vitamins and other components added to the feed must be known.

Vitamin K destruction will depend on the source used, so either the most stable form is used (menadione bisulfate) or the levels are increased to reach the desired levels in the final feed. Vitamin stability is also affected by other factors, such as the presence of choline chloride in the vitamin-mineral premix. Vitamin K is especially susceptible to choline chloride. Coelho (1996) determined that vitamin K content decreased by 47% of the original activity after 2 months of storage when choline chloride was included in the premix, whereas the activity remained at 98% of the original value when choline chloride was excluded from the premix. This effect will vary according to the choline chloride level in the premix, as well as the proportion carried on the premix. The addition of choline chloride directly to the main mixer in a liquid form can be a useful means of avoiding these problems.

11.8 Feed Presentation

Good-quality pellets are needed because of the aversion of rabbits to fines (Lebas, 1975): if a high proportion of fines is present in the final feed, rabbits almost stop eating for 2–3 days. This is why there is currently virtually no discussion on feed presentation to the rabbit; it is universally accepted that presentation must be as pellets and this is the only physical presentation form used commercially in industrial rabbit production. When considering small-scale rabbit farms without any feed-purchasing possibility, it is more profitable either to use locally grown raw materials or to supply the raw materials as such without any grinding. Whenever essential particle size reduction to facilitate feed manipulation is considered, grinding must be very coarse to prevent as much as possible the presence of fine particles.

An important practical point to consider is the ideal pellet size for the rabbit. A pellet diameter >5 mm promotes feed losses because the animal discards such pellets (Lebas, 1975). Several authors (Maertens, 1994; Maertens and Vermeulen, 1995) have attempted to clarify the situation for smaller diameters by comparing 2.5, 3.2 and 4.8 mm. At weaning, there were no statistically significant differences between the different diameters as far as growth and feed conversion rates are concerned. However, there was a negative trend as the diameter fell, which contradicts the general opinion that a small pellet favours feed intake of rabbit pups. After weaning, the best technical response was obtained with 4.8 mm pellets. Furthermore, if pups consumed a 4.8 mm pellet before weaning and they were then moved to a 2.5 mm pellet, the growth rate decreased. Therefore, the growing/finishing feed for rabbits must never have a diameter lower than the doe–pup feed.

As a general rule, it is advisable to use a pellet diameter between 3 and 5 mm. Pellet length will be between 2- to 2.5-times pellet thickness, that is to say from 6 to 12.5 mm. If the length is greater, the animal can waste feed because of poor cutter adjustment; when trying to eat the pellet, after biting it the rest of the pellet falls down. Another practical rule is to use the same pellet diameter for all rabbit ages and physiological stages. Rabbit feed should be sieved just before bagging or loaded onto bulk trucks to remove fines that could still be present after the cooling and transport of pellets to the loading area of the mill.
11.9 Quality Control

The main objective of a feed mill is to supply properly manufactured compound feeds to customers whenever they need them, and consistently including the necessary nutrients to satisfy animal requirements according to the kind of production (Jones, 1996). Consequently, quality control must cover all of the processes and services that facilitate the fulfilment of this objective, not only based on chemical analysis of raw materials and final feeds. This concept would represent more a quality assurance than a quality control.

Quality assurance is expanding in all economic sectors, including feed manufacturing. Currently, there are several systems that try to guarantee this quality to the consumer. In this way, the ISO 9001 and 22000 rules and others give a guarantee to the consumer that a processing methodology exists and that this methodology is externally audited. There are also other systems, including the Dutch rules on good manufacturing practice (GMP), which have the advantage that they are more orientated to the feed mill industry. It is a company decision to ask for this kind of certification, but, in any case, it is of fundamental importance to carry out these working philosophies in feed milling.

GMP is a very wide area but, in general, the following documents should be available:

- Specifications for the raw materials received, previous mixes, additives and medicated premixes.
- Specifications for the feeds to be supplied.
- A descriptive diagram of the feed manufacturing process, with critical points identified.
- A precise description of all the controls and inspections at the critical points of the production process from raw material until the final product.
- A description of the measurement methods to be used in controls, indicating, if necessary, the regulations or bibliography on which they are based.

Development of these approaches, as well as the regulations on residues, diffuse pollution and other aspects of feed milling, are very important for the quality assurance of rabbit feed.

11.10 Raw Material and Feed Control

As previously discussed, the feed manufacturing process consists of particle size reduction (grinding), blending of raw materials (mixing) and feed shaping (pelleting). There is no process that significantly transforms the raw materials; there is only a partial starch gelatinization and/or protein denaturing. Therefore, the nutritional quality of feeds depends on the nutritional quality of the raw materials and, consequently, their control is decisive in feed manufacturing.

Raw material quality must be evaluated through two different methods: (i) analytical values; and (ii) organoleptic parameters. All raw material loads that come to the feed mill, either by truck, railway or ship, must be sampled. The first evaluation of the raw material before unloading is the organoleptic evaluation. This includes the following:

- A check if load identification is correct.
- Detecting the presence of foreign materials such as other raw materials, soil, metals and a great diversity of substances that can contaminate the raw material during the harvest, transport or production process.
- Detecting the presence of insects.
- Recognizing colours that do not correspond to the raw material. These can be due to defects of the process.
- Identifying off or strange odours, which may be due to previous fermentation.

The reception operator of raw materials should thoroughly understand this subject, because it a basic tool for the quality assurance of the feed.

Chemical analysis of raw materials will help to assess their nutritional quality, either directly or indirectly, to complete the quality control. The information obtained can be classified according to origin, supplier and so on. Factors that should be routinely analysed
in raw materials as well as in final feeds are moisture, crude protein, fibre, ether extract and ash, as well as urease activity in soybean meal. Other analysis can be sporadically undertaken at the feed mill or external laboratories for amino acids, minerals, vitamins, fatty acid profiles, other type of carbohydrates and so on. Periodic controls of different ANFs of the raw materials used should also be undertaken, including tannins, antitrypsin factors, alkaloids and glucosinolates, depending on the feedstuff used.

11.10.4 Ether extract

This analysis is an indicator of the fat content. Because of the high energetic value of fats, it is important to know precisely not only the amount but also the quality of this fat. Raw materials that are very rich in fat, such as oilseeds, must be frequently limited because of their variation according to their origin. At the feed mill, when volumetric systems for fat addition are used, it is necessary to increase controls to prevent deviations from expected formulations.

11.10.5 Ash

This analysis is an indication of the mineral content. Higher than normal figures can indicate some degree of contamination, and a complementary analysis on insoluble material for chlorhidric acid would suggest the presence of silica (soil). In feeds, figures under or over those expected indicate incorrect additions of limestone, phosphate or salt. It is remarkable how important it is to have an accurate system for salt addition, because this can be the main reason for feed rejection problems by rabbits. An excess as well as a deficiency can cause problems.

11.10.1 Moisture

Water contents >140 g kg\(^{-1}\) stimulate microorganism growth, particularly of fungi, which can produce mycotoxins. Another reason to control moisture is that the dilution of the nutritive value of the feedstuff, and therefore a moisture level over that specified in the contract, will result in economic losses.

11.10.2 Crude protein

Protein variation in a raw material, as well as in the feed, implies amino acid compositional changes that can be important in terms of the performance of the animals. Rabbits are sensitive not only to protein deficiency, but also to protein excess because of the risk of digestive disturbances.

11.10.3 Crude fibre

An increase in fibre reduces digestibility and therefore the nutritive value. Because rabbits have specific fibre requirements for the regulation of intestinal motility, this is an important parameter to control not only in feedstuffs, but also in the finished feed. As discussed in other chapters, other kinds of fibre analysis (e.g. acid detergent fibre, neutral detergent fibre) or analysis of fractions (e.g. lignin) may be useful, especially for raw materials with an extreme content of any kind of these fractions (e.g. sugarbeet pulp is high in hemicelluloses, grape marc is rich in lignin), where abnormal intestinal behaviour can be expected.

11.10.6 Analysis

Information obtained from chemical analysis must be available as fast as possible to be effective. Action must be taken soon after a deviation from the expected values has been identified because the figure is not so useful after an excessive time. In any case, it is good to have historical values, even if not so recent, in order to identify trends according to the supplier or the year of harvest and
hence act to prevent problems that may arise.

As far as fast analysis is concerned, the near infrared reflectance technique allows online information if connected to the production line and, if not, supplies information in a few minutes. Another fast and low-cost technique is microscopy, which allows a qualitative and sometimes semi-quantitative evaluation of feed ingredients. This technique is very useful to detect contamination or adulteration in raw materials (Bates, 1994).

Microbiological analysis (of moulds, yeasts, coliforms, enterobacteria, Salmonella and so on) is essential, because rabbits are very sensitive to the bacteriological quality of their feed. With all livestock feeds, it is necessary to ensure the absence of microorganisms that can cause pathological problems, especially those that can transmit disease to the consumer.

Due to the low persistence of Salmonella in feed, analytical control is difficult, so it is more interesting to assess enterobacteria, which gives an insight into the effectiveness of treatments. After pelleting, the target value is \(<100\text{ c.f.u. g}^{-1}\), with action necessary if values are between 100 and 1000 c.f.u. g\(^{-1}\).

Mycotoxins are metabolites produced by different fungi. They produce various illnesses in animals that consume them and can be harmful at very low concentrations (parts per billion). There are many fungi, but those that can really cause problems are Aspergillus, Fusarium and Penicillium species (Meronuck and Concibido, 1996). The most frequent mycotoxins produced by Aspergillus are aflatoxins, specifically B1 and B2. From the genus Fusarium, the most common mycotoxins are the trichothecene family, especially T-2, as well as zearalenone and deoxynivalenol.

There is little information available on the effects of mycotoxins in rabbits. Most data come from other species, but, generally speaking, the mycotoxins included in the international regulations are the aflatoxins, where a maximum limit has been established in order to allow a raw material to be marketed. Different countries have limits for other mycotoxins, but currently it is still difficult to establish safe limits for rabbit health and residues. In 2006, the European Union gave guidance values for deoxynivalenol, zearalenone, ochratoxin A, T-2, HT-2 and fumonisins (Official Journal of the European Union, August 23, 2006). Mycotoxin detection is an indicator of mould growth in the raw material or in the feed analysed, but many other mycotoxins than those detected can be present.

Mycotoxin control can be undertaken by chromatography and different commercial kits are available to quantitatively determine the presence of the most frequent and dangerous mycotoxins.

### 11.11 Pellet Quality

Because of their particular way of consuming feed, rabbits are extremely sensitive to the presence of fines in the feeder; when fines are present, they can enter the respiratory system and cause respiratory problems. To solve this situation, feeders with small holes at the bottom that allow the fall of feed fines are used. Unfortunately, this implies a feed loss because the feed falls into the faeces pit. This loss will increase the feed conversion ratio proportionally to the fines content of the feed. This is the reason why a high-durability pellet must be produced at the feed mill. However, pellet hardness must not be too high because this can cause rabbits, especially rabbit pups, to refuse the feed.

Different methods can be used to measure pellet durability and hardness. Hardness is defined as the pellet’s resistance to pressure breakage. This parameter is measured by means of a spring device (hard meter), where pressure is gradually increased on the pellet with a screw, up to when the breakage occurs. The pressure on the pellet is recorded on a scale. This parameter assesses pellet hardness, but not durability. A very hard pellet with a low elasticity can be very fragile and can produce a high amount of fines.

The determination of pellet durability is done with a simple mechanism that was originally developed by Professor H.B. Pfost at Kansas State University, and is currently used at many feed mills with minor changes...
This equipment consists of a normalized box, which turns at a rate of 50 rpm for 10 min, with a specific amount of feed inside. Subsequently, the pellets and fines obtained are weighed. As a general rule, pellet durability for rabbit feed must not be <97%. Devices such as the Holmen pellet tester also exist. This can undertake online measures when the pellets are produced and, with this information, corrections on one or several parameters can be made. Both systems are reliable, and each feed compounder should generate its own figures and draw up the optimum standards for every batch of pellet feeds produced (Acedo-Rico, 2006).

11.12 Feed Labelling

Substantial legislation exists on feeds and their labelling rules. The objective is to inform the purchaser on feed composition, the inclusion of additives, recommended periods of use and any withdrawal period, if necessary. Another basic objective of the legislation is to guarantee that feeds do not contain undesirable substances or microorganisms, either for the animals or the consumer. Specific legislation exists for medicated feeds, the main aims of which are the obligatory nature of using licensed products and their inclusion in the feed through veterinary prescription.

11.13 Processing Control

Each feed mill must establish its own processing control, well adapted to its specific requirements and the capacity to follow it (e.g. personnel, laboratory). As a general rule, it is necessary to take into account the following aspects (Jones, 1996):

- Raw materials inventory, which must be taken at least once a day. This measure allows the mill to detect if any raw material has not been properly used.
- Silo-bin cleaning. The frequency will vary according to the raw material stored.
- Checking the equipment at the cleaning stage.
- Grinding.
- Weighing systems.
- Mixing.
- Pelleting and cooling.
- Conditioning temperatures.
- Truck cleaning and control.

The following steps must be followed when a problem arises:

1. Is the analysis correct? First, the laboratory result must be checked or repeated.
2. How was the sample taken? The sample may have been incorrectly taken and it is advisable to repeat the analysis on another sample from the same batch.
3. Is only one nutrient or are several nutrients out of the established range? The latter may indicate the absence of a raw material from the formulated feed.
4. Was the process undertaken by the usual person?
5. Check the inventories to rule out discrepancies that could indicate mistaken identifications.
6. Check the measurement equipment.
7. Check the raw material and finished feed silo bins.
8. Re-evaluate the mixing times.
9. Check the values of the raw materials used to detect possible sporadic lot failures.
10. Check the formulation of the raw material matrix and the formulation itself to verify that the figures are up to date.

It is obvious that if serious problems arise, it is necessary to proceed rapidly to avoid animals consuming a defective feed. Rabbits are probably one of the most sensitive species to feed faults.

11.13.1 Process controls

Documentation is important not only to guide the feed compounder in what is to be done, but also to show to external inspectors how the process works at the feed mill:

- Control of documentation: documents that are required by the feed safety system must be maintained.
• Control of records: records must be established and maintained to provide evidence of compliance with requirements and of the effective operation of the feed safety system.

Management responsibility
Senior management must demonstrate their involvement in the development and implementation of the feed safety system and the continuous improvement of its effectiveness.

Management of resources
Personnel who perform work affecting feed safety must be competent, based on appropriate education, training, skills and experience. The company must have sufficient personnel with the skills and qualifications required for the production of safe feed.

Production must be carried out in an environment in which it is not possible for the presence of potentially hazardous substances to lead to an unacceptable level of those substances in feed.

Production buildings may not stand on or near places that clearly present a danger to feed safety, such as contaminated sites, waste sites and so on. If the environment entails risks for feed safety, the company must show by way of a risk analysis that the risks are sufficiently controlled.

Work environment
• Clearing: dust, dirt and feed remains can form a major breeding ground for bacteria that can contaminate feed materials. The accumulation of such substances must therefore be avoided as much as possible.
• Cleaning: cleaning programmes must be introduced. These should describe responsibilities and methods, frequency and times.
• Pest control: effective programmes must be used for combating harmful organisms. Everything that is reasonably possible and effective must be done to keep birds, pets and vermin away from production areas.

• Waste control: waste and material that is not appropriate as feed must be identified as such and kept separate. If such materials contain hazardous concentrations of feed medicines, contaminants or other hazards, they must be removed in a proper fashion and may not be used as feed. Waste must be collected and stored in clearly designated bins or containers. Places in which waste is collected and stored must be included in the cleaning and disinfection programmes.

Identification and traceability
The factory must take appropriate measures to ensure that the feed produced can be traced effectively. It must maintain a register with the relevant details with respect to purchase, production and sale, which can be used to trace the feed from reception to delivery, including export to the final destination (Product Board Animal Feed, 2008c).

11.14 Carry-over Control
In order to avoid carry-over (or cross-contamination) it is necessary to know the factory risk situation and its limits to avoid it. When measuring the carry-over of additives and veterinary medical products in an installation, there must be an examination using a diagram and the actual layout of the factory to determine which areas may be subject to carry-over. A basic principle in determining carry-over in a factory is that the degree of carry-over as a result of return flows is known and controlled.

The greatest carry-over of additives and veterinary medical products occurs in the weighing process, mixing and transport. The place where premixes are added should be as close to the mixer as possible. In addition, a considerable amount of carry-over can occur in the press line and during loading.

The most popular method of controlling carry-over is based on cobalt. The control procedure includes processing three batches from the same feed mix. The first
batch serves to determine the natural cobalt level in the feed in question. A cobalt mix is added to the second batch and the third production batch gives a picture of the carry-over in the installation (Product Board Animal Feed, 2008a). If the undesired carry-over of critical additives and veterinary medical products is expected then a company may take measures by drawing up a mandatory production sequence.

11.15 Hazard Analysis and Critical Control Points

A hazard can be describe as the contamination of animal feed, or a condition leading to the contamination of animal feed, with possible negative implications for human or animal health (Product Board Animal Feed, 2008b).

Three types of hazard can be defined:

- Chemical: residues of pesticides, hormones, additives and veterinary drugs, heavy metals, environmental pollution, mycotoxins, polychlorinated biphenyls, dioxins, cleaning agents, lubricants, mineral oils and so on.
- Microbiological hazards: veterinary risk (animal diseases) and pathogenic organisms such as Salmonella, enterobacteria and fungi (the latter group as indicator organisms).
- Physical hazards: glass, plastic, metal parts, stones, bone and pieces of packaging.

From these three types of possible hazard, the HACCP team should determine which are actually a risk – this is a risk assessment. The word ‘risk’ is defined by two elements: the seriousness and probability of a potential hazard. The hazard must be of such a nature that it realistically could be expected to occur (probability) and that eliminating or reducing it to an acceptable level is essential for manufacturing safe animal feed (seriousness).

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12 Feed Formulation

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12.1 Introduction

This chapter deals with nutritional allowances under practical conditions for intensive meat rabbit production. In recent years, the performance of intensively reared rabbits has regularly increased because of improvements in genetics, management and pathology. Currently, the rate of improvement in productivity is comparable to that obtained in other intensively farmed domestic species. Breeding does are able to wean >60 pups and produce ten times their weight in milk per year, whereas the fast growth rate allows multiplication of their birth weight by 40–50 at the end of the fattening period (60–70 days of age). Rabbits are herbivorous animals and require a high dietary fibre content (about one-third of cell wall constituents on an as-fed basis) to prevent digestive disorders. Furthermore, rabbit diets must be designed to allow a sufficient nutrient intake to meet the high nutritional requirements per unit of body weight. Therefore, factors affecting feed consumption, such as nutrient imbalances, inadequate raw material composition and pellet quality, are a major concern in this species. The average composition of commercial feeds in Spain (Table 12.1) reflects this situation, as feeds typically simultaneously contain a high proportion both of fibrous and highly concentrated ingredients.

Prior to establishing practical feeding standards, the effect of varying dietary energy and nutrient content on rabbit performance will be discussed. This information allows the formulation of diets on a performance–cost basis according to market prices. The effects of diet composition on meat quality and pathology should also be considered, as reviewed in Chapters 9 and 10.

12.2 Level of Fibre

Rabbits are capable of achieving a good growth performance on high-fibre diets as a result of their peculiar digestive physiology (see Chapter 1). As shown in Fig. 12.1, maximal growth rates are reached with diets containing around 180–210 acid detergent fibre (ADF) g kg\(^{-1}\), which corresponds to approximately 9.7–10.3 MJ digestible energy (DE) kg\(^{-1}\) when no fat is added. Above this fibre level, fattening rabbits are not able to maintain DE intake. High-fibre diets (350 g ADF kg\(^{-1}\) dry matter (DM)) decrease the average daily gain and feed conversion rate by 30% and 50%, respectively, as compared with diets containing the optimal values. This impairment might be higher in young animals (de Blas et al., 1995; Feugier et al., 2006). High-fibrous diets are frequently formulated to limit the incidence of diarrhoea. However, several
studies have shown that an increase in dietary ADF content from 190–210 to 240–260 g kg\(^{-1}\) in fact increases fattening mortality (Gutiérrez et al., 2002; Romero et al., 2009) and sanitary risk (mortality plus morbidity; Feugier et al., 2006) and leads to an impairment in the structure of the mucosa (Álvarez et al., 2007).

Conversely, a minimal content of dietary fibre is required to decrease total and caecal mean retention time (see Chapter 5) and to maximize DE intake and weight gain (Fig. 12.1). An adequate fibre level also dilutes dietary and ileal starch and protein content and reduces total microbial growth (García et al., 2000), digestive disorders and fattening mortality (see Chapter 10).

Three long-term studies (>1 year) conducted with rabbit does have compared seven diets containing from 162 to 216 g ADF kg\(^{-1}\) and no added fat (Méndez et al., 1986; Barreto and de Blas, 1993; Cervera et al., 1993). The results indicate that rabbit does maintain DE intake by increasing consumption as the dietary fibre content increases. The type of feed had no influence on reproductive performance, but litter weight at weaning decreased (by about 11%) when dietary ADF content was >180 g (equivalent to 10 MJ DE kg\(^{-1}\)).

De Blas et al. (1995) studied the effect of the substitution of starch for fibre in rabbit does using five iso-energetic diets (10.6 MJ DE kg\(^{-1}\)) formulated with increasing levels of ADF (from 167 to 221 g kg\(^{-1}\)) and ether extract (from 20 to 51 g kg\(^{-1}\)) at the expense of the level of starch, which decreased from 237 to 117 g kg\(^{-1}\). The type of diet had little effect on DM intake. However, regression analyses indicated that dietary levels of neutral detergent fibre (NDF), ADF and starch of around 320, 170 and 180 g kg\(^{-1}\), respectively, were optimal for maximal reproductive performance,

### Table 12.1. Usual range of ingredient composition of feeds for rabbits in Spain (g kg\(^{-1}\)).

<table>
<thead>
<tr>
<th>Ingredient</th>
<th>Amount</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cereal grains*</td>
<td>100–200</td>
</tr>
<tr>
<td>Animal and vegetable fats</td>
<td>5–30</td>
</tr>
<tr>
<td>Molasses</td>
<td>0–30</td>
</tr>
<tr>
<td>Beet, apple and citrus pulp, soy hulls</td>
<td>0–100</td>
</tr>
<tr>
<td>Cereal co-products(^\text{h})</td>
<td>150–350</td>
</tr>
<tr>
<td>Lucerne hay</td>
<td>150–300</td>
</tr>
<tr>
<td>Lignified fibrous co-products(^\text{c})</td>
<td>50–150</td>
</tr>
<tr>
<td>Protein concentrates(^\text{d})</td>
<td>120–220</td>
</tr>
</tbody>
</table>

\(^*\)Mainly barley and wheat.  
\(^\text{h}\)Mainly wheat bran, maize gluten feed and distillers’ co-products.  
\(^\text{c}\)Mainly wheat straw, olive and grape co-products.  
\(^\text{d}\)Mainly sunflower, soybean, rapeseed and palm kernel meal.
growth of young rabbits and feed efficiency (Fig. 12.2). The impairment observed in rabbits fed the highest levels of fibre might be explained by higher fermentation losses in the caecum, together with an insufficient uptake of glucose from the gut to meet the requirements for pregnancy and milk lactose synthesis. The negative effects of high starch concentrations in the diet were related to an increase in the incidence of diarrhoea.

12.3 Type of Fibre

Several studies have shown that cell wall composition and physical structure influence feed digestion in iso-fibrous diets (see Chapter 5). Lucerne hay is the most widely used fibre source in rabbit diets, accounting for around one-quarter of commercial feeds in Spain (see Table 12.1). Lucerne hay is highly palatable and provides both long and digestible fibre, which allows an adequate transit time of the digesta and a balanced growth of the caecal flora.

Dietary inclusion of fibrous by-products at levels of 100–150 g kg⁻¹ has little effect on rabbit performance (Motta et al., 1996; García et al., 2002; Nicodemus et al., 2002). However, an excessive substitution of lucerne hay with highly lignified sources of fibre depresses energy digestibility and caecal fermentative activity (García et al., 1999, 2000) and impairs average daily gain and feed efficiency by 10 and 20%, respectively, in diets with a 50:50 ratio of lucerne hay to grape marc (Parigi-Bini and Chiericato, 1980; Motta et al., 1996).

The inclusion of moderate levels of soluble fibre (120 g soluble NDF kg⁻¹) in post-weaning diets has been shown to improve the immune response and reduce the deterioration of mucosa after weaning, pathogen proliferation in the gut and fattening mortality (Fabre et al., 2006; Gómez-Conde et al., 2007; see Chapters 5 and 10). However, the substitution of high levels of lucerne hay with digestible fibre sources, such as beet and citrus pulps, increases the relative weight of caecal contents and the retention time in the gut (Fraga et al., 1991; García et al., 1993, 1999). As a result, there is a decrease in feed intake and performance in both fattening rabbits and breeding does (Perez et al., 1994; Nicodemus et al., 1999).
Similarly, a minimal proportion of particles >0.315 mm seems to be required to maximize feed intake, growth and lactation performance in rabbits (Nicodemus et al., 2006).

These results indicate a benefit of combining different sources of fibre when trying to substitute a high proportion of lucerne hay in the diet (Nicodemus et al., 2007). However, further research is needed to establish feeding recommendations based upon this issue.

12.4 Fat Supplementation

The effect of the addition of 30 g kg\(^{-1}\) of different sources of fat (tallow, lard, deodorized oleins or sunflower oil) in iso-fibrous diets for fattening rabbits has been studied by several authors (Partridge et al., 1986; Santomá et al., 1987; Fernández and Fraga, 1992). In these studies, dietary digestible protein (DP) content was increased with fat addition to keep the DP:DE ratio as constant as possible. Fat inclusion had a positive effect on energy digestibility (5% on average) and feed efficiency (7%), but not on growth rate, as feed intake decreased by 6%. No interaction was found between the type and level of supplemental fat. Therefore, the value of fat addition to fattening feeds should be established on an energy-cost basis also taking into account the effects of fat quality on carcass quality and pellet stability (see Chapters 9 and 11).

Several long-term (9–24 months) studies (Fraga et al., 1987; Maertens and De Groote, 1988a; Barreto and de Blas, 1993; Cervera et al., 1993) have studied the effect of fat addition in iso-fibrous diets (200 g ADF kg\(^{-1}\)) on the performance of breeding does. The beneficial effects of fat inclusion were more pronounced for does than for growing rabbits. The inclusion of 35 g fat kg\(^{-1}\) in doe diets increased DE intake by 14.5% on average, which promoted an increase in milk yield, and litter weight at weaning by 8.5%. Neither the body weight of breeding does nor fertility or prolificacy were affected by the type of diet, but pup mortality decreased in litters with more than nine pups (Fraga et al., 1987). These results indicate that the use of fat to increase the energy concentration of feeds (>11–11.5 MJ DE kg\(^{-1}\)) maximizes milk production and litter growth in highly productive rabbits when the remaining components of the diet (fibre, protein and starch) are kept in balance.

Researchers have also shown that diets enriched in n-3 polyunsaturated fatty acids either from linseed (Maertens et al., 2005) or fish oil (Lleonart, 2005) decrease mortality during lactation and improve the reproductive efficiency of breeding rabbit does. Another study (Castellini et al., 2003) has demonstrated a positive effect of dietary linseed supplementation on the semen quality of bucks.

12.5 Level and Source of Protein

The energy concentration of rabbit diets varies widely. Therefore, it is advisable to express total protein requirements as a ratio between DP and DE. The effect of a variation in this ratio on the performance of fattening rabbits has been studied by de Blas et al. (1981) and Fraga et al. (1983) using 12 diets containing from 7.9 to 11.7 g DP MJ\(^{-1}\) DE. Maximal DE intake and average daily gain were obtained for diets with a DP:DE ratio of 10 g DP MJ\(^{-1}\) DE (see Fig. 12.3). Accordingly, the optimal DP content should be increased from 95 to 115 g kg\(^{-1}\) when dietary DE increases from 9.5 to 11.5 MJ kg\(^{-1}\). Dietary DP:DE ratios below and above this optimum impair fattening performance and feed efficiency. It has been reported that dietary crude protein contents of around 140 g kg\(^{-1}\) do not impair growth performance if the DP:DE ratio is maintained around 9.5–10 g MJ\(^{-1}\) and the amino acid supply is adequate (Carabaño et al., 2009). Low DP:DE values (<9.5 g MJ\(^{-1}\)) also promote a curvilinear decrease in water and protein and an increase in body fat (see Fig. 12.3). On the other hand, an excess of protein content related to energy increases environmental pollution (Maertens et al., 1997; Xiccato, 2006).
Several studies (Gutiérrez et al., 2003; García-Ruiz et al., 2006; Chamorro et al., 2007) have also observed that a reduction in dietary protein content or the use of highly digestible protein sources decreases ileal protein flow and reduces the proliferation of pathogens and mortality during the fattening period (see also Chapter 10).

The effects of the DP:DE ratio in breeding does have been reviewed by Santomá et al. (1989) and Xiccato (1996). Optimal recommended values are in the range 11.0–12.5 g DP MJ⁻¹ DE; about 20% higher than that for fattening rabbits. The higher values correspond to females under intensive breeding systems. Dietary protein contents below the optimal level decrease milk production, growth of suckling rabbits and fertility and body weight of does.

12.6 Amino Acid Requirements

Until recently, no consideration was given to the quality of protein in rabbit feeds, because all the essential amino acid requirements were believed to be supplied through caecotrophy. However, soft faeces represent only about 0.14 of the total protein intake in intensively reared rabbits (see Chapter 3). Consequently, essential amino acid requirements, along with total protein, must be taken into account in practical feed formulation.

Several authors have studied the amino acid requirements of rabbits on a dose–response basis (Tables 12.2 and 12.3). Dietary amino acid content had a quadratic effect on productivity for some of the traits studied (see Fig. 12.4). This type of response indicates the negative effects of excess amino acids. This problem seems to be of especial interest for threonine. For this amino acid, a level slightly greater than the optimal reduced performance, which indicates the need of establishing a maximal concentration for this nutrient in the diet.

As for other species, there are more data available for growing rabbits than for breeding does, as well as considerable variation between different studies. Part of this variation can be explained by differences in the methods used: purified versus commercial diets, the genetic potential of the animals and the energy concentration of the diets.

Other causes of variability are related to the different availabilities of the sources of amino acids used (see Chapter 3). To take into account this effect, several studies (Taboada et al., 1994, 1996; de Blas et al., 1998) have determined the lysine, sulphur and threonine requirements, expressed in

Fig. 12.3. Effect of the dietary digestible protein (DP) to digestible energy (DE) ratio on the average growth rate in the fattening period and content of fat in the empty body of rabbits at 2.25 kg (de Blas et al., 1981; Fraga et al., 1983). ADG, average daily gain; E, energy; P, protein.
Table 12.2. Total amino acid requirements of growing-fattening rabbits (g kg⁻¹, as-fed basis).

<table>
<thead>
<tr>
<th>Reference</th>
<th>DE (MJ kg⁻¹)</th>
<th>Growth rate (g day⁻¹)ᵃ</th>
<th>Lys</th>
<th>TSAAᵇ</th>
<th>Thr</th>
<th>Trp</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adamson and Fisher (1973)</td>
<td>–</td>
<td>25.5</td>
<td>7.0</td>
<td>6.0</td>
<td>5.0</td>
<td>1.5</td>
</tr>
<tr>
<td>Colin (1975)</td>
<td>9.41</td>
<td>39.2</td>
<td>5.8</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Colin (1978)</td>
<td>11.13</td>
<td>37.6</td>
<td>–</td>
<td>6.3</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Davidson and Spreadbury (1975)</td>
<td>10.46ᶜ</td>
<td>36.5</td>
<td>9.0</td>
<td>5.5</td>
<td>6.0</td>
<td>2.0</td>
</tr>
<tr>
<td>Colin and Allain (1978)</td>
<td>10.88</td>
<td>35.0</td>
<td>6.2</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Spreadbury (1978)</td>
<td>–</td>
<td>41.0</td>
<td>9.4</td>
<td>6.2</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Berchiche and Lebas (1994)</td>
<td>11.17</td>
<td>40.2</td>
<td>–</td>
<td>6.2</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Taboada et al. (1994)</td>
<td>10.70</td>
<td>40.7</td>
<td>7.6</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Taboada et al. (1996)</td>
<td>10.75</td>
<td>40.4</td>
<td>–</td>
<td>5.4</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>De Blas et al. (1998)</td>
<td>10.13</td>
<td>43.2</td>
<td>–</td>
<td>–</td>
<td>6.0</td>
<td>–</td>
</tr>
</tbody>
</table>

DE, digestible energy; Lys, lysine; Thr, threonine; Trp, tryptophan; TSAA, total sulphur amino acids.

ᵃAt the optimal amino acid concentration.

ᵇMethionine must represent at least 0.35 of TSAA (Colin, 1978).

ᶜMetabolizable energy.

Table 12.3. Total amino acid requirements of breeding does (g kg⁻¹, as-fed basis).

<table>
<thead>
<tr>
<th>Reference</th>
<th>DE (MJ kg⁻¹)</th>
<th>Lys</th>
<th>TSAAᵇ</th>
<th>Thr</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maertens and de Groote (1988b)</td>
<td>10.46</td>
<td>8.0</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Taboada et al. (1994)</td>
<td>10.70</td>
<td>8.0ᵃ</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Taboada et al. (1996)</td>
<td>10.75</td>
<td>–</td>
<td>6.3</td>
<td>–</td>
</tr>
<tr>
<td>De Blas et al. (1998)</td>
<td>10.13</td>
<td>–</td>
<td>–</td>
<td>6.4</td>
</tr>
</tbody>
</table>

DE, digestible energy; Lys, lysine; Thr, threonine; TSAA, total sulphur amino acids.

ᵃFor maximal milk production. Reproductive performance did not improve at >6.8 g kg⁻¹.

Fig. 12.4. Effect of dietary threonine content on feed intake, reproductive performance and feed efficiency of breeding does (base 100 = diet containing 3.44 g of digestible threonine kg⁻¹) (de Blas et al., 1998).
Table 12.4. Digestible (faecal apparent) amino acid requirements of rabbits (g kg⁻¹, as-fed basis).

<table>
<thead>
<tr>
<th>Amino acid</th>
<th>Breeding does</th>
<th>Fattening rabbits</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lysine</td>
<td>6.4*</td>
<td>6.0</td>
<td>Taboada et al. (1994)</td>
</tr>
<tr>
<td>Methionine + cystine</td>
<td>4.9</td>
<td>4.0</td>
<td>Taboada et al. (1996)</td>
</tr>
<tr>
<td>Threonine</td>
<td>4.4</td>
<td>4.0</td>
<td>De Blas et al. (1998)</td>
</tr>
</tbody>
</table>

*For maximal milk production. Reproductive performance was not improved with levels >5.2 g kg⁻¹.

digestible (apparent faecal) instead of crude units. The results are shown in Table 12.4. Optimal values for growth were consistent with those obtained by Moughan et al. (1988) based on the amino acid composition of the whole body of 53-day-old rabbits (Table 12.5), although the latter method does not consider the amino acid requirements for maintenance or the amino acid supply by the caecotrophes. Although the use of digestible amino acids in practical feed formulation is still limited, recent information on this subject is provided in Chapter 8.

12.7 Recommended Nutrient Concentration of Diets

The nutrient requirements of intensively reared rabbits are presented in Tables 12.6 and 12.7. Values are given for the three types of diets more commonly used in practice: breeding does, fattening rabbits and a mixed feed for all animals. When rabbits are slaughtered at heavy weights (around 2.5 kg), more than one fattening feed is recommended. In this situation, Carabaño et al. (2009) proposed increasing the dietary protein and amino acid content by about 10% for the first 2 weeks after weaning (up to 11 g DP MJ⁻¹ DE) to take into account the relatively higher amino acid requirements for tissue accretion, intestinal growth and maintenance of mucosa functionality. The main objective of this feed is to optimize gut health by substituting starch with fat and increasing the concentration of easily fermentable fibre (up to 120 g kg⁻¹ soluble NDF or 120 g kg⁻¹ hemicellulose, see Chapter 10).

Energy concentrations in Table 12.6 have been determined from estimates based on the optimal proposed levels of carbohydrates and fat. Essential nutrient recommendations have then been referred to those concentrations. However, the DE content of fattening feeds can vary from 9.7 to 11.5 MJ kg⁻¹ without detriment to rabbit performance. Changes in the DE concentration with respect to the values given in this table should be accompanied by proportional parallel corrections in the contents of essential nutrients.

Minimal levels of fibre and maximum levels of starch are more critical than maximum levels of fibre and minimum levels of starch, as they affect not only performance but also mortality.

Recommendations for the type of fibre include an optimal concentration for lignin and a minimum level for long fibre particles. Both restrictions should be followed simultaneously, as some highly lignified by-products can have an insufficient content of long fibre.

Only the well-established amino acid requirements are presented in Table 12.6.

Table 12.5. Amino acid composition (mg g⁻¹ nitrogen) of the whole body of 53-day-old New Zealand White rabbits (Moughan et al., 1988).

<table>
<thead>
<tr>
<th>Amino acids</th>
<th>Absolute value</th>
<th>Relative to lysine</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lysine</td>
<td>383</td>
<td>100</td>
</tr>
<tr>
<td>Methionine</td>
<td>77.5</td>
<td>20.2</td>
</tr>
<tr>
<td>Cystine</td>
<td>158</td>
<td>41.3</td>
</tr>
<tr>
<td>Arginine</td>
<td>415</td>
<td>108</td>
</tr>
<tr>
<td>Histidine</td>
<td>193</td>
<td>50.4</td>
</tr>
<tr>
<td>Threonine</td>
<td>245</td>
<td>64</td>
</tr>
<tr>
<td>Leucine</td>
<td>429</td>
<td>112</td>
</tr>
<tr>
<td>Iso-leucine</td>
<td>194</td>
<td>50.7</td>
</tr>
<tr>
<td>Valine</td>
<td>239</td>
<td>62.4</td>
</tr>
<tr>
<td>Phenylalanine</td>
<td>249</td>
<td>65</td>
</tr>
<tr>
<td>Tyrosine</td>
<td>192</td>
<td>50.1</td>
</tr>
</tbody>
</table>
Table 12.6. Nutrient requirements of intensively reared rabbits, as concentration kg\(^{-1}\) corrected to a dry matter content of 900 g kg\(^{-1}\).

<table>
<thead>
<tr>
<th>Nutrient</th>
<th>Unit</th>
<th>Breeding does</th>
<th>Fattening rabbits</th>
<th>Mixed feed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Digestible energy</td>
<td>MJ</td>
<td>10.7</td>
<td>10.2</td>
<td>10.2</td>
</tr>
<tr>
<td>Metabolizable energy</td>
<td>MJ</td>
<td>10.2</td>
<td>9.8</td>
<td>9.8</td>
</tr>
<tr>
<td>NDF(^{a})</td>
<td>g</td>
<td>320 (310–335)</td>
<td>340 (330–350)</td>
<td>335 (320–340)</td>
</tr>
<tr>
<td>ADF</td>
<td>g</td>
<td>175 (165–185)</td>
<td>190 (180–200)</td>
<td>180 (160–180)</td>
</tr>
<tr>
<td>Crude fibre</td>
<td>g</td>
<td>145 (140–150)</td>
<td>155 (150–160)</td>
<td>150 (145–155)</td>
</tr>
<tr>
<td>ADL</td>
<td>g</td>
<td>55(^{c})</td>
<td>50</td>
<td>55</td>
</tr>
<tr>
<td>Soluble NDF</td>
<td>g</td>
<td>Free</td>
<td>115</td>
<td>80</td>
</tr>
<tr>
<td>Starch</td>
<td>g</td>
<td>170 (160–180)</td>
<td>150 (140–160)</td>
<td>160 (150–170)</td>
</tr>
<tr>
<td>Ether extract</td>
<td>g</td>
<td>45</td>
<td>Free</td>
<td>Free</td>
</tr>
<tr>
<td>Crude protein</td>
<td>g</td>
<td>175 (165–185)</td>
<td>150 (142–160)</td>
<td>159 (154–162)</td>
</tr>
<tr>
<td>Digestible protein(^{d})</td>
<td>g</td>
<td>128 (115–140)</td>
<td>104 (100–110)</td>
<td>111 (108–113)</td>
</tr>
<tr>
<td>Lysine(^{e})</td>
<td>g</td>
<td>81</td>
<td>73</td>
<td>78</td>
</tr>
<tr>
<td>Digestible</td>
<td>g</td>
<td>64</td>
<td>57</td>
<td>61</td>
</tr>
<tr>
<td>Sulphur(^{f})</td>
<td>g</td>
<td>63</td>
<td>52</td>
<td>59</td>
</tr>
<tr>
<td>Digestible</td>
<td>g</td>
<td>48</td>
<td>40</td>
<td>45</td>
</tr>
<tr>
<td>Threonine(^{g})</td>
<td>g</td>
<td>67</td>
<td>62</td>
<td>65</td>
</tr>
<tr>
<td>Digestible</td>
<td>g</td>
<td>46</td>
<td>43</td>
<td>45</td>
</tr>
<tr>
<td>Calcium</td>
<td>g</td>
<td>105</td>
<td>60</td>
<td>100</td>
</tr>
<tr>
<td>Phosphorus</td>
<td>g</td>
<td>60</td>
<td>40</td>
<td>57</td>
</tr>
<tr>
<td>Sodium</td>
<td>g</td>
<td>23</td>
<td>22</td>
<td>22</td>
</tr>
<tr>
<td>Chloride</td>
<td>g</td>
<td>29</td>
<td>28</td>
<td>28</td>
</tr>
</tbody>
</table>

ADF, acid detergent fibre; ADL, acid detergent lignin; NDF, neutral detergent fibre.
\(^{a}\)The proportion of long fibre particles (>0.3 mm) should be >0.22 for breeding does and >0.205 for fattening rabbits.
\(^{b}\)Values in parentheses indicate the range of minimal and maximal values recommended.
\(^{c}\)Values in italics are provisional estimates.
\(^{d}\)The digestibility of crude protein and essential amino acids is expressed as faecal apparent digestibility.
\(^{e}\)Total amino acid requirements have been calculated for a contribution of synthetic amino acids of 0.15.
\(^{f}\)Methionine should provide a minimum of 35% of the total sulphur amino acid requirements.
\(^{g}\)Maximal levels of 50 and 72 g kg\(^{-1}\) of digestible and total threonine, respectively, are recommended for breeding does.

Dietary tryptophan content can be estimated at 0.18–0.20 of the optimal lysine concentration. For other essential amino acids, the ideal protein pattern (Table 12.5) can be of help.

There is a lack of research on mineral and vitamin requirements. The standards proposed in Tables 12.6 and 12.7 are mostly based on the practical levels used by the industry.

Table 12.7. Trace element and vitamin requirements of intensively reared rabbits, as concentration kg\(^{-1}\) corrected to a dry matter content of 900 g kg\(^{-1}\).

<table>
<thead>
<tr>
<th>Nutrient</th>
<th>Unit</th>
<th>Breeding does</th>
<th>Fattening rabbits</th>
<th>Mixed feed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cobalt</td>
<td>mg</td>
<td>0.3</td>
<td>0.3</td>
<td>0.3</td>
</tr>
<tr>
<td>Copper</td>
<td>mg</td>
<td>10</td>
<td>6</td>
<td>10</td>
</tr>
<tr>
<td>Iron</td>
<td>mg</td>
<td>50</td>
<td>30</td>
<td>45</td>
</tr>
<tr>
<td>Iodine</td>
<td>mg</td>
<td>1.1</td>
<td>0.4</td>
<td>1.0</td>
</tr>
<tr>
<td>Manganese</td>
<td>mg</td>
<td>15</td>
<td>8</td>
<td>12</td>
</tr>
<tr>
<td>Selenium</td>
<td>mg</td>
<td>0.05</td>
<td>0.05</td>
<td>0.05</td>
</tr>
<tr>
<td>Zinc</td>
<td>mg</td>
<td>60</td>
<td>35</td>
<td>60</td>
</tr>
</tbody>
</table>

Continued
Table 12.7. Continued.

<table>
<thead>
<tr>
<th>Nutrient</th>
<th>Unit</th>
<th>Breeding does</th>
<th>Fattening rabbits</th>
<th>Mixed feed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vitamin A</td>
<td>mIU</td>
<td>10</td>
<td>6</td>
<td>10</td>
</tr>
<tr>
<td>Vitamin D</td>
<td>mIU</td>
<td>0.9</td>
<td>0.9</td>
<td>0.9</td>
</tr>
<tr>
<td>Vitamin E</td>
<td>IU</td>
<td>50</td>
<td>15</td>
<td>40</td>
</tr>
<tr>
<td>Vitamin K₃</td>
<td>mg</td>
<td>2</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Vitamin B₁</td>
<td>mg</td>
<td>1</td>
<td>0.8</td>
<td>1</td>
</tr>
<tr>
<td>Vitamin B₂</td>
<td>mg</td>
<td>5</td>
<td>3</td>
<td>5</td>
</tr>
<tr>
<td>Vitamin B₆</td>
<td>mg</td>
<td>1.5</td>
<td>0.5</td>
<td>1.5</td>
</tr>
<tr>
<td>Vitamin B₁₂</td>
<td>µg</td>
<td>12</td>
<td>9</td>
<td>12</td>
</tr>
<tr>
<td>Folic acid</td>
<td>mg</td>
<td>1.5</td>
<td>0.1</td>
<td>1.5</td>
</tr>
<tr>
<td>Niacin</td>
<td>mg</td>
<td>35</td>
<td>35</td>
<td>35</td>
</tr>
<tr>
<td>Pantothenic acid</td>
<td>mg</td>
<td>15</td>
<td>8</td>
<td>15</td>
</tr>
<tr>
<td>Biotin</td>
<td>µg</td>
<td>100</td>
<td>10</td>
<td>100</td>
</tr>
<tr>
<td>Choline</td>
<td>mg</td>
<td>200</td>
<td>100</td>
<td>200</td>
</tr>
</tbody>
</table>

References


13 Feeding Behaviour of Rabbits

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13.1 Introduction

As a non-ruminant herbivore, the rabbit has a unique feeding behaviour compared to other domestic animals. It belongs to the Lagomorpha order (Leporidae family: rabbits and hares; Grassé and Dekeuser, 1955) and, consequently, expresses a main specificity that is caecotrophy. In brief (see details in Chapter 1) caecotrophy is a complete behaviour involving the excretion and immediate consumption of specific faeces, named soft faeces or ‘caecotrophes’. Consequently, the daily intake behaviour of the rabbit is comprised of two meals: feeds and caecotrophes. Although the rabbit is not a rodent, one of the main features of its feeding behaviour is to gnaw. Information about feeding behaviour has mainly been obtained with the domestic rabbit, bred for meat or fur production or as a laboratory animal. It has basically involved rabbits receiving ad libitum a balanced complete pelleted feed, supplemented or not with dry forages or straw, but generally without a real free choice of feed.

This chapter reviews regulation of the intake behaviour according to several factors: age, type of feed and so on. The last part of the chapter is devoted to the feeding behaviour of wild and domestic rabbits in a situation of free choice.

13.2 The Behaviour of Caecotrophy

Caecotrophy plays an important role in rabbit nutrition, providing proteins and B vitamins from bacterial sources. The physiological mechanisms implicated in caecotrophy are detailed in Chapter 1. It is not fully known when caecotrophy behaviour commences in young rabbits, but it probably starts around 25 days of age, when a significant dry feed intake occurs that leads to both caecal and colon filling (Gidenne et al., 2002a; Orengo and Gidenne, 2007).

Hard pellets are voided, but soft pellets are recovered by the rabbit directly upon being expelled from the anus. To do this the rabbit twists itself around, sucks in the soft faeces as they emerge from the anus and then swallows without chewing them. The rabbit can retrieve the soft pellets easily, even from a mesh floor. By the end of the morning there is a large number of these pellets inside the stomach, where they may comprise three-quarters of the total contents. The intriguing presence of these soft pellets in the stomach was at the origin of the first correct description of caecotrophy by Morot (1882): the production of two types of faeces and the systematic ingestion of one of the two types (the soft ones). This makes caecotrophy different from the coprophagy classically described...
for rats or pigs, where only one type of faeces is produced.

13.3 Feeding Behaviour in the Domestic Rabbit

13.3.1 Feeding behaviour of the young rabbit: from milk to solid food

Females give birth to naked and blind young in a nest after 31 days of gestation. There is subsequently a period of rapid development for the young, ending in weaning around 1 month later. During this period, kits progress from a diet comprised almost exclusively of milk, available only once a day, to several meals of solid food.

Milk intake

Initial nursing occurs during parturition. Suckling is induced by the mother when she stands motionless over the kits in the nest. She gives no direct assistance to the offspring to suck (Hudson and Distel, 1982, 1983). Therefore, locating the nipples and ingesting milk depends on the individual abilities of each kit to behave efficiently under the female.

It was demonstrated a long time ago that the rabbit suckles her litter for 4–5 min once a day only during the initial 2 weeks after birth (Zarrow et al., 1965). More recently, however, data have suggested that some does (wild or domestic) nurse their young twice a day (Hoy and Selzer, 2002). In any case, suckling represents <0.0035 of the time budget of kits. Under experimental conditions, if two different females are presented to the litter, the young are able to suckle twice a day or more (Gyarmati et al., 2000). However, double suckling on its own offers few if any nutritional benefits: the weight of kits at 21 days increased by 4.6% according to Etchegaray-Torres et al. (2004) and was clearly not influenced by suckling frequency according to Tudela et Balmisse (2003). On the other hand, under normal breeding conditions, it may happen relatively frequently that one or two kits from the same litter do not obtain milk at one nursing (0.14 of the litter on day 1 according to Coureaud et al., 2007).

The first suckling bouts occur after parturition and within the first hour after the birth (colostrum), and are essential to the subsequent survival of kits. Starvation is indeed one of the key causes of mortality, usually peaking during the initial days post-partum (Coureaud and Schaal, 2000; Coureaud et al., 2000), in addition to other factors such as maternal inexperience and behaviour (Verga et al., 1978, 1986). During suckling, competition for access to nipples is very high. Indeed, in domestic rabbit breeds there are frequently more kits in the litter than nipples, with seven to ten kits per litter according to breed and selection and generally four pairs of nipples (Drummond et al., 2000; Hudson et al., 2000; Bautista et al., 2005), although does from breeds or lines selected for prolificacy may have up to 12 nipples (Fleischhauer et al., 1985; De Rochambeau et al., 1988; Szendrő et al., 1991; Coisne, 2000). Notwithstanding the actual number of nipples available, newborn rabbits do not appropriate a single nipple but change from one to another approximately every 20 seconds within the same sucking bout. This is contrary to other newborn mammals (e.g. kittens, piglets), where newborns retain the same nipple throughout lactation. Bautista et al. (2005) showed that the availability of milk across the eight nipples is equal during the first days post-partum, but that more milk is available from the two middle pairs by the end of the first week.

During the first week post-partum, kits drink about 0.15 of their live weight (LW) in milk each day in one nursing session, and up to 0.25 for some individuals (around 15–25 g; Lebas, 1969). Their nipple-searching behaviour is very stereotyped and controlled by a pheromonal signal (Schaal et al., 2003). During the first week post-partum (between 4 and 6 days of age) kits also consume some hard faeces deposited by the doe in the nest, thus stimulating the caecal microbiota maturation (Kovacs et al., 2004). Thereafter, individual milk
intake increases gradually to reach a peak of about 25 g day\(^{-1}\) between 17 and 25 days of age (Fig. 13.1). During this period, milk intake is highly variable between kits due to individual ability, competition between littermates and milk availability (Fortun-Lamothe and Gidenne, 2000). After day 20–25, maternal milk production progressively decreases. If food resources are sufficient and the female is not fertilized again, milk production can continue to 5–6 weeks or even longer. If the female is fertilized just after parturition, however, and sustains a concurrent pregnancy and lactation, milk production decrease significantly at the end of pregnancy and ceases 2–3 days before the following parturition (Lebas, 1972; Fortun-Lamothe et al., 1999). This frequently occurs in wild rabbits in the spring, when females mate again on the day of parturition. In this situation, young rabbits may be weaned from 3 weeks of age. In commercial systems, weaning is generally carried out between 28 and 35 days of age, even if milk production has not completely stopped.

**Solid food intake and evolution of nutrient and energy supply**

Young rabbits begin to eat significant quantities of solid food at around 16–18 days of age, when there are able leave the nest and move easily to access a feeder (with pelleted feed) and drinker. Nevertheless, the first contacts with solids occur during the first week of life, when the young consume some hard faeces deposited by the doe in the nest during suckling (Kovacs et al., 2004; Moncomble et al., 2004).

Initially, the young eat very small quantities of feed (<2 g day\(^{-1}\) per rabbit before 20 days of age). The solid food intake increases from 25 days of age to reach 40–50 g day\(^{-1}\) by 35 days (Gidenne et al., 2002b), although this is highly variable between litters. Consequently, the feeding behaviour changes considerably in a few days, as the young switch from a single daily meal of milk to 25–30 solid and liquid (water) meals in 24 h. The ingestion of solid food and water exceeds that of milk during the fourth week of life.

![Fig. 13.1. Milk, water and dry feed intake of the young rabbit (adapted from Szendrö et al., 1999; Fortun-Lamothe and Gidenne, 2000). Values are means for litters of seven to nine kits with pelleted dry feed and one lactating doe available, and weaned at 30 days (does remated 11 days after kindling).](image-url)
It is interesting to note that when suckling rabbits begin to eat solid food, they prefer to eat from the same feeder as their mother rather than from a specific feeder for young animals (Fortun-Lamothe and Gidenne, 2003). This suggests that the start of solid food ingestion is influenced by initiation or imitation of the mother. In addition, for the early-weaned rabbit, the watering system (nipple or ‘open air’ drinker) does not affect solid feed intake, while a too-small pellet diameter increases hardness and impairs feed intake (Gidenne et al., 2002a, 2003).

In parallel to modifications in feeding behaviour, the nutrients ingested by young rabbits change significantly between birth and weaning (Fig. 13.2). Indeed, rabbit milk is very rich in lipids (13 g 100 g⁻¹) and proteins (12 g 100 g⁻¹), but contains only traces of lactose (Maertens et al., 2006). On the other hand, pelleted feed mainly contains carbohydrates (80 g 100 g⁻¹, with varying digestibility ranging from very high for starch to low for fibre), some protein (15–18 g 100 g⁻¹) and only a small quantity of lipids (2–5 g 100 g⁻¹), all of vegetable origin. Therefore, digestive capacities must evolve rapidly, in parallel with the evolution of feeding patterns (Gidenne and Fortun-Lamothe, 2002). The ingestion of vegetable proteins becomes equal to that from the milk at around 25 days of age, and then exceeds it within a few days. Conversely, lipids come mainly from milk until weaning. While the ingestion of carbohydrates is virtually zero (<0.3 g day⁻¹) until 17 days of age, it becomes significant from day 21 in the form of fibre and starch. However, proteins and fats in the milk constitute the main sources of energy until weaning.

Regulation of feeding behaviour in young rabbits

The individual feeding behaviour of kits before weaning and its regulation are not easy to study due to the interactions of each kit with its littermates and mother. Nevertheless, it is well known that the availability of milk is a key regulating factor of solid food ingestion before weaning. Thus, if the size of the litter is reduced from ten to four kits or if milk production increases, the start of solid food ingestion is

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**Fig. 13.2.** Evolution of the composition of food ingested by young rabbits between birth (day 0) and weaning (day 35) in breeding conditions.
delayed by 2–4 days (Fortun-Lamothe and Gidenne, 2000) and the feed intake of the whole litter is reduced (Pascual et al., 2001). Similarly, offering a second milking to the young (using a second doe) delays dry feed intake (Gyarmati et al., 2000). On the other hand, early weaning (before 25 days of age) stimulates and considerably accelerates dry feed intake (Gallois et al., 2005; Xiccato et al., 2005).

The influence of feed nutritional composition on feeding behaviour is poorly understood, although some authors have used an original model of a cage to measure the intake of the litter without separation from the mother (Fortun-Lamothe et al., 2000). However, results obtained with young rabbits indicate that the variability among littermates is very high (up to 45%) and that the control of intake before weaning through the nutrient and energy supply is not consistent. For instance, Pascual et al. (1998, 1999) suggested that suckling rabbits regulate their food consumption according to dietary digestible energy (DE) content, as do weaned rabbits. Conversely, greater feed intake has been found for a high- compared to a moderate-energy diet (Debray et al., 2002; Gidenne et al., 2004). Finally, other factors, such the form of presentation of food and pellet size and quality (e.g. hardness, durability) probably play a key role in the starting of solid feeding behaviour.

Despite this, the individual feeding behaviour of kits (e.g. regulation factors, number of meals) is largely unknown, since no method is presently available to assess their intake when reared collectively (until weaning).

### 13.3.2 Feeding behaviour of the growing and adult rabbit

From weaning (classically between 4 and 5 weeks), the daily feed intake of the domestic rabbit (fed a complete pellet feed) increases in relation to metabolic LW (Fig. 13.3) and stabilizes at about 5 months of age. Taking as a reference an adult animal fed ad libitum (140–150 g dry matter DM day$^{-1}$, for example, for a 4 kg New Zealand White): (i) at 4 weeks a young rabbit eats 0.25 of the amount an adult eats, but its LW is only 0.14 of that of the adult; (ii) at 8 weeks the

![Fig. 13.3. Dry matter (DM) intake from pelleted feed and caecotrophes and live weight from weaning (28 days) until adulthood. Data are from the domestic rabbit, fed a pelleted feed ad libitum (Gidenne and Lebas, 1987). *Data on caecotrophe excretion were obtained from rabbits wearing a collar.](image-url)
relative proportions are 0.62 and 0.42; and (iii) at 16 weeks, 1.00–1.10 and 0.87 respectively. Between weaning (4–5 weeks) and 8 weeks of age, weight gain is at its highest (Table 13.1) and feed conversion is optimal. The rate of increase of feed intake and growth rate subsequently decrease, with intake stabilizing at around 12 weeks of age for current hybrid lines of domestic rabbit.

Similarly to other mammals, the rabbit regulates its feed intake according to energy requirements. Chemostatic mechanisms are involved, by means of the nervous system and blood levels of compounds used in energy metabolism. In non-ruminants, however, glycaemia plays a key role in food intake regulation, while in ruminants the plasma levels of volatile fatty acids have a major role. Since the rabbit is a non-ruminant herbivore, the main blood component regulating feed intake is not clear, but it is probably glucose. Voluntary intake, proportional to metabolic LW \( (\text{LW}^{0.75}) \), is about 900–1000 kJ DE day\(^{-1}\) kg\(^{-1}\) LW\(^{0.75}\), and chemostatic regulation appears only with a dietary DE concentration >9–9.5 MJ kg\(^{-1}\) (see Chapter 6). Below this level, a physical-type regulation is prevalent and linked to gut fill.

The intake of soft faeces increases only until 2 months of age and then remains steady (Fig. 13.3). Expressed as fresh matter, the intake of soft faeces increases from 10 g day\(^{-1}\) (1 month old) to 55 g day\(^{-1}\) (2 months), thus representing 0.15–0.35 of the feed intake (Gidenne and Lebas, 1987). However, the classic method of calculating caecotrophy probably underestimates this proportion, since installing a collar around the neck of the rabbit to avoid the intake of soft faeces from the anus is stressful. Recently, Belenguer et al. (2008) developed methods based on microbial marker analysis that are less intrusive for the animal.

The rabbit divides its voluntary solid intake into numerous meals: about 40 at 6 weeks of age, and a slightly lower number in adulthood (Table 13.2). This meal fractionation is probably linked to the relatively weak storage capacity of the stomach (as detailed in Chapter 1), particularly when compared to herbivorous animals or even carnivorous or omnivorous ones (such as dogs and pigs).

For 6-week-old rabbits fed a pelleted diet, the time spent feeding every 24 h is slightly >3 h. Subsequently, it drops rapidly to <2 h. If a ground non-pelleted diet is offered, the time spent on eating doubles (Lebas, 1973). The number of liquid meals increases in parallel to that of feed, and less time is spent drinking than eating. Furthermore, at any age, feeds containing >0.70 water, such as green forage, provide rabbits with sufficient water at temperatures <20°C and, in these circumstances, rabbits may not drink at all. In growing rabbits fed with pellets, the normal ratio of water to DM is about 1.6–1.8. In the adult or breeding doe it is increased up to 2.0–2.1.

### Table 13.1. Feeding behaviour of the domestic rabbit after weaning. Mean values from rabbits (current commercial lines) fed a pelleted diet (890 g dry matter kg\(^{-1}\)) \textit{ad libitum} with free access to drinkable water.

<table>
<thead>
<tr>
<th>Age (weeks)</th>
<th>Solid feed intake (g day(^{-1}))</th>
<th>Weight gain (g day(^{-1}))</th>
<th>Food conversion</th>
</tr>
</thead>
<tbody>
<tr>
<td>5–7</td>
<td>100–120</td>
<td>45–50</td>
<td>2.2–2.4</td>
</tr>
<tr>
<td>7–10</td>
<td>140–170</td>
<td>35–45</td>
<td>3.4–3.8</td>
</tr>
</tbody>
</table>

### Table 13.2. Feeding and drinking behaviour of the domestic rabbit from 6 to 18 weeks old. Mean values from nine New Zealand White rabbits fed a pelleted diet (89 g dry matter kg\(^{-1}\)) \textit{ad libitum} and with free access to drinkable water (Prud’hon et al., 1975b).

<table>
<thead>
<tr>
<th>Age in weeks</th>
<th>Solid feed intake (g day(^{-1}))</th>
<th>No. of meals per day</th>
<th>Average quantity per meal (g)</th>
<th>Water intake (g day(^{-1}))</th>
<th>No. of drinks per day</th>
<th>Average weight of one drink (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>6</td>
<td>98</td>
<td>39</td>
<td>2.6</td>
<td>153</td>
<td>31</td>
<td>5.1</td>
</tr>
<tr>
<td>12</td>
<td>194</td>
<td>40</td>
<td>4.9</td>
<td>320</td>
<td>28.5</td>
<td>11.5</td>
</tr>
<tr>
<td>18</td>
<td>160</td>
<td>34</td>
<td>4.9</td>
<td>297</td>
<td>36</td>
<td>9.1</td>
</tr>
</tbody>
</table>
Solid intake fluctuates over a 24-h period (Fig. 13.4). Over 0.60 of the solid feed (excluding soft faeces) is consumed in the dark period for a domestic rabbit submitted to a 12-h light, 12-h dark schedule. The circadian changes in liquid meals are strictly parallel to those of solid meals for the domestic rabbit fed pellets (Prud’hon et al., 1975b), but no correlation can be established between the time or intervals of solid and water meals. Peak intake is observed at the end of the light period, about 1 h before the start of the dark period. Prud’hon et al. (1975b) reported intense feed consumption in the 6-week-old rabbit. According to Horton et al. (1974) and Jolivet et al. (1983), intake is usually spread over two periods: (i) one at the end of the dark interval (or early in the day); and (ii) another more important period at the end of the light interval (or early night).

With older rabbits, the nocturnal feeding behaviour becomes more pronounced. The feeding habits of wild rabbits are even more nocturnal than those of domesticated rabbits. In fact, the domestic rabbit no longer has prolonged periods without eating, since it has >20 meals of dry feed a day, and it also consumes caecotrophes (early in the light period). Moreover, Hirakawa (2001) pointed out that leporids (including rabbits) also consume a portion of their own hard faeces, which are masticated (in contrast to soft faeces, which are swallowed). In rabbits, meals of soft faeces (and sometimes hard) increase in proportion when feed availability is insufficient.

Obviously, the feed intake level is modulated by the physiological status of the animal. For instance, the voluntary intake of does varies considerably during the reproductive cycle (Fig. 13.5), with intake falling markedly during the final days of pregnancy. Some does refuse solid food just before kindling. Water intake, however, never stops completely. After kindling, feed intake increases very rapidly and can exceed 100 g DM kg⁻¹ LW day⁻¹. Water intake is also increased at that time, from 200 to 250 g day⁻¹ kg⁻¹ LW. When a doe is both pregnant and lactating, she eats a similar amount to a doe that is only lactating.

### 13.4 External Factors Modulating the Feeding Behaviour of the Domestic Rabbit

#### 13.4.1 Feed composition and presentation form

One of the main dietary components implicated in feed intake regulation, after weaning, is the DE concentration. The domestic rabbit (fed a pelleted balanced diet) is able to regulate its DE intake (and thus its growth) when the dietary DE concentration is between

![Fig. 13.4](image-url)  
**Fig. 13.4.** Circadian pattern of feed intake in the growing or adult rabbit. Mean values for domestic rabbits (n = 6) fed a pelleted feed *ad libitum* (daily feed intake of 80 and 189 g day⁻¹, respectively, for 6- and 16-week-old rabbits) and bred under a 7:00–19:00 light schedule (Bellier et al., 1995).
9 and 11.5 MJ kg\(^{-1}\), or when the dietary fibre level is between 10% and 25% acid detergent fibre. The intake level is thus well correlated with the dietary fibre level, compared to the dietary DE content (Fig. 13.6). However, the incorporation of fat in the diet – while maintaining the dietary fibre level – increases the dietary DE level, but leads to a slight reduction in intake. Other nutrients in the diet, such as proteins and amino acids, are able to modify the food intake (Tome, 2004). For example, an excess of methionine has been observed to reduce the feed intake of the growing rabbit by at least 10% (Colin et al., 1973; Gidenne et al., 2002b).

The presentation of the diet is an important factor that modulates feeding behaviour in the rabbit. Compared to meals, pelleted feeds are preferred at 97% when offered in free choice (Harris et al., 1983). Furthermore, meals seem to modify the circadian cycle of feed intake (Lebas and Laplace, 1977). Pellet size and quality (hardness, durability) also affect feeding behaviour (see Chapter 14). A reduction in pellet diameter, which also increases the hardness, reduces the feed intake of young and growing rabbits (Maertens, 1994; Gidenne et al., 2003), although the time spent on feeding is increased.

### 13.4.2 Environmental factors affecting the feeding behaviour of the rabbit

Energy expenditure and hence the requirements and feed intake of the rabbit depend on the ambient temperature. Studies on growing rabbits have shown that the intake of pelleted feed drops from 180 to 120 g day\(^{-1}\) and water intake rises from 330 to 390 g day\(^{-1}\) at temperatures between 5°C and 30°C (Table 13.3) (Eberhart, 1980). A closer analysis of feeding behaviour shows that the number of solid meals eaten in 24 h drops as temperature increases, from 37 solid feeds at 10°C to only 27 feeds at 30°C (for 6-week-old New Zealand White rabbits; Prud’hon, 1976). The amount eaten at each meal also decreases with higher temperatures (from 5.7 g per meal at 10–20°C to 4.4 g per meal at 30°C). Water intake increases, however, from 11.4 to 16.2 g per meal between 10°C and 30°C (Prud’hon, 1976).

The negative effect of hot ambient temperatures (29–32°C) on daily feed intake may be partly counterbalanced by distribution of cooler drinking water (16–20°C). With ‘cold’ water distribution, the average feed intake may be increased by 4–6% for fatteners and breeding does, with corresponding improvements in performance (Duperray et al., 1998).
In an experiment by Selim et al. (2004), feed intake was increased by up to 11% for 7-week-old fatteners with 6 h of hot temperatures (29–32°C) during each 24-h cycle. The feeding and drinking behaviour of does and their litters according to climatic conditions is discussed in Chapter 15.

If drinking water is not provided and the only feed available is dry with a moisture content of <140 g kg⁻¹, DM intake drops to zero within 24 h. With no water at all, and depending on temperature and humidity, an adult rabbit can survive from 4 to 8 days without any irreversible damage, although its weight may drop by 20–30% in less than a week (Cizek, 1961). Rabbits with access to drinking water but no solid feed can survive for 3–4 weeks. Within a few days they will drink four to six times as much water as normal. Sodium chloride in the water (0.0045 g kg⁻¹) reduces this high water intake, but potassium chloride has no effect (sodium loss through urination). Although the rabbit is very resistant to hunger and relatively resistant to thirst, any reduction in the water supply, in terms of water requirements, causes a proportional reduction in DM intake, with a consequent drop in most performance criteria. For example, limiting water availability for breeding does to 20 min day⁻¹ decreases their feed intake, milk production and growth of kits by about 17–18%, but has no effect on reproduction parameters or kit mortality (Carles and Prud’hon, 1980).

![Intake and dietary lignocellulose level (ADF)](image1)

\[ y = -0.079x^2 + 5.05x + 49.0 \]

\[ R^2 = 0.92 \]

![Intake and DE concentration of the feed](image2)

\[ y = -0.029x + 186.6 \]

\[ R^2 = 0.65 \]

**Fig. 13.6.** Feed intake prediction in the domestic rabbit after weaning. ADF, acid detergent fibre; DE, digestible energy; DFI, daily feed intake (measured between weaning (4 weeks) and 11 weeks of age) (Gidenne, 2000).

**Table 13.3.** Feeding behaviour of the growing rabbit according to ambient temperature (data from Eberhart, 1980).

<table>
<thead>
<tr>
<th>Ambient temperature</th>
<th>5°C</th>
<th>18°C</th>
<th>30°C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Relative humidity (%)</td>
<td>80</td>
<td>70</td>
<td>60</td>
</tr>
<tr>
<td>Pelleted feed eaten (g day⁻¹)</td>
<td>182</td>
<td>158</td>
<td>123</td>
</tr>
<tr>
<td>Water intake (g day⁻¹)</td>
<td>328</td>
<td>271</td>
<td>386</td>
</tr>
<tr>
<td>Water to feed ratio</td>
<td>1.80</td>
<td>1.71</td>
<td>3.14</td>
</tr>
<tr>
<td>Average weight gain (g day⁻¹)</td>
<td>35.1</td>
<td>37.4</td>
<td>25.4</td>
</tr>
</tbody>
</table>
Other environmental factors have also been studied in the domestic rabbit, including the lighting schedule and housing systems. In the absence of light (24-h dark) the feed intake of fattening rabbits is increased, as compared to rabbits submitted to a natural sunlight programme (Lebas, 1977). Under these conditions, rabbits organize their feeding pattern in a regular 23.5- to 23.8-h programme, with about 5–6 h devoted to soft faeces ingestion and the remaining part of the cycle to feed intake. Under continuous lighting, the feeding pattern is organized in an approximate 25-h programme (Jilge, 1982; Reyné and Goussopoulos, 1984). For breeding does, reduction of the lighting duration during a 24-h cycle by the introduction of two 4-h periods of dark during the normal 12 h of lighting in a 12-h light, 12-h dark programme (intermittent lighting) did not modify the average daily feed intake, despite an increase in milk output leading to a better feed efficiency for milk production (Virag et al., 2000).

As previously mentioned, the type of caging also influences the daily feed intake and feeding pattern of rabbits. For instance, feed intake is affected by the stocking density of rabbits in the cage. An increase in stocking density seems to lead to greater competition for feeders among the animals and reduced feed intake (Aubret and Duperray, 1993). However, this is not necessarily a result of a competition for feeders since it is also observed with rabbits in individual cages (Xiccato et al., 1999).

In comparisons of cage and pen housing, enlarging the cage size for a group (with or without variations in stocking density) allows rabbits to move more and reduces daily feed intake (Maertens and Van Herck, 2000). At the same density, rabbits caged in groups of two or six had the same daily feed intake, but those in cages of two spent a lower proportion of their time budget on feed consumption: 0.058 versus 0.099 during the 10-h light period during which they were observed (Mirabito et al., 1999). Finally, according to the feeding pattern, the number of places at a feeder (one to six) for a group of ten rabbits did not influence daily feed intake (Lebas, 1971).

### 13.5 Feeding Behaviour in Situations of Choice

All of the studies described above were conducted with domestic rabbits, generally fed with complete and more-or-less balanced diets. In the wild or in situations of free choice for caged rabbits, another dimension must be added to the feeding behaviour: how rabbits select feeds.

#### 13.5.1 Feeding behaviour of the wild rabbit or the rabbit in an open situation (grazing)

The feed resources available to wild rabbits invariably include a wide range of plant material. Rabbits clearly prefer graminaceous plants (*Festuca*, *Brachypodium* or *Digitaria* species) and graze only a few dicotyledons if insufficient grasses are available (Williams et al., 1974; Leslie et al., 2004). Within the dicotyledonous plants, rabbits graze some leguminous plants and some *Compositae*. However, it should be underlined that consumption of carrots (*Daucus carota*) is minimal, and this plant is not preferred by rabbits (CTGREF, 1978).

The proportion of grazing of dicotyledonous species may increase during some seasons, depending on the availability of plants (Bhadresa, 1977). In winter and early spring, grazing of cultivated cereals by rabbits may completely compromise the crop, especially up to a distance of 30–100 m from the warren (Biadi and Guenezan, 1992). When rabbits can choose between winter cereals cultivated with or without mineral fertilization (phosphorus and/or nitrogen), they clearly prefer the latter (Spence and Smith, 1965).

Grazing rabbits may be very selective and, for example, choose one type or part of the plant with the highest nitrogen concentration (Lebas, 2002). Similarly, in a test performed in Ireland, wild rabbits grazed one variety of spring barley more intensively than four others, probably in relation to the plant’s composition. However, differences in the sugar content of the varieties did not fully explain this varietal selection (Bell and Watson, 1993).
The considerable winter appetence of rabbits for buds and young stems of some woody plants is important. Grazing of very young trees or shoots may completely compromise the regeneration of forests (CTGREF, 1980) or, more specifically, the regeneration of shrubs such as juniper (Lebas, 2002) or common broom (M. Sabourdy, personal communication, 1971). In winter rabbits like to eat the bark of some cultivated trees (not only young stems), especially that of apple trees and, to some extent, cherry and peach trees. The bark of pear, plum or apricot trees is generally not so frequently consumed (CTGREF, 1980). In forests rabbits clearly prefer broad leaved trees, but may also consume the bark of conifers (mainly spruce and some types of pines); however, when very young trees are available, rabbits prefer to eat apical or lateral sprouts of spruces or firs instead of oaks (CTGREF, 1978).

The basic reasons for these choices remain unclear, even if they are constant. They are regulated by the hypothalamus, since hypothalamic lesions clearly modify the choice pattern of rabbits (Balinska, 1966).

Many experiments have been conducted, especially in Australia and New Zealand, to study the behaviour of wild rabbits when offered different manufactured baits (the ultimate objective being the eradication of imported wild rabbits). Many variations have been observed, depending on both the type of bait and the season. For example pollard plus bran pellets (5:1 in weight) is consumed throughout the year; in contrast, the acceptability of carrots or oats varies seasonally. The addition of salt (10 or 50 g NaCl kg$^{-1}$) or lucerne meal (150 g kg$^{-1}$) to the pollard plus bran pellets significantly reduces bait consumption (Ross and Bell, 1979).

### 13.5.2 Free choice for the domestic caged rabbit

When a choice is proposed between a control diet and the same diet plus an appetiser, rabbits generally prefer the latter. However, when the same two diets are offered alone to rabbits, both the daily feed intake and growth performance are exactly the same (Fekete and Lebas, 1983). This means that the pleasant smell of the proposed food is not essential for feed intake regulation. This has also been shown with a repellent diet (the addition of formalin), which was clearly rejected in a free-choice test but consumed in the same quantity in a long-term single food test (Lebas, unpublished data).

Similarly Cheeke et al. (1977) have demonstrated that rabbits prefer lucerne with a saponin (a bitter component) content of up to 3 mg g$^{-1}$ diet, whereas rats always prefer the control diet without saponin in the range of 0.4–5 mg g$^{-1}$ (Fig. 13.7). However,
when single feeds with different levels of saponin are offered to rabbits (saponin from 1.8 to 6.4 mg g$^{-1}$ complete diet), feed intakes and growth rates are independent of the saponin level (Auxilia et al., 1983).

Conversely, when a toxin is present (e.g. aflatoxins) rabbits completely refuse to consume the diet or consume it in very low quantities (Fehr et al., 1968; Morisse et al., 1981; Saubois and Nepote, 1994). This regulation may be relevant in protecting the animal against food-borne pathologies.

When a concentrate (low-fibre compound diet) and a fibrous material are offered as free choice to rabbits, they prefer the former. The fibrous material is consumed in only small quantities and the growth rate may be reduced (Lebas et al., 1997). A further consequence is an immediate increase in the health risk for rabbits with digestive disorders through lack of fibre (Gidenne, 2003). This is the result of the specific search by rabbits for energy sources (scarce in the wild), the dominant regulation system of feed intake in rabbits.

In fact when Gidenne (1985) offered a free choice of two energy concentrates with a complete diet and fresh green bananas, the growth rate was similar among the two groups and the DE daily intake was identical. Nevertheless, it must be underlined that, in this study, the proportion of bananas in the DM intake decreased from 0.40 at weaning (5 weeks) to 0.28 at the end of the experiment 7 weeks later.

Similarly, rabbits receiving a diet deficient in one essential amino acid (lysine or sulphur amino acids) and drinking water with or without the missing amino acid in solution clearly prefer the solution with the missing amino acid (Lebas and Greppi, 1980).

To add a last constituent to this section on free choice, it should be remembered that a simple variation in the humidity of one component may change the balance of choice. For example, when dehydrated lucerne and normally dried maize grains (110 g moisture kg$^{-1}$) are offered ad libitum, the result of the choice is 65% lucerne to 35% maize. If, however, the water content of the maize grains is increased up to 140–150 g kg$^{-1}$ the balance changes to 45% lucerne and 55% maize (Lebas, 2002). In this case the choice seems motivated more by the immediate palatability of the feeds than by their nutritive value.

As described above, regulation of intake in a free-choice situation is difficult to predict. Thus, in most practical situations of rabbit production, the utilization of a complete balanced diet is advisable.

### 13.6 Feeding Behaviour in a Situation of Feed Restriction

#### 13.6.1 Quantitative limitation

When a limited quantity of pelleted food is distributed to a rabbit, the animal consumes its daily allocation within a few hours. For example, for rabbits caged individually or in pairs, a quantity representing 0.85 of the ad libitum intake is ingested in a maximum of 16 h; if the quantity is reduced to 0.70, however, the time taken to ingest this quantity is reduced to 10 h (Bergaoui et al., 2008).

When restricted-fed rabbits are caged in groups, the time spent on feed intake is shorter and depends on the number of rabbits able to eat pellets at the same time. For example, according to Tudela and Lebas (2006), fattening rabbits caged in groups of eight, with feed restriction at 0.85 of ad libitum, will consume all of the daily allocation within 8 h if only one rabbit has access to the feeder; but if two rabbits can access the feeder simultaneously, only 0.89 of the daily allocation is consumed in the same 8 h. According to the same authors, if the daily allocation is distributed in two equal halves at 8:00 and 18:00 to groups of eight fattening rabbits with only enough space for one at the feeder, all of the feed is consumed within 2 h of distribution (0.93 during the first hour). If two rabbits can consume feed simultaneously, 3 h are necessary (0.76 during the first hour).

A feed restriction at 0.85 of ad libitum is not associated with real competition for feed intake between eight rabbits (as indicated from LW measurements), whether there
are one or two places at the feeder or one or
two meal distributions per day. Moreover,
the within-cage standard deviation of LW is
also independent of these factors and iden-
tical to that of the ad libitum control group.
If the feed restriction is more severe (0.60 of
ad libitum), however, the average LW is not
affected by the number of feed distributions,
but the standard deviation of LW is signifi-
cantly increased by 20% when compared to
that obtained with groups restricted at 0.85
or fed ad libitum – a situation that can be
interpreted as the result of real competition
between rabbits (Tudela and Lebas, 2006).

13.6.2 Limitation of daily access
to the feeder or drinker

Restricted access to the feeder

Feed intake is reduced if access to the feeder
is <14–16 h day\(^{-1}\), as demonstrated by the dif-
ferent studies conducted in Hungary (Szendrö
et al., 1988; Tal El Den et al., 1988) and sum-
marized by Lebas (2007) in Fig. 13.8. For
example feed restriction to 8 h day\(^{-1}\) was asso-
ciated, on average, with a reduction in feed
intake of 0.80 of ad libitum. Nevertheless, it
must be highlighted that reducing access time
to feeders induces a greater reduction in the
intake of young rabbits than in older fattening
rabbits. A reduction to 0.64, 0.73 and finally
0.81 of the ad libitum intake during each of
the 3 weeks following weaning at 32 days has
been demonstrated with 8 h of access to feed-
ers (Foubert et al., 2007); a reduction to 0.73
of the ad libitum intake is seen with 4- to
5-week-old rabbits feeding for 9 h day\(^{-1}\)
(Matics et al., 2008); and intake almost
identical to that of an ad libitum control at
12 weeks is seen with continuous 8 h day\(^{-1}\)
limitation of access (Szendrö et al., 1988). If a
breeder hopes to induce a known quantita-
tive restriction for a group of fattening rabbits
(e.g. 0.85 of ad libitum, or adjustment to a
theoretical curve of intake) by reducing the
feeding time, it would be necessary to regu-
larly determine the real feed intake in some
cages in order to adjust, once or twice per
week, the duration of access to feeders for the
whole group.

The same Hungarian group has also
observed the time taken by rabbits to con-
sume their food in conditions of restricted
access to feeders. The total number of meals
per day is not affected by time limitations
(30–35 day\(^{-1}\) on average at 12 weeks), but
meals are concentrated in the smaller number
of hours ‘available’, without a significant
increase in the duration of each meal.
Nevertheless, with 9 h day\(^{-1}\) available for feed

Fig. 13.8. Pelleted feed intake of rabbit with a limited time of access to the feeder (Lebas, 2007; data from
Szendrö et al., 1988; Tag El Den et al., 1988).
intake, the total duration spent on feed consumption is 1 h 20 min day$^{-1}$, compared to the 1 h 45 min day$^{-1}$ spent by rabbits of the same age fed \textit{ad libitum} (Szendrő \textit{et al}., 1988).

\textit{Restricted access to drinking water}

Limitation of the access time to drinkers is another method by which to reduce feed intake. Some time ago, Prud'hon \textit{et al}.
(1975a) demonstrated that after 1 week of adaptation, rabbits receiving free access to drinking water for only 10 min day$^{-1}$ reduced their feed intake to 0.76–0.86 of that of rabbits drinking *ad libitum*, depending on the age: 0.86 for 6- to 9-week-old rabbits, 0.84 for 11- to 14-week-old rabbits and 0.76 for adults. The adaptation period was introduced because of the drastic reductions in water and feed intake (~63% and ~53%, respectively) in the 1–2 days following the institution of the restriction, followed by 6–8 days of adaptation to the new situation (Lebas and Delaveau, 1975).

In practical conditions with fattening rabbits, limiting access to drinking water to 1.5–4 h induces a reduction in water intake that is proportionally greater than the concomitant reduction in pelleted food intake, mainly for short durations of watering (Fig. 13.9). As a consequence, the water to feed ratio is reduced from 1:74 for rabbits fed *ad libitum* to 1:54 for those receiving water during only 1.5–4 h day$^{-1}$.

Table 13.4. Effect of limiting daily drinking duration or reducing the quantity of pellets distributed on relative water and feed intakes (Boisot et al., 2005). Observation during the 3 weeks following weaning at 31 days.

<table>
<thead>
<tr>
<th>Feeding and watering conditions</th>
<th>Ad libitum control</th>
<th>Water available for 1 h day$^{-1}$ (theoretical 0.65)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Feed intake</td>
<td>136 g day$^{-1}$</td>
<td>0.78</td>
</tr>
<tr>
<td>Water intake</td>
<td>228 g day$^{-1}$</td>
<td>0.56</td>
</tr>
<tr>
<td>Water to feed ratio</td>
<td>1.7</td>
<td>3.5</td>
</tr>
</tbody>
</table>

It must be pointed out that with restricted access to drinkers, the water to feed ratio is always reduced as consequence of the drastic reduction in water intake compared to the *ad libitum* control. However, when feed intake is reduced even more than after water access restriction (Boisot et al., 2005), the water intake is clearly enhanced above the *ad libi-
tum* intake (Table 13.4) and the water to feed ratio is increased above that of the control.

13.7 Conclusion

The feeding behaviour of rabbits is very particular compared to that of other mammals, with special features such caecotrophy associated with a particular digestive physiology, intermediate between the non-ruminant and the herbivore. As a herbivore, the feeding strategy of the rabbit is almost opposite to that of ruminants. The feeding strategy of ruminants consists or retaining food particles in the rumen until they reach a sufficiently small size. The rabbit has adopted the reverse strategy, characterized by a preferential retention of fine digesta particles in the fermentative segment (caecum and proximal colon), with rapid removal of the coarse particles (such as poorly digested fibre) in hard faeces. This is associated with numerous meals, thus favouring a quick digesta rate of passage and digestion of the most digestible fibre fractions.

Therefore, the rabbit is adapted to various feeding environments, from desert to temperate and even cold climates, and is able to consume a very wide variety of feeds, from seeds to herbaceous plants.

References


14 Feeding Systems for Intensive Production

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14.1 Introduction

Rabbits are primarily raised as meat producers and secondarily as wool or fur producers. They are also an important pet and exhibition animal in many countries and widely used in biomedical research. In recent years, interest has been increasing in biotechnology to produce protein-linked substances with transgenic rabbits. The high daily output (50 g kg\(^{-1}\) live weight day\(^{-1}\)) of protein-rich milk (120 g kg\(^{-1}\)) makes female rabbits suitable for the production of human drugs (Maertens et al., 2006).

In intensive production systems, rabbits are almost exclusively fed with a balanced compound diet in order to fulfil their dietary requirements, with a view to optimizing their production records and feeding management. The size of commercial farms has been dramatically increased due to the introduction of artificial insemination and the batch management system. As an example of intensive rabbit production, the average production records obtained from commercial farms in France are presented in Table 14.1.

In rabbit meat production, as with other animal species, feeding costs represent the largest part of the production costs. Depending mainly on investment costs, they amount to 0.60–0.70 of the total costs. In fact, the production costs for meat rabbits are twice as high as those for broilers and 25–35% higher than for pigs. In view of being competitive with these animal productions, a reduction in feeding costs is of primary importance. For this reason, this chapter considers in detail different possibilities for optimizing the feed conversion ratio (FCR) in rabbit production.

14.2 Diet Presentation

In intensive rabbit production, dried and ground raw materials are used to prepare balanced compound diets. These concentrated diets are generally pelleted because rabbits show a strong preference for pellets over the same diet in meal or mash form. The processing costs for pelleting rabbit diets are more than compensated for by a number of benefits. Significantly lower amounts of feed are consumed on meal diets, resulting in lower daily weight gain, inferior FCR and lower slaughter yield (Table 14.2). When offered a choice between meal and pellet form, 0.97 of the total feed intake is of the pelleted diet (Harris et al., 1983).

Other benefits of pelleting are comparable to those for other animals: segregation or selection between the different raw materials is impossible, higher amounts of
Table 14.1. Average production records in 2006 from commercial rabbit farms in France (Lebas, 2007).

<table>
<thead>
<tr>
<th>Criteria</th>
<th>2006</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of farms considered</td>
<td>1089</td>
</tr>
<tr>
<td>Does per farm</td>
<td>495</td>
</tr>
<tr>
<td>Replacement rate (%)</td>
<td>113</td>
</tr>
<tr>
<td>Kindling per artificial insemination (%)</td>
<td>79.4</td>
</tr>
<tr>
<td>Number of parities per female year⁻¹</td>
<td>6.85</td>
</tr>
<tr>
<td>Litter size at birth (alive)</td>
<td>9.5</td>
</tr>
<tr>
<td>Litter size at weaning</td>
<td>8.1</td>
</tr>
<tr>
<td>Mortality (plus eliminated)</td>
<td>15.8</td>
</tr>
<tr>
<td>Mortality after weaning (%)</td>
<td>8.5</td>
</tr>
<tr>
<td>Fatteners produced per doe year⁻¹</td>
<td>50.7</td>
</tr>
<tr>
<td>Market weight of growers (kg)</td>
<td>2.45</td>
</tr>
<tr>
<td>Feed per rabbits produced (kg)²</td>
<td>3.58</td>
</tr>
</tbody>
</table>

²Total feed consumption including young parent stock, does and fatteners.

co-products can be fed and feed wastage is minimal. Pellets further reduce dust problems in houses and automatic or semi-automatic rabbit feeders work much more easily with pellets than with meal or mash.

Several efforts have been undertaken with other presentation forms. When a limited number of raw materials are mixed and supplied, rabbits select those raw materials according to their palatability. As a result of this unbalanced intake, performances deteriorate (Schlolaut, 1995). When cereals and protein sources are covered with molasses, however, rabbits are less able to distinguish between the different dietary components.

With low cereal prices, efforts have been made to feed high amounts of whole grains together with a concentrated pellet. Rommers et al. (1996) compared pellets with a mixture of 0.85 pellets and 0.15 whole wheat or barley for fatteners. The biological performance was not significantly different. However, the cereals accumulated in the feeders because the rabbits showed preference for the pellets. Because feed wastage was not observed, mainly due to the construction of the feeders, it was concluded that a mixture of pellets and whole grains could reduce feeding costs. However, attention must be drawn to the need to avoid feed wastage and to feed a homogenous mixture.

Instead of pelleting, rabbit diets can be extruded. Rabbits accept such a presentation if the durability and hardness are acceptable, but performances tended to decrease, especially in young rabbits (Maertens and Luzi, 1995). The decreased daily weight gain could be related to degradations in protein quality due to the high temperature during the extrusion. Moreover, the intended higher starch digestibility was not obtained and consequently extrusion failed to reduce the mortality rate of high-starch diets (Maertens and Luzi, 1995). Similarly, Fernández-Carmona et al. (1983) obtained a lower intake and growth rate and considerable variability in FCR when rabbits from 18 to 42 days of age were fed an extruded diet as opposed to the pelleted diet. The authors

Table 14.2. Effect of diet presentation on the performances of growing rabbits (as a proportion of pellet).

<table>
<thead>
<tr>
<th>Reference</th>
<th>Presentation form</th>
<th>DWG</th>
<th>DFI</th>
<th>FCR²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lebas (1973)</td>
<td>Pellet</td>
<td>=1.00</td>
<td>=1.00</td>
<td>=1.00</td>
</tr>
<tr>
<td></td>
<td>Meal</td>
<td>0.87</td>
<td>0.83</td>
<td>1.06</td>
</tr>
<tr>
<td>King (1974)</td>
<td>Pellet</td>
<td>=1.00</td>
<td>=1.00</td>
<td>=1.00</td>
</tr>
<tr>
<td></td>
<td>Meal</td>
<td>0.93</td>
<td>0.90</td>
<td>1.03</td>
</tr>
<tr>
<td>Machin et al. (1980)</td>
<td>Pellet</td>
<td>=1.00</td>
<td>=1.00</td>
<td>=1.00</td>
</tr>
<tr>
<td></td>
<td>Meal</td>
<td>0.98</td>
<td>0.80</td>
<td>1.23</td>
</tr>
<tr>
<td></td>
<td>Mash (0.40 water)</td>
<td>0.75</td>
<td>0.84</td>
<td>0.89</td>
</tr>
<tr>
<td>Candau et al. (1986)</td>
<td>Pellet</td>
<td>=1.00</td>
<td>=1.00</td>
<td>=1.00</td>
</tr>
<tr>
<td></td>
<td>Meal</td>
<td>0.60</td>
<td>0.75</td>
<td>1.23</td>
</tr>
<tr>
<td>Sánchez et al. (1984)</td>
<td>Pellet</td>
<td>=1.00</td>
<td>=1.00</td>
<td>=1.00</td>
</tr>
<tr>
<td></td>
<td>Meal</td>
<td>0.64</td>
<td>0.52</td>
<td>2.79</td>
</tr>
</tbody>
</table>

DWG, daily weight gain; DFI, daily feed intake; FCR, feed conversion ratio. ²A higher figure indicates worse FCR.
explained these inferior results by the lower quality of the pellets in the extruded diet (lower durability and hardness).

In intensive rabbit meat production, a pelleted balanced diet is the basis for meeting nutrient and energy requirements for maximizing biological performance. All ‘alternative’ methods (e.g. meal, mash, roughages, mixture of raw materials) decrease the daily dry matter intake. Most of these methods are labour-intensive because they have to be fed daily and are difficult to distribute automatically; they are therefore not suitable for large-scale production.

14.2.1 Pellet size and quality

The length of pellets is preferentially between 0.8 and 1 cm. If longer, there is a higher risk of breaking during handling. Moreover, losses of single pellets or parts of pellets by the rabbits are more frequent at sizes >1 cm. The preferential pellet diameter is in the range of 3–4 mm, which is also suitable for use in rabbit feeders and minimizes production costs. At diameters >5 mm, the risk of pellet wastage increases (Lebas, 1975a).

Small pellet size (diameter <2.5 mm) tends to decrease feed intake, probably due to the increased feeding time (Maertens, 1994). This effect was partly confirmed in the choice feeding trial of Gidenne et al. (2003a) with early-weaned rabbits. Between 18 and 31 days of age, rabbits consumed 40% fewer 2.5 mm pellets than control pellets of 3.5 mm. However, the hardness of the small pellets was 18% higher and it is not clear if a small pellet size or higher durability is responsible for the decreased feed intake at a smaller size.

Changing from a large pellet diameter (4.8 mm) to a small diameter (2.5 mm) at weaning leads to a 20% reduction in feed intake and weight gain, while the opposite change induces a 10% increase in feed intake and weight gain shortly after weaning (Maertens, 1994).

Pellet durability and hardness are the major quality characteristics of rabbit pellets because rabbits do not eat the fines between the pellets. Several types of device for measuring pellet quality have been used by the industry. Generally, these devices can be classified into those testing the resistance of pellets to crushing (hardness) or those testing fragmentation when rubbed or shaken (durability). The pneumatic-powered hardness testers determine the power (in kg) for crushing pellets (Payne et al., 1994). Although this method is quick, sufficient pellets (>ten) have to be tested in order to have good repeatability. Equipment using a motor drive instead of manual handling is preferable because it excludes effects due to the operator. A minimum hardness of 8 kg is necessary to avoid excessive fines being produced during handling or transport, especially when using automatic feeders.

To test the durability of pellets, a standard method using a square tumbling can has been developed (Phost, 1963). The can is rotated at a speed of 50 rpm using a perpendicular axis centred on both sides. A quantity of 500 g of pellets, after sieving out the fines, is used for the test. The sample is placed in the tumbling can and rotated for 10 min; after sieving again (standard mesh size just smaller than the nominal pellet diameter), the remaining pellets are weighed and the pellet durability index (g pellets after/g pellets before tumbling × 10) is obtained. Under correct processing and handling conditions, <0.02 of ‘fines’ may be produced in quality pellets during transport, in silos or bags and in tubes and rabbit feeders.

When the resistance to crushing is between 7 and 13 kg, the biological performance of rabbits is not influenced by the hardness of the pellets (Morisse et al., 1985).

14.3 Feed Storage

With the increasing size of rabbit breeding units, feeds are mainly delivered in bulk. Packaging in bags is still used for small units or for special feeds (e.g. weaning diets). Storage time should be limited to 3–4 weeks, employing outdoor silos. Due to temperature variations, feed may sweat and
become mouldy. Taking into account the fact that about 4 t feed week\(^{-1}\) is consumed in a unit of 500 does and corresponding fatteners, a storage capacity of about 15 t is necessary for bulk feed. When only two different diets are supplied (for lactation and growth), the minimal silo sizes are 5 and 10 t for does and fatteners, respectively.

If stored in a dry location, rabbit feed with a dry matter content of at least 890 g kg\(^{-1}\) can be stored for several months, which implies fewer diet changes for a growing cycle. Cages equipped with manual-filled feeders must contain at least the quantity consumed daily. With automatic feeding systems, tubes supplying a number of cages (rather than individual feeders) are used. In such systems, feed is distributed several times per day. Although it is claimed that rabbits eat more when fresh feed is served, no experiments have demonstrated this.

**14.4 Number of Diets**

With increasing knowledge of the specific requirements of the different categories of rabbits, a series of diets can be proposed. However, based on practical considerations and because of the relatively small differences in nutrient and energy concentrations between the different diets, the number of diets should be limited.

In practice, two or three silos (diets) are economically optimum for a middle-sized rabbitry, otherwise the quantities involved are too small to operate with bulk feed. Furthermore, automatic or semi-automatic feeding systems are increasingly being used in large units. These do not allow the distribution of a different diet to each category. However, rabbit management is changed from individual handling to a batch system. In this way, animals in the same reproductive phase or of the same age are grouped together in one building or battery. Such a management system allows the use of phase feeding programmes. The same silo is progressively filled with an adapted diet according to the age of the fatteners.

In a rabbitry, depending on the weaning date and slaughter weight, about 0.5–0.6 of the feed is consumed in the fattening unit and 0.4–0.5 in the reproduction unit (Fig. 14.1a). Young parent stock, males (if present) and does in pre-gestation cages have similar requirements. They can be fed a fattening diet, sometimes on a restricted basis.

After weaning, about 0.65 of the feed is consumed in the second half of the fattening period (Fig. 14.1b). A specific finishing diet (high energy level, reduced protein content) favours feed efficiency and reduces the nitrogen output to the environment.

![Fig. 14.1](image-url). Distribution of the feed consumption in a rabbitry using a 42-day reproduction cycle, weaning at 35 days and a production level of 50 fatteners per doe year\(^{-1}\). (a) Closed farm; (b) in the fattening unit.
14.5 Feed and Water Intake

The average feed intakes and feed efficiencies of weaned rabbits until slaughter weight are given in Table 14.3. Data reflect results obtained with a quickly growing strain and weaning at 30 days. Growth, and consequently feed intake curves, show an irregular development during the fattening period; therefore, the data presented in Table 14.3 are mean values of several batches of hybrid rabbits. Feed intake increases with age, but not when expressed as kg\(^{-1}\) live body weight. The highest feed intake per unit of weight is reached before the maximal growth rate occurs.

The feed intake of does varies considerably during the reproductive cycle, from 150 to 450 g day\(^{-1}\). Feed intake patterns during the lactation period correspond largely to the milk yield of the doe and consequently drop dramatically after weaning.

Rabbits fed a pelleted diet have a water requirement that exceeds the dry matter intake. The ratio of feed to water consumption increases during the fattening period, from 1.55 to 1.65 (Laffolay, 1985). This ratio is about 1.9 for non-lactating does or adults at maintenance. Lactating does have a water intake that is about twice the feed intake.

If water is not available, feed intake drops quickly and will stop within 24 h. Limited drinking water leads to reduced feed intake and is sometimes used as an indirect way of inducing restricted feeding (Boisot et al., 2004). However, this management system cannot be defended from a welfare viewpoint.

14.6 Practical Feeding of the Different Categories of Rabbits

In commercial rabbitries, as a rule, rabbits are fed on an *ad libitum* basis (Table 14.4). This is not only for practical considerations, but also because of the rapid reproductive rate and the adjustment of the voluntary feed intake in response to changes in dietary energy concentration. However, some categories of rabbits are fed on a restricted basis to prevent excessive fattening or overcome digestive disturbances. In Table 14.4, a feeding scheme for commercial rabbit meat production is presented.

When restricted feeding is applied with a pelleted diet, no advantage has been found for feeding the total quantity once a day instead of spreading it over two meals (Tudela and Lebas, 2006). Moreover, in fatteners the number of feeding places does not need to be increased when feed is restricted (Tudela and Lebas, 2006).

### 14.6.1 Young parent stock

Feeding young parent stock properly is very important because it affects the lifetime reproductive capacity of the animals. The optimal feeding regime for young does

<table>
<thead>
<tr>
<th>Age (days)</th>
<th>Weight (g)</th>
<th>Weight gain (g day(^{-1}))</th>
<th>Feed intake</th>
<th>Feed conversion ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>g day(^{-1})</td>
<td>g kg(^{-1}) LW</td>
</tr>
<tr>
<td>21–30</td>
<td>400–740</td>
<td>38</td>
<td>35 + milk</td>
<td>–</td>
</tr>
<tr>
<td>30–37</td>
<td>740–1050</td>
<td>44</td>
<td>84</td>
<td>94</td>
</tr>
<tr>
<td>37–44</td>
<td>1050–1395</td>
<td>49</td>
<td>114</td>
<td>93</td>
</tr>
<tr>
<td>44–51</td>
<td>1395–1750</td>
<td>51</td>
<td>136</td>
<td>86</td>
</tr>
<tr>
<td>51–58</td>
<td>1750–2085</td>
<td>48</td>
<td>148</td>
<td>77</td>
</tr>
<tr>
<td>58–65</td>
<td>2085–2395</td>
<td>44</td>
<td>160</td>
<td>71</td>
</tr>
<tr>
<td>65–72</td>
<td>2395–2680</td>
<td>41</td>
<td>171</td>
<td>67</td>
</tr>
</tbody>
</table>

LW, live weight.

*"Diet: 10 MJ digestible energy kg\(^{-1}\). Moderate temperature conditions (15–23°C), no assumed mortality.*
depends to a large extent on the age of the first desired mating. Although evidence is found in the literature that *ad libitum* feeding together with early mating (0.75–0.80 of the adult weight) leads to favourable results in obtaining a first litter, in practice it is recommended to restrict feeding in young does and postpone the first mating until the age of at least 17 weeks, with a target of 0.85–0.90 of the adult weight (Rommers *et al*., 2006). This improves litter size. Restricted feeding during rearing also results in a higher milk yield and increased weaning weight of the kits at the end of the first lactation. Flushing 4–5 days prior to mating or insemination leads to oestrous synchronization, high pregnancy rates and a greater number of follicles (Rommers *et al*., 2006).

Another method to restrict feeding in young parent stock is to use a low-energy, high-fibre diet (<8 MJ digestible energy (DE) kg⁻¹). Such a diet, even fed *ad libitum*, induces growth retardation, but the rabbit develops a higher intake capacity in the first lactation (Cervera *et al*., 2008).

When restricted-fed, a daily quantity of 40 g kg⁻¹ live weight is sufficient to cover the nutrient and energy requirements when a moderately concentrated diet (9.5 MJ DE kg⁻¹) is fed. Requirements increase rapidly during the second half of the gestation period, but the intake capacity decreases because of the development of fetuses in the abdomen. Subsequently, *feed is provided ad libitum*.

After weaning, non-pregnant does or does in early pregnancy have to be restricted-fed to prevent excessive fattening, which would lead to both high perinatal mortality and suppression of voluntary feed intake in early lactation (Partridge *et al*., 1986; Pascual *et al*., 2003). The same quantity as mentioned for young does is recommended. In late gestation, feed restriction is no longer necessary.

### 14.6.2 Males

Males increase their voluntary feed intake until the age of 5 months. Subsequently, feed intake drops by about 0.30 or a natural feed restriction takes place. In comparison with restricted-fed littermates (0.75 of *ad libitum*), libido or semen characteristics are not negatively influenced by *ad libitum* feeding (Luzi *et al*., 1996). Excessive feed restriction in males is therefore not recommended. However, males from heavy lines frequently show sore hocks in wire mesh cages; feed restriction reduces their adult weight by about 0.5 kg and consequently

### Table 14.4. Feeding scheme for commercial rabbit meat production.

<table>
<thead>
<tr>
<th>Category</th>
<th>Quantity</th>
<th>Diet</th>
</tr>
</thead>
<tbody>
<tr>
<td>Young does</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Early mating (15–16 weeks)</td>
<td><em>Ad libitum</em></td>
<td>Fatteners</td>
</tr>
<tr>
<td>Late mating (17–20 weeks)</td>
<td>Restricted (40 g kg⁻¹ live weight, followed by a 4-day flushing before insemination)</td>
<td>Fatteners or specific rearing diet</td>
</tr>
<tr>
<td>Does</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Late gestation</td>
<td><em>Ad libitum</em></td>
<td>Lactation</td>
</tr>
<tr>
<td>Lactating</td>
<td><em>Ad libitum</em></td>
<td></td>
</tr>
<tr>
<td>Kits &lt;3 weeks</td>
<td></td>
<td>Lactation</td>
</tr>
<tr>
<td>Kits &gt;3 weeks</td>
<td></td>
<td>Weaning</td>
</tr>
<tr>
<td>In pre-gestation cages</td>
<td>Restricted (40 g kg⁻¹ live weight), but <em>ad libitum</em> 4 days prior to insemination</td>
<td>Fatteners</td>
</tr>
<tr>
<td>Males</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Young (until 18 weeks)</td>
<td><em>Ad libitum</em></td>
<td>Fatteners</td>
</tr>
<tr>
<td>Adult</td>
<td>Restricted (40 g kg⁻¹ live weight)</td>
<td>Fatteners</td>
</tr>
<tr>
<td>Weaned rabbits</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4–6/7 weeks</td>
<td>Restricted, 0.75 of <em>ad libitum</em></td>
<td>Fatteners</td>
</tr>
<tr>
<td>6/7–10/11 weeks</td>
<td><em>Ad libitum</em></td>
<td>Fatteners/finishing</td>
</tr>
</tbody>
</table>

After weaning, non-pregnant does or does in early pregnancy have to be restricted-fed to prevent excessive fattening, which would lead to both high perinatal mortality and suppression of voluntary feed intake in early lactation (Partridge *et al*., 1986; Pascual *et al*., 2003). The same quantity as mentioned for young does is recommended. In late gestation, feed restriction is no longer necessary.
favourable effects on longevity may be expected.

### 14.6.3 Lactating does and their young

Lactating females have a high nutrient and energy demand due to their concentrated milk production (Maertens et al., 2006). A concentrated high-energy lactation diet stimulates daily nutrient and energy intake, and reduces the energy deficit at the end of the lactation (see Chapter 6). Feed intake gradually increases as milk production increases (Fig. 14.2). Feeding the lactating doe *ad libitum* is a common habit to fulfil the high nutrient and energy demands.

Lactating does and their young eat out of the same feeder. Specific starter diets (creep feeding) as for piglets are not commonly used with rabbits. Although a system has been developed to feed the female and her litter separately (Fortun-Lamothe et al., 2000), it is not actually in use in practice. Before the age of 3 weeks, only small amounts of feed are consumed by the young. Therefore, a lactation diet adapted to the requirements of the doe is fed in early lactation.

Once the young start to eat significant amounts of solid feed, from the age of 3 weeks, preference can be given to the young. A diet more adapted to their requirements has been shown to not only promote higher weaning weights, but also favour their intestinal health (Xiccato et al., 2006; Gidenne et al., 2007).

### 14.6.4 Weaned young

If a specific weaning diet is fed from the age of 3 weeks, this may be continued after weaning until the age of 7–8 weeks. Once the critical period is passed (7–8 weeks of age), rabbits are fed a more concentrated fattening diet. The increased energy concentration favours the conversion ratio.

A phase-feeding programme during the fattening period is designed to reduce mortality, increase biological performance and minimize mineral excretion in order to protect the environment. However, such a programme requires scheduled production in large groups.

Besides dietary qualitative aspects, quantitative aspects of feeding have proved to be helpful in overcoming losses due to diarrhoea (see Chapter 10). Based on studies and success under practical conditions, many farms no longer feed weanlings *ad libitum*. A reduction of feed intake by at least 25% has proven to be very helpful in overcoming enteritis problems between the ages of 5 and 8 weeks. Gidenne et al. (2003b) found the mortality rate to be halved in restricted-fed rabbits compared to those fed *ad libitum*. On intensive farms, increasing use is therefore being made of automatic feeding systems, which allow the distribution of a restricted quantity of

![Fig. 14.2. Feed intake (g day⁻¹) and milk yield (g day⁻¹) of does if pregnant (P) or non-pregnant (NP) 11 days post-parturition (data from Maertens and De Groote, 1991; Maertens et al., 2006).](image-url)
feed in relation to the age of the growing rabbit.

An indirect method of restricting feed intake is to restrict water intake. Rabbits have a relatively small stomach, which limits a high water and feed intake during a short period of time. Therefore, when the water distribution is limited to 2–3 h (continuous) day⁻¹, feed intake is only 0.70 of the ad libitum intake. Under such conditions, both in experimental studies as on commercial farms, positive results have been obtained in reducing enteritis and losses due to diarrhoea (Boisot et al., 2003, 2004). As already mentioned, however, restricting water cannot be defended from a welfare viewpoint and direct feed restriction should be applied to prevent enteritis in young rabbits (see also Chapter 11).

14.7 Feed Conversion Ratio

Numerous experimental FCR data are available in fatteners, but only very few data are available for the reproduction unit. Nevertheless, to improve FCR, possibilities have to be considered for both females and fatteners. The most important factors are the use of efficient stock, the quality of the feed, limitation of losses (mortality) and farm management (e.g. reproduction efficiency, slaughter age). The impact of some of the factors of primary importance in reducing FCR will be discussed.

14.7.1 Definition of feed conversion ratio

When speaking about FCR, in practice the most extensively used parameter for estimating feed efficiency in intensive systems is the overall global (farm) feed conversion ratio. This global FCR is defined for a closed unit (maternity and fattening) as the ratio between the kg of feed consumed (bought) per kg of rabbits produced (sold). Consequently, it is very valuable from a practical and economic viewpoint.

Recent overviews of farm data have shown average FCRs of 3.60, 3.82 and 3.63 in France, Italy and Spain, respectively (Lebas, 2007; Rosell and González, 2007; Xiccato et al., 2007). However, all of these studies stressed the big differences between farms (from <3.0 to >4.5) (Fig. 14.3). In this index, reproduction efficiency and

![Figure 14.3](image_url)
slaughter weight are the main factors that influence the FCR. When the same mortality is considered (10% after weaning), the cumulative effect of both variables results in an increase from 3.07 to 4.03, or 31.3% (Table 14.5).

When the FCR is calculated in fatters then the FCR is defined as the ratio of kg of feed consumed per kg weight gain of rabbits (finishing weight minus weaning weight). In this FCR, the feed consumption of rabbits lost (mortality and removed) is included, while no weight gain for them is considered. This is correct from an economic viewpoint, and is therefore defined as the economic FCR. If we calculate this FCR in the reproduction unit then the FCR is the ratio between kg of feed consumed and kg of rabbits weaned plus sold old females.

However, if mortality is not one of the target variables in nutrition experiments, the effect of mortality is eliminated and the result is the technical FCR. In this method, only the feed consumed by rabbits reaching the end of the experimental period is taken into account. As a consequence, the technical FCR is lower than the economic FCR. For this correction, it is assumed that no feed was consumed during the 2 days preceding death (Maertens et al., 2005b).

In addition to FCR, efficacy of the feed utilization is sometimes presented as feed efficiency (de Blas et al., 1998). From a scientific point of view this inverse ratio, namely kg of weight gain per kg feed consumed, shows a figure that better expresses the efficiency and is therefore suggested for experimental purposes.

### 14.7.2 Feed conversion ratio as affected by age

Young and fast-growing animals have a far more favourable FCR in the early fattening stage than when near slaughter weight. The different content of tissue accretion (fat versus protein and water) and increased maintenance requirements are responsible for the very fast increase in FCR above a weight of 2.0 kg (FCR >3.25). In Table 14.3, recent data obtained at our experimental unit are presented for the technical FCR with a fast-growing strain.

### 14.7.3 Diet concentration

Feed efficiency is negatively correlated with dietary DE content, as was originally shown 30 years ago by Lebas (1975b) and confirmed in many later experiments. A rabbit regulates its feed intake according to energy requirements, as for other mammals. In non-ruminants glycaemia plays a key role in food intake regulation, while in ruminants the levels of plasma volatile fatty acids have a major role. Since rabbit is a non-ruminant herbivore, the main blood component regulating feed intake is unclear, but it is likely to be the blood glucose level (Gidenne and Lebas, 2005). However, because of the close relationship between dietary fibre and DE content, daily feed intake (and by consequence FCR) is even more correlated with lower digestible fibre (acid detergent fibre) than with the higher DE content (Gidenne and Lebas, 2005).

Based on the relationship between dietary DE content and intake, an improved

<table>
<thead>
<tr>
<th>Slaughter weight (kg)</th>
<th>Number of rabbits produced per doe year⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>40</td>
</tr>
<tr>
<td>2.00</td>
<td>3.64</td>
</tr>
<tr>
<td>2.25</td>
<td>3.79</td>
</tr>
<tr>
<td>2.50</td>
<td>4.03</td>
</tr>
</tbody>
</table>

Table 14.5. Global feed conversion ratio for different slaughter weights and the number of rabbits produced per doe year⁻¹ (adapted from Maertens et al., 2005a).
FCR can be obtained with diets of high energy concentration. However, due to the dietary fibre requirements of rabbits and the low digestibility of different fibre classes (Gidenne, 2003), rabbit diets have a low energy content (DE or metabolizable energy) compared to poultry and pig diets.

While respecting fibre requirements, diets of high energy concentration can be obtained by adding fat (and to a lesser content digestible fibre). The DE content of fats (or oils) is nearly three times as high as that of cereals (Maertens et al., 2002). However, because of the necessity for rabbit diets to be pelleted, the addition is limited to 20–30 g kg\(^{-1}\) because of its negative impact on the pellet quality (Maertens, 1998). If it is taken into account that a replacement of 20 g cereal with 20 g fat (oil) kg\(^{-1}\) results in an increase in the dietary DE content of 0.44 MJ kg\(^{-1}\), a decrease in the FCR by about 0.15, or 5–7%, can be expected. This effect has again been demonstrated by Corrent et al. (2007); rabbits did not reduce their feed intake, and consequently the higher daily energy intake resulted in a more favourable FCR (Table 14.6). Because amino acids were adjusted to the dietary DE content, daily weight gain also tended to be higher with the higher energy concentration diets.

The use of diets of higher energy concentration to improve the FCR is especially interesting during the finishing stage. Shortly after weaning, feed consumption is low and optimizing digestive health is of primary importance. However, in the second fattening stage rabbits are less sensitive to digestive disorders and about 0.66 of the feed is consumed during this period. A phase feeding programme, including higher energy concentration diets in the finishing stage, improves FCR. Based on several studies, an improvement in FCR of 0.15–0.20 for 0.5 MJ DE kg\(^{-1}\) can be expected (Maertens, 2009). However, more trials are necessary to verify if this relationship is linear (especially with fat addition) and between which margins of dietary energy content.

### 14.7.4 Mortality

It is evident that mortality has a very large impact on FCR (Table 14.7). For this calculation, the weight gain and feed intake data for a 5-week fattenning period (between 30 and 65 days of age), as presented in Table 14.3, were used. The effect of both increasing mortality (from 0% to 20%) and the timing of mortality (week 1, week 2–3 or during the last week) are presented.

If mortality occurs in the early fattening stage, the economic FCR deteriorates only slightly. However, if the losses (mortality and culled rabbits) are concentrated at the end of the fattening period, the FCR is 11.2% and 26.1% worse for mortality rates of 10% and 20%, respectively (Table 14.7) (Maertens, 2009).

Losses in the fattening unit also have consequences on the FCR in the reproduction unit. Before weaning these rabbits have consumed feed and, moreover, the feed consumption of the mother has to be divided between fewer weaned rabbits. This will be discussed further in the management paragraph.

| Table 14.6. Effect of dietary digestible energy (DE) content on growth and feed conversion ratio during the finishing period (Corrent et al., 2007). |
|-----------------|-----------------|-----------------|-----------------|-----------------|
| **Energy content of diet (MJ DE kg\(^{-1}\))** | **10.25 (24.5)** | **10.67 (34.4)** | **11.08 (39.5)** | **P value** |
| Weight gain (g day\(^{-1}\)) between 48 and 70 days | 47.2 | 48.2 | 50.3 | 0.06 |
| Feed intake (g day\(^{-1}\)) between 48 and 70 days | 168.8 | 163.5 | 168.4 | >0.10 |
| Feed conversion ratio | 3.60 | 3.40 | 3.36 | <0.01 |

\(^a\)Values in parentheses are ether extract (g kg\(^{-1}\)).

\(^b\)\(^c\)Data with different letter are statistically different (\(P <0.05\)).
Table 14.7. Economic feed conversion ratio in the fattening unit as affected by mortality and age of losses.

<table>
<thead>
<tr>
<th>Age when mortality occurs</th>
<th>Mortality (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0</td>
</tr>
<tr>
<td>Week 1</td>
<td>2.72</td>
</tr>
<tr>
<td>Week 2–3</td>
<td>2.72</td>
</tr>
<tr>
<td>Week 4–5</td>
<td>2.72</td>
</tr>
</tbody>
</table>

14.7.5 Management

In practice, a 42-day reproduction cycle is generally used. However, fertility rate, litter size and pre-weaning mortality have a very large impact on the number of rabbits weaned per doe and, as a consequence, on the FCR of the reproduction unit. Data concerning this FCR are very scarce in the literature. Therefore, a calculation is presented for a rabbit unit with weaning at 35 days, based on recent feed intake data obtained at our institute (Table 14.8) (Maertens, 2009). During the entire lactation period, productive does and their young consume on average 18.5 kg of feed. Furthermore, their feed consumption outside of the lactation period has to be considered (110 days year⁻¹), in addition to the feed consumption of the young females and females in pre-gestation cages (together 45 days year⁻¹). For the calculation of FCR in a productive maternity, we have assumed an average of 7.3 litters per doe year⁻¹ and 8.5 weaned kits per litter.

The FCR obtained in such a productive maternity unit is only 2.79, but this does not take into account weanlings losses in the fattening unit. The feed consumption before weaning of these rabbits is lost and the FCR worsens in the maternity unit. In Table 14.9, the effect of post-weaning losses is presented for different production levels.

When 10% losses are considered, the FCR worsens to 3.45 at a production level of 57 young. On the other hand, an increase of five young per doe year⁻¹ leads to an improved FCR of 3.09, a decrease of 11%. The simultaneous impact of an increase of five weaned young and a decrease of 5% of post-weaning mortality results in an improved FCR (e.g. from 3.45 to 2.93) (Table 14.9).

14.7.6 Other factors involved in the FCR

Restricted feeding in the fattening unit has proved to be helpful in overcoming digestive disorders, especially shortly after weaning, but it has also a favourable effect on FCR. According to Gidenne et al. (2003b), the following relationship is found during the 5-week fattening period:

$$\text{FCR} = 2.88 - 0.021 \times \text{feed restriction (proportion)}$$

This means that an improvement of 0.21 in FCR can be obtained when rabbits are 0.10 restricted-fed (i.e. 0.9 of ad libitum). However, this gain has to be considered

Table 14.8. Calculation of the feed conversion ratio in a productive reproduction unit (for 100 does).

<table>
<thead>
<tr>
<th>Stage</th>
<th>Feeds consumed</th>
<th>Product</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lactation: 18.5 kg per litter × 7.3 litters per doe year⁻¹</td>
<td>13.505</td>
<td>8.5 weaned per litter × 7.3 litters or 62 weaned per doe year⁻¹ with a weight of 1.0 kg</td>
</tr>
<tr>
<td>Only pregnant: 110 days × 160g day⁻¹</td>
<td>1.760</td>
<td>Sold females: 50 with an economic weight of 3 kg</td>
</tr>
<tr>
<td>Young females and females in rearing cages: 45 × 365 days × 150g day⁻¹</td>
<td>2.464</td>
<td>Total</td>
</tr>
<tr>
<td>Total</td>
<td>17.729</td>
<td>Total</td>
</tr>
</tbody>
</table>

FCR 2.79
under the restriction plan that was applied in their trials.

Females that do not immediately become pregnant have to be restricted-fed because over-fattening impairs their subsequent reproductive performance and leads to a reduced output in the subsequent lactation (Pascual et al., 2003). Based on the data in Table 14.8, an over-consumption of 10 g day$^{-1}$ leads to a deterioration of 2–3% of the FCR in the maternity unit.

Fattening rabbits are mainly caged in a group size of six to eight. However, several comparative trials have shown that individually caged rabbits have a higher daily weight gain and better FCR. In a Spanish study, the difference in favour of individual caging was 11.8% (Garcia-Palomares et al., 2006). Housing in large groups (pens) or on an alternative floor (e.g. straw) always leads to a deterioration in the FCR (Dal Bosco et al., 2002).

In addition, environmental conditions affect the FCR because of their effect on thermoregulation. During the summer, a better FCR is obtained than during the winter despite the lower growth rate. On the other hand, higher growth rates but worse FCRs are observed at low temperatures (winter) compared to fattening under heat stress (Ramon et al., 1996).

Finally, feed wastage due to the feeder design or meal losses can have a significant impact on the FCR. Pregnant females can waste large amounts of feed by scratching it out of un-modified feeders. Another important wastage results from rabbits not eating fines. Any mash present in the pellets or formed in the feeding system worsens FCR. Farm data indicate that this loss can approach 1.5–2% of the total amount of feed.

<table>
<thead>
<tr>
<th>Table 14.9. Feed conversion ratio in the maternity unit, as affected by post-weaning mortality and production level.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Losses in the fattening unit (%)</td>
</tr>
<tr>
<td>0</td>
</tr>
<tr>
<td>5</td>
</tr>
<tr>
<td>10</td>
</tr>
<tr>
<td>15</td>
</tr>
</tbody>
</table>

References


15 Nutrition and the Climatic Environment

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15.1 General Aspects of Environment

Biometeorology is the study of the relationship between the environment and living organisms. In homeothermic animals, the goal is to maintain a stable body core temperature under most conditions. The thermoregulatory system employs all of the systems of the body and integrates their activities into appropriate and coordinated reactions. This chapter considers one specific area of this by focusing on nutrition.

The variables that define an environment are temperature, humidity, light, altitude, smell and noise. Little is known about the last three, apart from some data relating levels of carbon dioxide or ammonia to some productive parameters of animals, which are essential in the control of the frequency of air exchange in intensive farms. The reciprocal problem of the contaminating effect of the animals themselves on the atmosphere and soil also appears to be very interesting, and numerous studies have been undertaken on species other than rabbits that show a relationship between nutrition and the production of ammonia, methane, phosphorus and sodium.

Lighting schedules are programmed to control reproduction and, together with feed restriction, can marginally improve feed efficiency in growing rabbits. This is a controversial idea because the effect depends on the age of the rabbit, length of feeding and time of feeding. Feeding usually occurs in the late afternoon and at night, so feed must be available at these times (Maertens, 1992).

Ambient temperature and humidity are the variables that most affect nutrition. Both directly influence the energy equilibrium of the animal, changing the flow of heat between the animal and the environment. In particular situations for species other than rabbits, correlations have been found between different functions of temperature and humidity that permit the most reliable to be selected; for example, the temperature humidity index (THI), wet bulb temperature, radiant temperature, equivalent temperature and effective temperature. The higher THI value in humid tropical climates compared to that found in temperate and subtropical areas elicits a more stressful environment for rabbit production (Ogunjimi et al., 2008). Other indices define the environment in terms of the animal’s response, including operative temperature, iso-ambient lines, thermoneutral zone (TNZ) and comfort zone.

Air temperature alone may be acceptable in laboratory conditions, but it becomes an inadequate measure of the degree of thermal stress on animals exposed to the natural environment (Young, 1977). Unfortunately, insufficient information is available to express all the climatic variables in one unit, such as the effective ambient temperature.
or others, and mean air temperature is employed instead as the usual index.

The lack of research work on rabbits limits the discussion of climatic variables solely to the effect of temperature, daily minimum temperature (Fuquay, 1981) or daily average temperature. This can lead to substantial errors where other parameters have a significant effect, for example wind, solar radiation or ambient humidity. Taking these factors into account, the dry temperature is the most important and representative index, and humidity (wet bulb temperature) can also be used when its incidence has been measured. Future research will perhaps define a THI similar to that used for other non-sweating species.

The environment is sometimes defined by the season of the year and even by the particular system of production, such as building interior versus open air. This type of loose definition adds even more imprecision to the conditions and makes it impossible to replicate observations or experimental work, although it may have practical value for specific zones or purposes.

Another difficulty in measuring temperature, in terms of minimum, maximum or mean, results from diurnal and seasonal fluctuations. Many experiments have been designed with animals in climate chambers at a constant temperature, making comparisons with animals exposed to a changing environment of limited relevance. In a naturally fluctuating environment, animals appear to partially overcome adverse effects by taking advantage of the more favourable parts of the cycle. It follows that a constant temperature is less well tolerated than a cyclic one, and the NRC (1981) suggested that the effect should be similar to that of a constant temperature equivalent to the mean of the cycle.

As a consequence of the small and fragmentary amount of work undertaken on rabbits to date, a review of experimental data raises more questions than it solves. This chapter tries to include the most valuable published work describing a general approach to the complex nutrition–environment relationship.

Interest in the subject is not recent, but has increased lately because it is a crucial element in the nutrition of domestic animals in cold climates and even more in sub-tropical and tropical environments.

Tables of nutrient requirements have been developed for rabbits from work carried out in intensive production systems in temperate countries under moderate conditions relatively free of thermal stress, where animals can realize their full genetic potential. Application of these data can lead to considerable errors in feeding animals exposed to acute cold or heat stress, because the physiological responses involve changes in voluntary water intake, feed intake, maintenance energy requirements and level of production.

It seems that some corrections need to be introduced, depending upon the environment to which animals are acclimatized or temporarily exposed.

### 15.2 Thermoneutral Zone

Homeothermic animals maintain a constant core temperature, compensating for heat loss through morphological, physiological and behavioural mechanisms. The definition of thermal neutrality accepted by the International Union of Physiological Sciences is: ‘The range of ambient temperature as an expression of thermal environment within which metabolic rates are at minimum and temperature regulation is achieved by non-evaporative physical processes alone’ (Bligh and Johnson, 1973). Including a phrase such as ‘in normal productive animals’ should make the concept of TNZ more acceptable to farmers. It implies that a non-stressful situation means not only normal body temperature and no shivering, sweating or panting, but also that feed intake does not change. Net energy for productive purposes is the difference between metabolizable energy (ME) intake and heat production, which in turn involves maintenance needs and the heat increment (HI) of food.

Therefore, level of nutrition and production of heat increase together, lowering
critical temperatures with maximum energy retention for a given energy intake expected to be in the range between them (Fig. 15.1). HI contributes to the maintenance of body temperature in cold conditions, but compromises the heat balance in hot environments.

In the TNZ range the animal invokes mainly postural and vasomotor mechanisms to conserve or dissipate body heat. Rabbits take on a ball posture at <10°C to decrease their surface area for conduction or radiation losses. The spread posture at 30°C allows more sensible heat to be dissipated.

The energy-demanding behaviours of rabbits include maternal feeding and digging burrows. Many animals dig burrows underground to protect themselves in both tropical countries and the Arctic. Different types of burrows are connected with survival of rabbits in arid areas of New South Wales, as described by Hall and Myers (1978). Some systems in New Mexico (Gentry, 1983) and Tunisia have been designed to exchange conventional cages or burrows for concrete burrows. In these deep pits, temperatures remain up to 9°C lower than outside (Finzi et al., 1989).

Vasoconstriction of peripheral blood vessels helps the rabbit to keep warm in cold conditions, so that metabolism need not increase to offset heat loss. In particular, the amount of heat conserved in the ears (with an area of 0.026 m² in adults) is considerable. McEwen and Heath (1973) reported that heat loss was 0.2 W °C⁻¹ linear over the range of 0–30°C ambient temperature, about half of the theoretical loss if the ears were maintained at core body temperature. Responses to cold stress rely on more carbohydrates being utilized and fat tissue being easily mobilized. Long-term adaptation to cold involves increased insulation.

In a hot environment rabbits have to dissipate metabolic heat when the thermal gradient between them and the ambient temperature is small or even negative. First, they use the least expensive heat loss procedure of skin vasodilation (Kruk and Davydov, 1977). When this becomes insufficient, a decrease in food intake, which decreases HI, and evaporation of water from the respiratory tract are the mechanisms used to lose excess heat.

The lower and upper critical temperatures should be assessed from metabolic

![Fig. 15.1. Schematic representation of heat production and energy intake. — Non-acclimatized animals; ... heat-acclimatized animals. HP, heat production; MEI, metabolizable energy intake; TNZ, thermal neutral zone.](image-url)
heat production figures. The great variability between published data may be due more to the experimental procedure than to any question related to breed (Table 15.1). The type of chamber, method of measurement, restlessness and adaptation of animals to the temperature and individual differences change the limits of the TNZ.

The TNZ given by several studies between the 1940s and 1960s varied from 20°C to 30°C. Later research has found heat production to decrease from 5°C to 35°C (Gonzalez et al., 1971), 10°C to 30°C (Kluger et al., 1973), 0°C to 30°C (McEwen and Heath, 1973), 18°C to 28°C (Scheele et al., 1985) and 20°C to 30°C (Jin et al., 1990).

Table 15.1. Heat production (kJ kg⁻¹ body weight⁻⁰.⁷⁵).

<table>
<thead>
<tr>
<th>Source</th>
<th>Temperature °C</th>
<th>0</th>
<th>5</th>
<th>10</th>
<th>15</th>
<th>20</th>
<th>25</th>
<th>30</th>
<th>35</th>
<th>40</th>
</tr>
</thead>
<tbody>
<tr>
<td>Johnson et al. (1958)ᵃ</td>
<td>–</td>
<td>–</td>
<td>660</td>
<td>–</td>
<td>630</td>
<td>580</td>
<td>575</td>
<td>570</td>
<td>675</td>
<td></td>
</tr>
<tr>
<td>Johnson et al. (1958)ᵇ</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>660</td>
<td>–</td>
<td>620</td>
<td>570</td>
<td>640</td>
<td></td>
</tr>
<tr>
<td>Gonzalez et al. (1971)ᶜ</td>
<td>–</td>
<td>613</td>
<td>520</td>
<td>428</td>
<td>398</td>
<td>364</td>
<td>352</td>
<td>421</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td>McEwen and Heath (1973)ᵈ</td>
<td>352</td>
<td>–</td>
<td>312</td>
<td>–</td>
<td>300</td>
<td>–</td>
<td>273</td>
<td>–</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td>Nichelmann et al. (1974a)ᵉ</td>
<td>–</td>
<td>–</td>
<td>570</td>
<td>520</td>
<td>490</td>
<td>425</td>
<td>400</td>
<td>400</td>
<td>485</td>
<td></td>
</tr>
<tr>
<td>Scheele et al. (1985)ᶠ</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>396</td>
<td>–</td>
<td>–</td>
<td>331</td>
<td>–</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td>Sanz et al. (1989)ᵍ</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>550</td>
<td>520</td>
<td>440</td>
<td>400</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td>Jin et al. (1990)ʰ</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>488</td>
<td>–</td>
<td>378</td>
<td>–</td>
<td>–</td>
<td></td>
</tr>
</tbody>
</table>

ᵃFed females, 4 kg, reared at 9°C. (Values are approximate. Calculated from the original figure.)
ᵇFed females, 4 kg, reared at 28°C. (Values are approximate. Calculated from the original figure.)
ᶜFasting animals (assuming 3 kg live weight).
ᵈFasting animals, 3.9 kg.
ᵉFasting 42-day-old animals, approximately 1 kg live weight (points interpolated from the original response).
ᶠFed growing rabbits.
ᵍTen-day-old sucking rabbits (interpolating original values).
ʰFed growing rabbits, approximately 1.6 kg (mean of two diets).

The upper critical temperature has been estimated by all of the cited studies to be <30°C, when physiological reactions such as feed intake, respiration rate, panting and body temperature were examined, but lack of information for intermediate values from 20°C to 30°C makes it difficult to reduce the uncertainty. Most studies have found appreciable differences in heat production between 10°C and 20°C and, therefore, the lower critical temperature should be between these values. From a survey of the literature, McEwen and Heath (1973) calculated a value of approximately 15°C for the lower critical temperature.

Heat production has also been measured by Johnson et al. (1958) in fed mature New Zealand White rabbits exposed to temperature levels from 10°C to 40°C. Heat production decreased steadily up to 35°C and appeared to increase after this. From the data of heat production, feed intake and thyroid activity, the authors suggested an upper critical temperature of around 24°C.

These results have been confirmed in a series of experiments conducted by Nichelmann et al. (1973a, 1974a). They showed that heat production had the shape of a parabola, with the point of inflection at 25°C for adults, 30°C for 42-day-old rabbits and 35°C for 10-day-old pups. The TNZ lay between 15°C and 25°C for animals aged 80 days. This range coincides approximately with some estimates carried out on commercial farms. The shape of the response was not so clear in the work of Gonzalez et al. (1971), who reported a relatively constant heat production between 15°C and 30°C.

Thereafter, cooling of the animals is based upon evaporation, the rabbit being particularly ineffective at this process compared with other species. Relatively low
ratios of surface to skin vaporization and respiratory tract evaporation to heat production indicate that the rabbit has little ability to dissipate heat. Panting alone, even at 400 breaths min⁻¹ at 35°C, did not prevent an elevation of rectal temperature of 1.4°C (Gonzalez et al., 1971). In stressed non-acclimatized animals at 38°C, Johnson et al. (1958) reported that evaporation accounted for 0.30 of the total heat produced by adult animals housed at 35°C (0.40 was recorded at 40°C by Nichelmann et al. (1973b)), of which 0.60 was lost through panting: no increase was observed from 20°C to 30°C in young animals acclimatized for 7 days (Nichelmann et al., 1974b). Total evaporative heat loss has been estimated to be 0.6, 1.26 and 2.0 W kg⁻¹ at each ambient temperature of 15°C, 30°C and 35°C. Using the latent heat of evaporation as 0.7 W g⁻¹ h⁻¹, a 4 kg doe should evaporate around 7 g water h⁻¹ at 30°C.

The ears are a means of dissipating heat. The heat exchange coefficient is 9.1 W m⁻² °C⁻¹, about four times the coefficient for the whole animal (Kluger et al., 1973). In a wind of 60 m s⁻¹, fully dilated ears can lose twice as much heat as ears in non-forced convection. However, most rabbits die after a few days’ exposure to 40°C.

Stressed animals have lower productivity in the short term. The problem can be solved in temperate or even cold climates, where highly productive breeds can be satisfactorily reared in heated or insulated buildings. However, the production of meat and milk, and reproduction, suffer in this increasing order as a consequence of hot climates.

A lower basal or resting heat production reported in animals continuously exposed to environments of around 30°C would be of value in adaptation to hot environments. Alliston and Rich (1973) suggested that, following an 18-day acclimation period, there was a positive relationship between thermoregulatory efficiency and pregnancy. The results of Johnson et al. (1958) suggested that the influence of rising environmental temperature was less in New Zealand White rabbits reared at 28°C than in those reared at 9°C, as rectal minus air temperature, pulse rate and respiration rate were lower.

The heat production of newborn rabbits housed in metabolism cages and subjected to several ambient temperatures has been determined both for 10-day-old animals suckling normally (Nichelmann et al., 1974a) and 2 h after birth for fasting animals (Cardasis and Sinclair, 1972). These studies demonstrated a cold-induced increment of heat production. Kits were able to raise their basal level of heat production at 35°C, followed by temperature drops to 30°C, 20°C or 10°C; peak metabolism was achieved at around 15°C at 10 days.

Neonatal animals cannot maintain body temperature if unfed or if the ambient temperature drops abruptly (Hill, 1961; Rödel et al., 2008), although they tend to group together and curl up. The metabolic responses to both cold and fasting are the result of complex interactions (Schenk et al., 1975) that bring about a higher mortality rate compared with normal suckling rabbits.

Survival time and rate of weight loss of fasted newborn rabbits are strongly influenced by temperature, which is known to stimulate thermogenic activity of brown fat. The probability that large or small littermates survive could be related to the different lipid stores (Dawkins and Hull, 1964). Cardasis and Sinclair (1972) placed newborn rabbits at 35°C, 30°C and 25°C, and reported that smaller animals survived for fewer hours. Young animals with a birth weight of >50 g were able to maintain metabolic rate and body temperature for longer.

Heat production of newborn rabbits increases during the first days of life. A 10-day-old rabbit coordinates movement and already has improved insulation, gaining hair and tissue fat. The use of nest boxes with bedding, where young rabbits huddle, thereby reducing body-surface exposure, means that the optimal temperature range becomes wider with increasing age: 20–30°C at 20 days of life (Rafai and Papp, 1984). Practical observations have concluded that a 20°C temperature indoors leads to high viability in farms (Delaveau, 1982), but maternal behaviour significantly
affects the proper kindling and subsequent survival of litters under extreme climatic conditions in open sheds (Platukin and Konokhov, 1972).

15.3 Heat Stress

Exposure to high ambient temperatures induces rabbits to try to balance the excessive heat load by using different heat dissipation pathways. If such means are not sufficient then physiological traits deteriorate, including depression in feed intake, efficiency and utilization, disturbances in water, protein, energy and mineral metabolism balances, enzymatic reactions, hormonal secretions and blood metabolites.

In the late 1930s it was recognized that a high ambient temperature increases body temperature (Lee, 1939). The stress at ≥30°C seems to be very high; rectal temperature starts to increase at 27°C, rises abruptly at 32°C, together with a sudden decrease in feed consumption (Johnson et al., 1958), and reaches 42.5°C at 35°C (Nichelmann et al., 1973a). Above 35°C, rabbits can no longer regulate their internal temperature and heat prostration sets in.

A method to measure the severity of heat stress using the THI value has been proposed for rabbits under a subtropical climate and the values obtained are then classified as follows: <27.8 = absence of heat stress, 27.8–28.9 = moderate heat stress, 28.9–30.0 = severe heat stress and ≥30.0 = very severe heat stress. When comparing these values to those obtained for sheep and cattle (≥25.6 = very severe heat stress), it is evident that rabbits tolerate higher climatic stress than large mammals (Marai et al., 2002).

Thermal stress directly affects reproduction, health and nutrition, and all of these interact with each other. The overall result for animals exposed to thermal stress is always a reduction in productivity, which varies according to the severity of the stress and the acclimatization of the animal. Multiple factors cause the response of rabbits to a hot climate to be reduction in food intake, litters per year and offspring per litter. Normal production figures, as estimated by several experts, could be four or five litters, 20–25 animals weaned yearly and <20 g live weight gain day<sup>−1</sup> for growing animals (Colin, 1991, 1995).

Depressed feed intake and increased water consumption are the most important reactions to heat exposure. At 30°C rabbits consume only 60–70% of the feed intake recorded at 20°C and at 35°C the feed intake is decreased by 28–17%. In contrast, water requirements increase by 50% as the temperature rises from 18°C to 38°C. Blood metabolites such as glucose, serum total protein, serum total lipids and cholesterol decrease in rabbits exposed to heat stress conditions, which may be correlated to the decrease in energy metabolism during heat exposure.

Moreover, the increased energy requirement during panting, with the additional rise in body temperature, seems to be nonlinear, as opposed to the apparent linear increase in cold conditions. In severe heat stress, feed intake is so depressed that the maintenance requirements cannot be properly calculated.

It is important to predict the future resistance to thermal stress of animals that are likely to suffer it, and the selection of breeders must be based on an index linked to the production of heat, because this decreases in previously acclimatized animals. Probably the most useful indices are based on rectal temperature, such as the Iberia test (Rhoad, 1944), which is used in beef cattle and is also of proven validity in rabbits (Alliston and Rich, 1973; Finzi et al., 1988). Other indices may measure biochemical factors (Amici et al., 1995) or certain nutritional parameters, such as nitrogen retention, body fluids or fat (Kamal and Johnson, 1971).

Very little work to date has been designed to anticipate and understand the degree of re-adaptation or recovery of animals that have suffered thermal stress. Such re-adaptive behaviour can negate or change the conclusions obtained from short-term observations. Age, physiological condition and duration and intensity of stress should affect recovery to the original level of production, which in female breeding rabbits is
possible after 10 months at 30°C (Fernández Carmona et al., 1994c).

15.4 Nutritional Value of Feedstuffs and Environment

The nutritional value of rabbit feedstuffs is expressed in terms of digestible energy (DE) or ME. These biological values depend not only on the composition or quality of the feed, but also on the digestive or metabolic processes in the animal itself.

In moderate climates the quality of forages can vary greatly because of variety, maturity and harvesting. With regards to lucerne, the most frequent fibrous ingredient in rabbit diets, Garcia et al. (1995), studying a Spanish variety, reported a wide range of values for dry matter (DM), energy and amino acid digestibility.

The composition and nutritive value of tropical forages are extremely diverse. Digestible DM was found by Raharjo et al. (1988) to range from 123 to 463 g kg\(^{-1}\) for grasses and from 281 to 494 g kg\(^{-1}\) for non-woody legumes. Similarly, Carew et al. (1989) evaluated 30 plant species collected in Nigeria: whole plants contained 66–284 g crude protein kg\(^{-1}\) and 45–407 g crude fibre kg\(^{-1}\); results from the leaves of three tree species were 33–109 g crude protein kg\(^{-1}\) and 45–216 g crude fibre kg\(^{-1}\).

In tropical countries, the nutritive value of forages is relatively low, with high indigestible fibre. This problem has been linked to the four-carbon atom compounds, rapid lignification associated with environmental temperature and a low leaf to stem ratio. Some factors such as oxalates, cyanides, tannins and alkaloids limit the efficiency of nutrient utilization. The low nitrogen digestibility detected in some plants, such as Leucaena leucocephala (Harris et al., 1981) and Robinia pseudoacacia (Raharjo et al., 1990), is apparently due to protein–tannin complexes.

Most systems operating in tropical countries are based on small subsistence-level farms, where forage provides a major part of the requirements of rabbits. Forage alone cannot support high performance in either growth or lactation, and this disadvantage occurs in addition to the low quality mentioned above. In fact, Raharjo et al. (1988) reported daily intakes of tropical grasses ranging from 10 to 28 g of DM; ingestion of leaves, shrubs and woody legumes was generally higher, but rabbits lost weight on all diets. This poor performance derives not only from the lower quality of forage, but also from the low feed intake of any unpelleted ingredient or diet (Harris et al., 1983; Schlolaut, 1987).

Supplementation of pelleted diets with potential energy sources, including roots, tubers, fruits and grain by-products, has generally demonstrated that 0.50–0.75 of pellets can be replaced by green forages, by-products or roots without a significant reduction in growth performance (Pote et al., 1980; Sanchez et al., 1984; Partridge, 1988; Abdel-Samee et al., 1994). Certainly the variety of feeding methods does not allow any general conclusion and many green feeds, milled grains, roots and protein supplements can be supplied to rabbits, based on seasonal availability and economic factors.

There is little information about whether climate affects the DE or ME values of feedstuffs, in addition to its influence on composition. Sanz et al. (1973) reported that increasing the temperature to 34°C adversely affected the coefficient of digestibility of a restricted-fed and balanced diet, but other studies (Kasa et al., 1989) have failed to detect any significant change. Short-term estimates of digestibility could be altered by transient changes in rate of digesta passage and gut volume, related to sudden changes in ambient temperature.

The ME of a feed is affected by urinary losses and methane production, and is independent of its DE value. Although during exposure to extreme conditions there could be a shift in feed and tissue protein metabolism, the urinary losses increase and the ME value would decline (Gray and McCracken, 1974, in pigs). Usually the protein retention process is considered to be relatively independent of temperature.
No information is available for rabbits, where determined ME values are not abundant, and thus at present no recommendation can be made on how to adjust rabbit diets for the influence of temperature on DE or ME values.

15.5 Nutrient Allowances and Environment

The environment affects rate of intake and maintenance requirements. In a mildly cold situation, improved efficiency may be observed if voluntary intake increases more than the corresponding energy needs for heat production. In warm environments animals expend less energy on maintenance, and these savings might improve production or energy efficiency, despite the decreased feed intake. However, it appears unlikely that these theoretical approaches are borne out in practice, because most data show that increased heat requirements during cold conditions are not entirely compensated for by the consequent increased energy intake. Conversely, livestock exposed to high temperatures increase heat production while decreasing voluntary feed intake. Even in a situation where a thermal balance is maintained by reduced activity of the animal, these lower maintenance needs do not balance the lower intake.

Results showing improved efficiency can generally be explained by the composition of the animal product, mobilization of fat tissues to replace the energy deficit or the measurement of effective ambient temperature.

The adverse effect of temperature on efficiency and production should be minimized by adjusting nutrient levels. Assuming that maintenance needs for protein are not influenced by thermal stress, the protein/energy ratio is increased during both cold and heat stress, resulting in excess protein being used as an energy source. The practical approach in cold conditions is to increase dietary energy levels.

The consequences of hot environments on feed intake, which means less protein being ingested and reduced growth, have generally resulted in recommending higher levels of protein in warm climates or seasons. The addition of some amino acids, particularly lysine, has alleviated the effect of heat on pigs and poultry. It may be observed that equal daily intakes at different temperatures have resulted in comparable live weight gains.

In fact, levels of protein in the diet should be corrected according to body gains or milk protein yield, rather than being changed only as a result of the expected intake. The predicted performance of pigs and poultry is used to tabulate the adjustments for environmental stress, but insufficient information is available for rabbits.

Estimations of ME requirements based on heat production figures have been used for pigs and poultry exposed to different temperatures, but it would appear that no similar studies have been undertaken with rabbits.

High-energy diets have been reported to overcome the lower energy intake in hot environments when fed to cattle, pigs and poultry. Diets with a minimal HI should be beneficial; Jin et al. (1990) found that evaporative losses in 1.9-kg rabbits at 30°C were higher with a diet containing 231 g neutral detergent fibre (NDF) than for one based on 165 g NDF kg⁻¹. However, feed intake in that experiment was also higher, making it difficult to establish the relationship between fibre and stress.

Attempts to overcome the expected poor intake would require the use of high-fat, low-fibre diets. While the range of fibre is relatively narrow in feeding rabbits, the limit of fat incorporated into a diet seems to be controlled only by the physical structure of the pellet. Very few experiments have related the composition of rabbit diets to production outside the TNZ. However, some results suggest that the response of rabbit females at high temperature is especially poor when they are fed a low-energy diet (Simplicio et al., 1991), and significantly improved when a high-energy diet is supplied (Simplicio et al., 1991; Fernández Carmona et al., 1996).

At this point it may be emphasized that two different ways of enhancing performance
through dietary improvement can be considered (Fig. 15.2). The first may be defined as a general improvement of performance, but it is questionable whether this is really what is wanted. Had the previous diet not been deficient, it might have promoted a similar response, although there is usually scope to improve a diet. In fact, most diets are formulated using a least-cost programme, assuming optimal, non-maximal performance. The second approach can respond to actual attempts to obtain a better diet for severe climatic conditions. It should be noticed that a different response caused solely by a difference in temperature implies a significant diet–temperature interaction.

Increased voluntary intake in cold conditions tends to overcome any marginal deficiency in nutrients, although not in energy. Compared with a given diet in TNZ, a smaller proportion of dietary protein is needed for the above reasons, and more protein is utilized as an additional energy source. In view of their HI, proteins may temporarily exert a favourable effect in a cold environment. For many years a high-fat diet has been shown to be the most effective means of maintaining body temperature, coincident with the needs arising from the two-stage adaptation of rabbits to cold: (i) cold stress with depletion of fat reserves; and (ii) cold adaptation linked to lipid deposition.

The increment of ME requirement corresponds exactly to the extra heat produced. From data on heat production, ME requirements can be estimated as 0.15–0.20 of the requirements for a growing animal at 15–20°C (Table 15.1).

The HI of roughage has been useful for feed-restricted or low-productive cattle. Using indirect calorimetry trials on growing rabbits, Ortiz et al. (1989) reported that the DE value overestimated by 5% the net energy value expected when the acid detergent fibre level increased from 180 to 240 g kg⁻¹. Fibre could then be considered for rabbits as a moderately effective means of enhancing heat production, and conversely of limiting the total net energy intake. No reference work is available for cold-stressed rabbits in any of the subjects mentioned here.

Obviously, there is broad scope for research on the interaction between protein and energy allowances and the environment in rabbits fed ad libitum in hot or cold conditions. Virtually no attempts have been undertaken to test inputs other than energy and nutrients other than protein. There are some references to the addition of probiotics in hot climates, with little emphasis on the problem of temperature. Adding disodium or dipotassium carbonate has proved to be effective at high temperatures (Bonsembiante et al., 1989; Fayezy et al., 1994), probably preventing the action of hyperventilation on the acid–base balance.

The performance of rabbits in tropical countries is likely to be maximized by providing free access to drinking water at all times (Thwaites et al., 1990). Water-restricted rabbits, besides saving water output in faeces and urine, show a significant reduction in DM intake. Kits <21 days of age seem to learn how to drink water at high temperatures (McNitt and Moody, 1992). A water to food intake ratio of about 2 has been recorded for adult rabbits fed ad libitum by Prud’hon (1976) at 20°C, similar to that published by Jin et al. (1990) in growing females and Kasa et al. (1989) in fattening rabbits. There is a rise in the ratio of

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**Fig. 15.2.** Relationship between performance and diets. Response to diet B is always higher than diet A; response to diet C is only higher than diet B under extreme conditions.
water intake to DM intake up to 2.4 between 20°C and 30°C. Drinking cool water has sometimes been recommended in hot situations, but it should be noted that, besides the practical difficulty, the cooling effect is very small compared with the loss of heat through water vaporizing from the respiratory tract.

15.6 Effect of Heat Stress on Breeding Does and Litters

The effect of heat stress has been measured in experimental conditions on mating, fertility, embryo survival and litter size at birth (Howarth et al., 1965; Alliston and Rich, 1973; Shafie et al., 1979; Abo-Elezz, 1982; Kamar et al., 1982; Tramell et al., 1988; Marai et al., 2006). Poor productive performance of does has also been found in commercial farms: Masoero and Auxilia (1977) reported a decline in mating and fertility at 25°C. Summertime has brought about poor results in mating, numbers of live offspring, mortality and size of weaning litter (Sittmann et al., 1964; Pagano-Toscano et al., 1990). The worst overall productive results are mostly obtained in hot conditions (summer in southern European countries). In a rabbit mortality survey, Rosell (1996) found respiratory disorders to be the main cause of death in females, and certainly in winter the mortality of lactating rabbits can increase and respiratory pathology may become severe (Battaglini et al., 1986; Costantini and Castellini, 1990; Mori and Bagliacca, 1990). Reproductive traits in hot countries are far removed from European Standards (Cardelli, 1993), although some advances have been reported (Baselga and Marai, 1994).

High ambient temperature appears to act on reproduction both directly and through the depression of voluntary feed intake (Fig. 15.3). Experimental research, where feed intake during heat stress was

![Fig. 15.3. Feed intake of does at different minimum (min.) temperatures (data for 32°C constant from Wittorff et al. (1988); other data from Fernández Carmona et al. (1994b)). Regression line for original data for 22 days of gestation to partum (22d–p) and lactation: intake g dry matter (DM) kg\(^{-0.75}\) body weight = 81.72 + 10.45 × W – 0.048 × T\(^2\) (standard error = 15.8, \(R^2 = 0.71\); W = 1–6 weeks starting from 22 days gestation to partum; T, temperature (°C)).](image-url)
recorded, has confirmed low performance during summer (Mendez et al., 1986) or during a transitory temperature rise (Maertens and De Groote, 1990) and in a controlled environment (Rafai and Papp, 1984; Papp and Rafai, 1988; Wittorff et al., 1988; Simplicio et al., 1991; Fernández Carmona et al., 1995).

The work of Rafai and Papp (1984) examined daily milk output and food intake for temperatures between 5°C and 35°C. At 25°C a noticeable reduction in feed intake started, and subsequently milk, litter weight and doe weight were affected. Later work (Papp and Rafai, 1988) showed that does kept at 35°C die within 72 h.

Angora rabbits suffer considerable stress when shorn at temperatures below 20°C (Schlolaut, 1987) and very low wool yield and quality have been reported at temperatures of ≥30°C (Stephan, 1980; Kong et al., 1987). Cheng et al. (1991) recorded in summer, with a 23.1°C monthly average temperature, 5.6% less intake and 10.6% less wool yield than in spring. Shorter intervals between shearing can be employed in high-temperature conditions. Optimal temperatures for hair growth have been estimated at about 25°C after shearing, and not above 15°C before it (Schlolaut, 1987).

Cold seasons affect the mortality of suckling rabbits (Ferraz et al., 1991), but Lukefahr et al. (1983) did not observe this relationship. A survey of the literature (Partridge, 1988) gave a mortality rate in pre-weaning rabbits from 0.15 to 0.30. Around 0.80 of pups died as a result of chilling and starvation during the first days of life. The data demonstrated that survival increased up to 0.957 when nestboxes with a low-voltage heated floor were provided. In a study of a European rabbit population living in a field enclosure, Rödel et al. (2008) found that the temperatures inside the subterranean nest were positively correlated with soil temperature (from 3°C to 21°C) and litter size. They concluded that under colder soil temperature conditions, the thermal benefits of a greater number of littermates outweighs the negative consequences of competition for milk, leading to an environment-dependent shift in the optimal litter size for individual growth in this species.

The possibility that modification of diets formulated for normal environments can alleviate thermal stress by avoiding nutrient deficiencies or increasing voluntary intake has hardly been explored. One logical course of action would seem to be to increase the DE of diets with more cereal or by adding fat. Although under normal conditions does compensate for different diet density through corresponding changes in feed intake (Maertens and De Groote, 1988; Fraga et al., 1989), long-term experiments carried out by Mendez et al. (1986), Simplicio et al. (1991) and Cervera et al. (1993) showed that some added fat elicits a better response from does, perhaps related to high milk-fat output (Christ et al., 1996; Pascual et al., 1999).

Barreto and de Blas (1993) did not detect any improvement during summer in Madrid with diets varying from 8.9 to 11.9 MJ DE g⁻¹ DM, the last containing 35 g lard kg⁻¹. In an experiment connected to this one, low-energy diets gave a poorer response at 30°C constant temperature, while no statistical difference was found between the high-energy diets (Table 15.2). However, a diet containing 100 g fat kg⁻¹ at 30°C promoted better weight gains in litters than a normal control diet (Cervera et al., 1997). It has yet to be established whether this is a specific effect of fat or of energy intake.

A relationship between the HI of food and the nutrition of does can only be found in a study by Fernández Carmona et al. (1995), where 57 New Zealand crossbred does were fed on two iso-energetic (DE) diets, with 121 and 193 g crude fibre kg⁻¹ DM. Feed intake results showed the second diet to be less efficient, suggesting that does compensated for higher HI in terms of milk production.

Sanz et al. (1989) reported that milk intake was similar in rabbits aged 1, 10 or 20 days, reared at several temperatures between 20°C and 36°C. Suckling rabbits start to ingest solid food at about 18 days of age, and a measurable amount at 21 days. Fernández Carmona et al. (1991) reported that rabbits kept at 30°C ingested less DM in
a 35-day lactation than those at normal temperatures. The composition of pellets seems to be unimportant at these ages, at least from the results of Fernández Carmona et al. (1991), who reported no differences in ingestion between diets at 30°C and at normal temperatures. This agrees with the findings of Blas et al. (1990), who evaluated a diet with 100 g skimmed milk kg⁻¹.

15.7 Effects of Heat Stress on Males

High ambient temperatures have adverse effects in bucks, potentially producing temporary sterility, decreasing libido, delaying age at first mating and reducing semen quality and quantity. The effects of heat stress may be due to a decrease in testosterone concentration and spermatogenesis (Zeidan et al., 1997) and become more pronounced when relative humidity is high (Marai et al., 2002).

Semen characteristics and volume should be impaired in summer because of a low sperm concentration, and a decrease in the volume of seminal plasma occurs through secretion of testosterone, which is lowest in summer (Chiericatto et al., 1995). Sperm motility, cell concentration, total number of spermatozoa in an ejaculate and incidences of abnormalities and dead sperm show poorest values when temperatures are higher.

The management of rabbit males during the growing and rearing periods seems to affect their subsequent performance and semen production. During a hot rearing season, Pascual et al. (2004) found that feed intake decreased, energy and protein requirements were not covered and perirenal fat thickness of males, semen production and sperm concentration were lower 2 months later when semen collection started, although a high-energy diet alleviated such effects. Similarly, zinc supplementation has been found to reduce the depression of semen production that is usually observed in autumn in Mediterranean countries (Mocé et al., 2000), but increasing vitamin and mineral content had no effect (Lavara et al., 2000).

15.8 Effect of Heat Stress on Growing Rabbits

The effect of temperature on the growth of weaned rabbits during the fattening period has often been measured, confirming the fact that voluntary feed intake varies according to whether conditions are cold or warm. DM intake in terms of metabolic weight is shown in Fig. 15.4, where a regression equation has been calculated from the original data, discarding diets with a high DE content. From published works by Zicarelli et al. (1979), Stephan (1980), Mori and Bagliacca (1985), Bordi (1986), Casamassima et al. (1988) and Samoggia et al. (1988), a temperature range from 13°C to 20°C can be assumed to be suitable, though some authors have widened this range. Not everyone agrees, but it is generally accepted that a reduction in intake occurs at 25°C, and perhaps above 22°C (Casamassima et al., 1988; Table 15.2. Effect of diet and housing on daily feed intake of does and litter weight at 28 days.

<table>
<thead>
<tr>
<th>Diet DE (MJ kg⁻¹ DM)</th>
<th>12.9ᵃ</th>
<th>11.3</th>
<th>10.4</th>
<th>9.0</th>
</tr>
</thead>
<tbody>
<tr>
<td>30°C constantᵇ</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intake (g DM)</td>
<td>185</td>
<td>181</td>
<td>162</td>
<td>163</td>
</tr>
<tr>
<td>Litter weight (kg)</td>
<td>2.65</td>
<td>2.32</td>
<td>1.64</td>
<td>1.38</td>
</tr>
<tr>
<td>Traditional buildingᶜ</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intake (g DM)</td>
<td>283</td>
<td>277</td>
<td>304</td>
<td>320</td>
</tr>
<tr>
<td>Litter weight (kg)</td>
<td>3.80</td>
<td>3.42</td>
<td>3.24</td>
<td>3.16</td>
</tr>
</tbody>
</table>

DE, digestible energy; DM, dry matter.
ᵃIncludes 35 g tallow kg⁻¹.
ᶜCervera et al. (1993).
Fernández Carmona et al., 1994a) and certainly impaired growth is assured around 30°C (Table 15.3). Ogunjimi et al. (2008) showed that there is high correlation between both rabbit weight gain or feed efficiency and the thermal comfort level of the habitat measured by THI value. This outcome is less predictable when seasons of the year are considered, because of the usually large degree of variation in temperature and humidity; regardless of this, a substantial number of controlled experiments have recorded lower intakes and growth rates in summer than during the rest of the year (Masoero and Auxilia, 1977; Simplicio et al., 1988). It is hard to establish consistent differences between the results for winter, autumn and spring. Samoggia et al. (1988) found higher figures for intake and feed efficiency in winter, but other studies have been far from consistent.

Open-air systems tend to be slightly worse in terms of feed efficiency than indoor systems (Blocher et al., 1990), but opposing results have also been published (Crimella et al., 1996). It seems that a large rabbit farm should be provided with some means of regulating the internal environment, because the stress factors are strongly reinforced by a significant presence of pathogenic microbes and chemical pollutants in the air. Conversely, microbe colonies are non-existent in open-air systems, but climatic stress factors cannot be closely controlled.

The interaction between feeding and temperature remains almost unknown. A reduction of 25% in feed intake, comparable with the percentage observed in hot climates, should be balanced by about the same increment of dietary nutrients. Both Simplicio et al. (1988), increasing DE by some 10%, and Borgida and Duperray (1992), increasing protein and lysine, found no improvement in average daily gain in rabbits kept at 30°C. Neither increasing protein from 130 to 200 g kg⁻¹ nor increasing total digestible nutrients from 57% to 62% improved the average daily gain when these diets were fed to slow-growing rabbits in tropical conditions (Deshmukh and Pathak, 1991).

### Table 15.3. Prediction of growth for 1.5-kg rabbits at two different temperatures.

<table>
<thead>
<tr>
<th></th>
<th>18°C</th>
<th>30°C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Feed intake (g DM kg⁻⁰.⁷⁵ body weight) ¹</td>
<td>80</td>
<td>60</td>
</tr>
<tr>
<td>Energy intake (kJ DE) ²</td>
<td>1188</td>
<td>891</td>
</tr>
<tr>
<td>Maintenance requirements (kJ DE) ³</td>
<td>745⁴</td>
<td>633⁴</td>
</tr>
<tr>
<td>Growth allowances (kJ DE) ⁵</td>
<td>443</td>
<td>258</td>
</tr>
<tr>
<td>Growth (g day⁻¹) ⁶</td>
<td>37</td>
<td>21</td>
</tr>
</tbody>
</table>

DM, dry matter; DE, digestible energy.
¹Approximate, from Fig. 15.4.
²1.50.⁷⁵ = 1.35; diet 11 MJ DE kg⁻¹ DM.
³552 kJ DE kg⁻⁰.⁷⁵ body weight (de Blas et al., 1985).
⁴15% lower requirements at 30°C.
⁵Approximately 12 kg DE g⁻¹ live weight gain.

---

**Fig. 15.4.** Feed intake of growing rabbits.
1, Stephan (1980) (constant temperatures); 2, Lebas and Ouhayoun (1987) (mean temperatures); 3, Casamassima et al. (1988) (minimum temperatures); 4, Nizza et al. (1995), 12.5 MJ DE kg⁻¹ (mean temperatures); 5, Borgida and Duperray (1992) (mean temperatures); 6, Fernández Carmona et al. (1994a) (minimum temperatures); 7, Boiti et al. (1992), Chiericatto et al. (1995) (nearly constant temperatures); 8, Cervera et al. (1997), 11 MJ DE kg⁻¹ (minimum temperatures); 9, Cervera et al. (1997), 12.4 MJ DE kg⁻¹ (minimum temperatures).
Rabbits fattened at mean temperatures of 6°C, 16°C, 22°C and 26°C and fed on a diet with 210 g crude protein kg$^{-1}$ (Lebas and Ouhayoun, 1987) have been found to gain about 5g more at each temperature than those fed with 157 g crude protein kg$^{-1}$. When comparing low- and high-fat diets, while gains at moderate temperatures of 12°C and 18°C were similar, at 24°C, 30°C and 33°C the use of high-fat diets slightly improved growth performance as a consequence of small differences in DM intake (Cervera et al., 1997). At a temperature of 30°C it also led to around 50% more dissectible fat (Plá, 1999).

Carcass yield, carcass fat and the efficiency of energy for fattening alter the significance of live weight gain as the sole predictor of growth performance. Slower growth leads to lighter and leaner carcasses, so that any diet should produce less carcass fat at high ambient temperature.

References


16 Nutritional Recommendations and Feeding Management of Angora Rabbits

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16.1 Introduction

The Angora rabbit produces 1.0–1.4 kg year\(^{-1}\) of pure fine animal fibre without grease or plant material contamination, named 'Angora wool'. This represents some 0.30 of its live weight, the highest keratin production to live-weight ratio found in any fibre-producing animal. In sheep, goat or camelids, this figure is generally <0.10.

The capacity of the Angora rabbit to convert food to keratin requires that particular attention be given to its nutrition. There are two important nutritional objectives:

1. To provide all the nutrients the rabbit needs to realize its genetic potential for wool production.
2. To avoid any disorder that may reduce the life-time performance of the animal.

Individual productive longevity (3–4 years on average) is an important economic parameter in the Angora production system.

There is a considerable paucity of information on Angora rabbit nutrition compared with published work on the production of meat from rabbits or wool from sheep. This applies to the genetics and physiology of Angora wool growth, as well to other areas of study such as pathology. In practice, producers have observed that the nutrient requirements of Angora rabbits bred for wool production are similar to those of breeding does kept for meat production and consequently have used this knowledge as a basis for diet formulation. Nevertheless, some specific modifications are necessary.

For a long time, Angora rabbits were fed in the same way as rabbits kept for meat production on a mixture of cereals (oats, barley or wheat), lucerne hay and fresh forages such as cabbage or fodder beet. Since the 1960s, complete diets based on pelleted concentrates have been used extensively in rabbit meat systems; Angora rabbit farmers, however, continued with the traditional feeding method through the 1970s, while Angora wool yields remained <850 g year\(^{-1}\). To improve wool yields, a mixture of 0.75 traditional feed and 0.25 supplementary feed pellets was subsequently used in some practical systems (Rougeot and Thébault, 1984). Other producers began using pelleted concentrates alone for Angora breeding does. By the beginning of the 1980s, as the genetic potential for wool production exceeded 1 kg per animal year\(^{-1}\), the use of specific pelleted diets formulated for Angora production became general practice as feed quality and safety (absence of induced disorders) were also improved. Schlolaut (1985) quantified the production advantages of concentrate feeds. Taking the Angora wool yield obtained with these as 1.00, mixed feeding (raw products plus cereals) and...
hay-based feeding reduced the yearly wool production to 0.85 and 0.72, respectively.

16.2 Nutritional Requirements

This chapter considers the nutrient requirements of Angora wool-producing females, since males are not frequently employed because of their lower wool production (5–10% less). Animals producing Angora wool are assumed to be adults with no production other than wool. For breeding does or growing animals, the recommendations are those proposed for meat production rabbits (see Chapters 10 and 14).

16.1.1 Consequences of daily variations in wool production

The amount of hair covering the body plays an important role in thermal insulation and heat loss. In France, Angora rabbits are de-fleeced every 3 months and are consequently completely or relatively naked and without thermal protection for 2–3 weeks. Vermorel et al. (1988) demonstrated a large increase in heat production just after the harvest (Tables 16.1 and 16.2). To reduce heat loss, some form of protection is often provided, either in the form of a woollen jacket (‘jersey rabbits’) or by leaving a strip of fleece on the back (‘strip rabbits’). Such techniques are less common with the German strain because the animals are shorn (i.e. a few millimetres of stubble is always left above the skin), which limits heat loss. In addition, German Angora rabbits have a higher proportion of down in the fleece, which improves thermal insulation. Nevertheless, whatever the Angora strain, the period of 2–3 weeks after harvesting is when energy requirements for thermal regulation are at their highest.

A further source of variation for nutrient requirements is the hair growth rate (i.e. the rate of keratin synthesis). The highest growth rate is observed during the fourth week after harvesting (31.7 g week⁻¹), with a reduction in the weekly wool output after this period (Fig. 16.1). Between weeks 4 and 14, the wool output is halved.

According to these data, nutrient and energy requirements appear to be maximum for energy, protein and sulphur amino acids (SAA, the main components of keratin) in the first month following fleece harvesting. The weekly requirements vary during the 3 months between two consecutive harvests (Table 16.3) and have been summarized by Rougeot and Thébault (1984).

16.1.2 Nutrient recommendations

As previously mentioned, Angora rabbits are now fed with balanced pelleted feeds. The desirable composition of such feeds has

| Table 16.1. Skin temperature and total and net radiative heat flow of Angora rabbits before and after de-fleecing, with or without a strip of hair on the back or a jersey jacket (means of six different spots measured during the 2 days following harvest ± standard deviations) (from Vermorel et al., 1988). |
|---------------------------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| No. of animals                  | Before harvest  | After complete  | On the hair     | Naked           | With woollen     | Without woollen |
| Skin temperature at 10°C        |                 | de-fleecing     | strip           | areas⁻¹          | jacket           | jacket          |
| Skin temperature at 10°C        | 6               | 6               | 9               | 9               | 6               | 6               |
| Total radiative heat flow at 15°C (W m⁻²) | 38.8 ± 0.4      | 38.8 ± 0.4      | 38.8 ± 0.4      | 38.8 ± 0.4      | 38.8 ± 0.4      | 38.8 ± 0.4      |
| Total radiative heat flow at 15°C (W m⁻²) | 38.8 ± 0.4      | 38.8 ± 0.4      | 38.8 ± 0.4      | 38.8 ± 0.4      | 38.8 ± 0.4      | 38.8 ± 0.4      |
| Total radiative heat flow at 15°C (W m⁻²) | 38.8 ± 0.4      | 38.8 ± 0.4      | 38.8 ± 0.4      | 38.8 ± 0.4      | 38.8 ± 0.4      | 38.8 ± 0.4      |
| Net radiative heat flow at 15°C (W m⁻²) | 38.8 ± 0.4      | 38.8 ± 0.4      | 38.8 ± 0.4      | 38.8 ± 0.4      | 38.8 ± 0.4      | 38.8 ± 0.4      |
| Net radiative heat flow at 15°C (W m⁻²) | 38.8 ± 0.4      | 38.8 ± 0.4      | 38.8 ± 0.4      | 38.8 ± 0.4      | 38.8 ± 0.4      | 38.8 ± 0.4      |
| Net radiative heat flow at 15°C (W m⁻²) | 38.8 ± 0.4      | 38.8 ± 0.4      | 38.8 ± 0.4      | 38.8 ± 0.4      | 38.8 ± 0.4      | 38.8 ± 0.4      |

aMeans of values obtained on the thigh, thorax and abdomen.

bTemperature on the jersey jacket.
Table 16.2. Heat production (kJ kg⁻¹ W⁻⁰·⁷⁵ h⁻¹) of Angora rabbits before de-fleecing (at 10°C) and after de-fleecing, with or without a strip of hair or a jersey jacket (for 2 days) and after harvesting the strip of hair or removing the jersey jacket (for 2 days) (means ± standard deviations) (from Vermorel et al., 1988).

<table>
<thead>
<tr>
<th>Environmental temp.</th>
<th>n</th>
<th>Before de-fleecing</th>
<th>Strip of hair</th>
<th>Jersey jacket</th>
</tr>
</thead>
<tbody>
<tr>
<td>15°C</td>
<td>2</td>
<td>18.1 ± 2.0a</td>
<td>20.8 ± 0.2a</td>
<td>29.9 ± 1.3b</td>
</tr>
<tr>
<td>10°C</td>
<td>4</td>
<td>16.7 ± 0.3a</td>
<td>23.2 ± 2.4b</td>
<td>32.6 ± 1.5c</td>
</tr>
<tr>
<td>5°C</td>
<td>3</td>
<td>16.3 ± 2.6a</td>
<td>25.5 ± 3.3b</td>
<td>35.6 ± 2.7c</td>
</tr>
</tbody>
</table>

a,b,cFor the same type of animals and the same environmental temperature, values with different superscripts are significantly different (P<0.05 or P<0.01).

Fig. 16.1. Variations in wool production (g week⁻¹) between two harvests. From Rougeot and Thébault (1984).

Table 16.3. Monthly variations in nutrient and energy requirements for French Angora rabbits between two wool harvestings (recalculated from Rougeot and Thébault, 1984).

<table>
<thead>
<tr>
<th></th>
<th>Month 1</th>
<th>Month 2</th>
<th>Month 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crude protein (g)</td>
<td>190</td>
<td>175</td>
<td>160</td>
</tr>
<tr>
<td>Fat (g)</td>
<td>37</td>
<td>34</td>
<td>31</td>
</tr>
<tr>
<td>Crude fibre (g)</td>
<td>205</td>
<td>190</td>
<td>170</td>
</tr>
<tr>
<td>Sulphur amino acids (g)</td>
<td>10</td>
<td>9</td>
<td>8</td>
</tr>
<tr>
<td>Digestible energy (MJ)</td>
<td>12.6</td>
<td>11.6</td>
<td>11.5</td>
</tr>
</tbody>
</table>

16.1.3 Energy

Recommendations for dietary digestible energy (DE) content are in the same range for German (Schlolaut, 1985), Chinese (Liu et al., 1992) and French authors (Rougeot and Thébault, 1984; Charlet-Lery et al., 1985). Nevertheless, German and Chinese data are not very precise since the variation between the proposed minimum and maximum
represents 13–17% of the minimum. The Hungarian recommendations are also in the same range: 10.7 MJ kg⁻¹ (Tossenberger and Henics, 1988; Henics et al., 1989). The recommendation is accordingly 10.5 MJ kg⁻¹ of feed on an as-fed basis.

According to Charlet-Lery et al. (1985), metabolizable energy (ME) represents 0.95 of DE content; in addition, the same authors have indicated that energy utilization by Angora rabbits, as DE or ME, is independent of the season or the time since the previous wool harvest.

### Table 16.4. Nutrient recommendation for adult Angora rabbits.

<table>
<thead>
<tr>
<th>Nutrients</th>
<th>Unit kg⁻¹</th>
<th>Germanyb</th>
<th>Chinac</th>
<th>Current work</th>
</tr>
</thead>
<tbody>
<tr>
<td>Digestible energy</td>
<td>MJ</td>
<td>9.6–10.9</td>
<td>10.0–11.7</td>
<td>10.5</td>
</tr>
<tr>
<td></td>
<td>Kcal</td>
<td>2,300–2,600</td>
<td>2,400–2,800</td>
<td>2,500</td>
</tr>
<tr>
<td>Lipids</td>
<td>g</td>
<td>20</td>
<td>30</td>
<td>30</td>
</tr>
<tr>
<td>Crude fibre</td>
<td>g</td>
<td>140–160</td>
<td>120–170</td>
<td>140</td>
</tr>
<tr>
<td>Crude protein</td>
<td>g</td>
<td>150–170</td>
<td>150–160</td>
<td>160</td>
</tr>
<tr>
<td>Digestible protein</td>
<td>g</td>
<td>–</td>
<td>110</td>
<td>122</td>
</tr>
<tr>
<td>Lysine</td>
<td>g</td>
<td>7</td>
<td>7</td>
<td>7</td>
</tr>
<tr>
<td>Methionine + cystine</td>
<td>g</td>
<td>7</td>
<td>7</td>
<td>8</td>
</tr>
<tr>
<td>Arginine</td>
<td>g</td>
<td>6</td>
<td>7</td>
<td>6</td>
</tr>
<tr>
<td>Minerals</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Calcium</td>
<td>g</td>
<td>10</td>
<td>–</td>
<td>8</td>
</tr>
<tr>
<td>Phosphorus</td>
<td>g</td>
<td>3–5</td>
<td>–</td>
<td>4</td>
</tr>
<tr>
<td>Sodium</td>
<td>g</td>
<td>2.5</td>
<td>–</td>
<td>3</td>
</tr>
<tr>
<td>Potassium</td>
<td>g</td>
<td>7</td>
<td>–</td>
<td>13 maximum</td>
</tr>
<tr>
<td>Chloride</td>
<td>g</td>
<td>4</td>
<td>–</td>
<td>4</td>
</tr>
<tr>
<td>Sulphur</td>
<td>mg</td>
<td>–</td>
<td>–</td>
<td>400</td>
</tr>
<tr>
<td>Magnesium</td>
<td>mg</td>
<td>300</td>
<td>–</td>
<td>300</td>
</tr>
<tr>
<td>Iron</td>
<td>mg</td>
<td>50</td>
<td>–</td>
<td>50</td>
</tr>
<tr>
<td>Copper</td>
<td>mg</td>
<td>10</td>
<td>–</td>
<td>50</td>
</tr>
<tr>
<td>Zinc</td>
<td>mg</td>
<td>50</td>
<td>–</td>
<td>50</td>
</tr>
<tr>
<td>Manganese</td>
<td>mg</td>
<td>10</td>
<td>–</td>
<td>10</td>
</tr>
<tr>
<td>Vitamins</td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>IU</td>
<td>6,000</td>
<td>–</td>
<td>10,000</td>
</tr>
<tr>
<td>D₃</td>
<td>IU</td>
<td>500</td>
<td>–</td>
<td>800</td>
</tr>
<tr>
<td>E</td>
<td>mg</td>
<td>20</td>
<td>–</td>
<td>40</td>
</tr>
<tr>
<td>K</td>
<td>mg</td>
<td>1</td>
<td>–</td>
<td>1</td>
</tr>
</tbody>
</table>

aAs-fed basis with 890 g dry matter kg⁻¹.
bSchlolaut (1985).
cLiu et al. (1992).

Among German, Chinese and French data, there is agreement on dietary protein requirements, which are in the order of 160 g kg⁻¹. On the other hand, the Hungarian recommendations are higher at 196 g kg⁻¹ (Tossenberger and Henics, 1988; Henics et al., 1989). However, this latter recommendation is based on an experiment in which protein and SAA were studied simultaneously and where the lowest protein level tested was 175 g kg⁻¹ of feed on an as-fed basis.

### 16.1.4 Protein

Among German, Chinese and French data, there is agreement on dietary protein requirements, which are in the order of 160 g kg⁻¹.

### 16.1.5 Crude fibre

No specific study has been published on dietary fibre content as a possible source of...
variation in Angora wool production. The recommendations of various authors are easily calculated from the analysis of practical diets employed. The available recommendations are currently expressed only in terms of the level of crude fibre. However, one of the roles of dietary fibre is to remove hair swallowed by the rabbit from the digestive tract. To achieve this objective, a significant proportion of dietary fibre must be non-digestible; a minimum level of lignin seems reasonable to reduce fibre digestibility and, to achieve this latter objective, a value of 40 g acid detergent lignin (according to the Van Soest methodology) kg$^{-1}$ may be proposed.

16.1.6 Amino acids

Lysine

German recommendations for dietary lysine in Angora rabbit production are 5 g kg$^{-1}$ diet, significantly lower than the 7 g kg$^{-1}$ suggested by Chinese data; however, neither of these figures is based on direct experiments. Lysine is not an important component of keratin, but it does play a significant role in body protein turnover and assists the animal in restoring its live weight following the body weight loss observed after de-fleecing. Therefore, a level of 7 g of lysine kg$^{-1}$ feed is recommended for Angora rabbits.

Methionine and cystine

Several studies have been undertaken in Germany (Scholaut and Lange, 1983), Hungary (Henics et al., 1990) and France (Lebas and Thébault, 1990) on the requirements for SAA. From this last work (Table 16.5), it has been concluded that, for a level of wool production >1000 g year$^{-1}$, SAA intake is an important limiting factor. Practical recommendations for SAA are 8 g kg$^{-1}$ diet on an as-fed basis. A more recent study (F. Lebas and R.G. Thébault, unpublished data) indicates that efficient SAA supplementation can be achieved with either D,L-methionine or L-cystine. Under some conditions, a slight advantage can be attributed to cystine supplementation. Nevertheless, for economic reasons SAA supplementation, if necessary, is recommended in the form of D,L-methionine.

The Hungarian SAA recommendation is 9 g kg$^{-1}$ diet (Henics et al., 1990), but this figure was obtained after a comparison of only two SAA dietary levels: 5.6 and 9.0 g kg$^{-1}$. Because the highest level examined in the French study (8.8 g SAA kg$^{-1}$; Lebas and Thébault, 1990) failed to induce any improvement in wool production above that achieved with 8.0 g kg$^{-1}$, the Hungarian recommendation of 9 g kg$^{-1}$ leads to a significant SAA wastage and is not considered practical.

Other amino acids

No specific evaluation has been undertaken for the other amino acids. The current die-

<table>
<thead>
<tr>
<th>Performance</th>
<th>Dietary SAA level (g kg$^{-1}$)</th>
<th>Residual coefficient of variation</th>
<th>Statistical probability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of harvests</td>
<td>5.6</td>
<td>6.4</td>
<td>7.2 (control)</td>
</tr>
<tr>
<td>Fleece weight</td>
<td>0.948$^{a}$</td>
<td>1.008$^{b}$</td>
<td>1.000$^{b}$</td>
</tr>
<tr>
<td>Feed intake</td>
<td>0.991</td>
<td>1.000</td>
<td>1.000</td>
</tr>
<tr>
<td>Feed efficiency$^{d}$</td>
<td>0.951$^{a}$</td>
<td>1.005$^{bc}$</td>
<td>1.000$^{b}$</td>
</tr>
<tr>
<td>Live weight</td>
<td>0.990</td>
<td>1.020</td>
<td>1.000</td>
</tr>
</tbody>
</table>

NS, not significant.

$^{a,b,c}$Values with different superscripts are significantly different ($P < 0.05$ or $P < 0.01$).

$^{d}$Calculated as g wool produced per g feed intake.
tary recommendation for arginine (7 g kg\(^{-1}\)) is based only on the actual content observed in adequate Angora diets. In the absence of further information, the recommendations for growing rabbits are suitable.

### 16.1.7 Minerals and vitamins

As for most of the amino acids, the current recommendations for minerals (Table 16.4) are derived from the observed composition of Angora diets and from knowledge of the mineral requirements of growing and adult meat rabbits.

The German recommendation for vitamin A (6000 IU kg\(^{-1}\); Schlolaut, 1985) is lower than the recommendation of 10,000 IU kg\(^{-1}\) proposed in France by Rougeot and Thébault (1984). Hungarian experimental results (Table 16.6) indicate clearly that 5000 IU kg\(^{-1}\), which is very close to the German recommendation, is not adequate for Angora wool production (Kovácsné-Virányi, 1990). By comparison with meat rabbit reproduction, it can be assumed that the maximum level employed in the Hungarian experiments is too large and the proposed recommendation is 10,000 IU vitamin A kg\(^{-1}\), which is the same as for most meat rabbits. A complementary experiment included in the same Hungarian publication demonstrated that \(\beta\)-carotene can sometimes completely replace the supply of vitamin A, but the two experiments were not precise enough to support any calculation of the transformation of \(\beta\)-carotene into vitamin A.

It is important to note that dietary vitamin D levels should not exceed 800 IU kg\(^{-1}\). Adult females that are not reproducing, lactating or growing are susceptible to heart valve and kidney calcification with D hypervitaminosis (Thébault and Allain, 1995).

### 16.2 Feeding Management

As mentioned in the introduction, in practice Angora rabbits are fed balanced pelleted feeds (3–5 mm pellet diameter). In addition, they must have permanent access to clean fresh water. Daily water intake is about 0.33 l per animal day\(^{-1}\), with a large variation between animals and season. Significant mortality can be observed if insufficient water is available during a hot period. Dietary roughage, supplied once or twice a week as straw or hay or \textit{ad libitum} as straw bedding, is not essential for health or wool production in the Angora rabbit (Rougeot \textit{et al.}, 1980). However, when straw is fed, average daily intake falls from 19 to 13 g between the first and third months following the harvest. Greater variations are observed between individual rabbits (e.g. straw intakes from 43 to only 3 g day\(^{-1}\)) without any apparent effects on wool production.

#### 16.2.1 Feed restriction

Preliminary studies showed that feed restriction decreases wool production by 14.7\% (Rougeot and Thébault, 1977) or 9.2\% (Schlolaut and Lange, 1983). In both of these studies, however, feed restriction was severe and no account was taken of the variability in hair growth rate between harvests. More recently, Lebas and Thébault (1988) have shown that feed intake can be reduced by 61\% in winter

| Table 16.6. Relative effect of dietary supplementation with vitamin A or \(\beta\)-carotene on the quantity of hair produced by a surface of 14 cm\(^2\) of skin shaved once a week during 8 consecutive weeks (from Kovácsné-Virányi, 1990). Value for the control, 1.000 = 1.17 g. |
|-------------------------------|-----------------|-----------------|-----------------|
|                              | Control (5000 IU vitamin A kg\(^{-1}\)) | Vitamin A + 15,000 IU kg\(^{-1}\) | \(\beta\)-Carotene + 45 µg kg\(^{-1}\) |
| No. of rabbits               | 5               | 7               | 7               |
| Hair production              | 1.000\(^a\)     | 1.132\(^b\)     | 1.055\(^ab\)    |

\(^{a} \neq b (P = 0.05)\).
and 26% in summer with an adapted feed restriction (1200 g week$^{-1}$) during the first month following harvest without any adverse effects on wool production (Fig. 16.2 and Table 16.7).

However, the Angora rabbit seems unable to regulate daily intake and some does are able to consume $>400$ g day$^{-1}$ and exceptionally 500 g day$^{-1}$ during the first 2 weeks following harvest. This can cause nutritional disorders (e.g. enterotoxaemia), which occur when pellets are fed *ad libitum*.

A restricted feeding regime, as described in the next section, has been developed using the pattern (Fig. 16.1) of weekly hair production over the 3 months of hair growth between harvests (Rougeot and Thébault, 1984). This has now been adopted in commercial practice.

- First month: 1200 g per animal week$^{-1}$.
- Second month: 1100 g per animal week$^{-1}$.
- Third month: 1000 g per animal week$^{-1}$.

The weekly ration must be distributed equally over 6 days a week as Angora rabbits are not able to self-regulate their feed intake.

### 16.2.2 One fasting day a week

A fasting day is essential when fibres are long or when hair losses are observed. Angora rabbits, like most mammals, lick their fleece when grooming. Hair is swallowed, representing 0.3–0.4 g day$^{-1}$ during the last month between harvests (Charlet-Lery *et al*., 1985). As the rabbit is unable to vomit, long hair mixed with feed material is retained in the

![Graph](image-url)

Fig. 16.2. Change in daily feed intake of Angora rabbits restricted-fed or fed *ad libitum* during the 5 weeks following de-fleecing, in spring and summer (from Lebas and Thébault, 1988).

| Table 16.7. Live weight (g) 5 weeks after the last de-fleecing and wool production at the next harvest of Angora rabbits (mean ± standard error of the mean) with or without feed restriction during two different seasons (from Lebas and Thébault, 1988). |
|-----------------|-----------------|-----------------|
|                  | *Ad libitum*    | Feed restriction | Statistical probability |
| Live weight (g)  | Spring          | 4457 ± 106      | 4244 ± 47            | 0.014 |
|                  | Summer          | 4234 ± 73       | 4127 ± 44            | 0.08  |
| Wool production (g) | Spring          | 258.3 ± 8.7     | 259.8 ± 6.6           | NS    |
|                  | Summer          | 235.9 ± 6.4     | 246.5 ± 8.7           | NS    |

NS, not significant.
It rapidly forms a stomach hair ball (trichobezoar), which blocks the pylorus and prevents gastric emptying. The animal stops feeding and will die. Plitt-Hardy and Dolnick (1948) described this phenomenon and Rougeot and Thébault (1977) observed the death of five out of 11 females fed a pelleted diet *ad libitum*. Autopsy revealed the presence of a trichobezoar in the stomach of each animal. Feed restriction and fasting on 1 day week⁻¹, when only straw or bulky forage is available, will facilitate voiding of ingested hair in hard faeces. On the day following the fast, hard faecal pellets connected to each other are often observed.

### 16.3 Conclusions

As Angora rabbits are housed in individual cages, it is very easy to control their feeding regime. When traditional raw feeds such as hay and cereals are used, no specific nutritional problems occur. Angora rabbits that have been selected for wool production cannot, however, achieve their genetic potential on such a regime. In addition, when hay is floor-fed inside the cage or even distributed in a feeding rack, vegetable matter tends to 'contaminate' the fleece, which drastically reduces its commercial value. For these reasons, most commercial Angora rabbits are fed a specific pelleted balanced diet. Pelleted concentrates have the advantage that nutritional characteristics are precise and constant, feed storage is minimum and labour costs for feeding are reduced. Some precautions are necessary when using a complete pelleted diet. Finally, water must be supplied *ad libitum* using an automatic watering trough. To avoid wastage and nutritional disorders, a restricted feeding regime adapted to variations in both feed requirements and hair growth should be adopted. Fasting once a week will avoid the formation of a stomach hair ball, which, should it occur, is invariably fatal.

### References


17 Pet Rabbit Feeding and Nutrition

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17.1 Introduction

The predecessor of the modern rabbit – whose Latin name, *Oryctolagus cuniculus*, literally means ‘hare-like digger of underground passages’ – is known to have originated, based on Upper Pleistocene fossil records, in the Iberian peninsula. It appears to have been confined to Spain for some time after the last Ice Age. Interestingly, the rabbit was a symbol of fertility in ancient Egypt. The rabbit/hare hieroglyph has been translated as the verb ‘to be’ and the Pharaoh Unas (2375–2345 BC) is named using this hieroglyph. Stone Age cave drawings clearly indicate its presence and Phoenician traders reported large numbers of wild rabbits around 1100 BC. The spread of rabbits out of Spain during this period was probably hindered by the Pyrenees and the dense forestation of the rest of Europe. With the gradual deforestation of Europe the rabbit spread and diversified into Algeria, Morocco, the Azores, the Mediterranean and Russia, and then to Northern Europe. This initial spread was devoid of any true domestication.

Partial domestication was undertaken by the Romans around AD 1, with rabbits breeding in the wild and only being caught for fattening purposes. This partial domestication extended across the Mediterranean, with rabbit becoming a regular meat by AD 600, which is relatively recent compared with other species (Zeuner, 1963). The evidence for this timing is further supported by the depiction of the rabbit on the coins of the period AD 120–130 and in Roman art.

The first housed breeding and controlled feeding of rabbits appears to have been in French monasteries, in which rabbits were kept in large leporaria, between the 6th and 10th centuries. Subsequently, rabbits became more commonplace such that by the 16th century selection for tameness, size and variety was clearly evident. The rabbit does not feature in the art of the domestic animal until the appearance of a white rabbit in 1530 in the painting *Madonna of the Rabbit* by Titian.

While there are some records and evidence for the development of the domestic rabbit in mainland Europe, no such material as to the existence of the rabbit in Britain appears to be available until after the Norman Conquest. The rabbit was commonplace in Britain by the 14th century and captive by the 17th century, but only truly domesticated by the end of the 18th century. It was not, however, until the mid-19th century that the pet and show rabbit began to appear (Sandford, 1986). As the rabbit is very adaptable and is today distributed over the five continents, it is surprising that it was so late in becoming a domesticated species and is only now a significant pet.

Although it is extensively farmed in China, Italy, France and Spain (Costachescu and Hoha, 2006), the rabbit has become an...
increasingly popular and important pet in certain areas, in particular Germany, the UK, the USA and Canada (Santomá et al., 1989).

The number of pet rabbits in the UK has steadily risen over the last few years, with current estimates in the range of 1.0–1.4 million, making the rabbit the third most popular pet (excluding fish) and present in almost 0.7 million pet-owning households (PFMA, 2009). The US pet rabbit population has similarly risen, with estimates in the region of 5 million rabbits in around 2.2 million households in 2002 (Grannis, 2002) and 6.17 million rabbits in 2 million households in 2007 (AVMA, 2007).

The pet rabbit has a life expectancy of 8–12 years. It is a small and pleasant animal to handle, and can be kept as easily by the elderly and handicapped as by the child or fit adult. It has always been regarded as the ‘classic’ pet for children, but, with the advent of the house rabbit, has more recently begun to fulfil a similar position in the eyes of the pet-keeping public as the cosseted cat. The rabbit’s place as a significant pet in small-animal veterinary practice is well established (Hartmann et al., 1994; Malley, 1994, 1995, 1996), even to the extent of there being a lecturer’s post dedicated to rabbit medicine and surgery at the University of Edinburgh Veterinary School. More than 50 breeds of rabbits are now recognized, ranging in weight from 1 to >10 kg. Rabbit fanciers divide them into two categories referred to as ‘fur’ and ‘fancy’, with the smaller breeds (e.g. Netherland Dwarf and Mini-lop) dominating as the most popular pets.

Much of the detailed information on the nutrient requirements and feeding of the rabbit are derived from studies and publications that are concerned with the rabbit as a research animal (NRC, 1977) or farmed for meat or fur (Lebas, 1980, 1987; Schlolaut, 1982). There are, however, some studies specific to the pet animal (Hartmann et al., 1994; Schwabe, 1995; Haffar, 1996) as well as some useful veterinary and specific texts (Sandford, 1996; Brooks, 2004). In assessing the nutrient requirements of the pet rabbit, reference to the basic principles of these and similar published information has therefore been made. Appropriate adaptations of values for nutrient requirements have been determined using the more recent articles as a check for the feeding of the smaller rabbit, at maintenance, as a pet.

Considerations have also been given to the particular requirements that arise from the fact that the owner of the pet rabbit may wish to supplement the commercial diet with fresh material and the problems that may subsequently arise through mal-feeding practices. It is strongly recommended that when designing diets for pet rabbits or considering the pet rabbit’s specific needs, consideration be given to the welfare of the rabbit. It is therefore desirable for manufacturers to supply additional on-pack or supportive information to assist the pet owner in maintaining animal health and well-being.

17.2 Feeding Management

17.2.1 General considerations

It must be emphasized that keeping of rabbits will not be successful unless attention to detail is paid in terms of housing, the behaviour of the rabbit and the feed quality and balance of the diet, as well as the most suitable feeding practices for the rabbit. The rabbit is a social creature and requires companionship, ideally from another rabbit, and exercise on a daily basis. The rabbit also benefits from mental stimulus; if this is unavailable from other rabbits or human interactions then it should be provided with appropriate ‘toys’. Studies using Norway spruce sticks (Jordan et al., 2008) have, for example, been shown to provide behavioural enrichment.

The pet rabbit should be given adequate opportunity to feed in a quiet place. Feed should be provided on a regular basis (e.g. in the early morning and evening to reflect the rabbit’s crepuscular behaviour) and with appropriate recognition of individual habits and changes to the routine (e.g. in the summer rabbits tend to eat more at night, when it is cooler). While rabbits dislike dust in their food, it is important to ensure that the
rabbit consumes all of the components of a coarse or flake-mix proprietary product to ensure a balanced diet. Removal of any dusty or fouled portion of the diet is important, but must not be such that the rabbit continually leaves the same component each day. It is sometimes suggested that the rabbit should have non-forage components of food withheld once each week to ensure that the digestive system is clear of furballs and to encourage the consumption of essential roughage, usually in the form of hay.

Rabbits like variety in their diet and mixtures are often considered more palatable than single-component diets. However, the importance of avoiding selective feeding and the consequential provision of an imbalanced diet and resultant health problems must be emphasized. For simplicity, and with modern production processes, palatability can be maintained with a single pelleted complete compound diet to which the only additional provision required is hay and fresh drinking water. With the exception of long fibre, it is not wise to dilute such a complete compound feed. Changing the diet to provide variety may also inadvertently result in obesity or digestive upsets. This comes about as a result of the rabbit consuming the diet for pleasure rather than nutritional needs, with an excess consumption of compound feed compared to forage. Sudden or inappropriate dietary changes often cause diarrhoea, which if inappropriately managed may lead to dehydration and death or predispose the rabbit to fly-strike.

With home-made diets, variety often consciously or unconsciously offsets inadequacies in one or more of the foods. It is important to offer only clean and dust-free food. Where a cereal or bran that is prone to dustiness is included, this can be moistened with a little warm water to a crumbly texture to encourage intake. All foods must be free from mould and frost and green foods must be fresh. Detailed considerations of each foodstuff are given later in this chapter. The rabbit will selectively take concentrates if the palatability of roughage is variable (Van Soest, 1982); however, this behaviour will readily result in a scour from the consumption of too much protein or starch relative to hay. A simple yet effective treatment for this is to remove the feed and provide warm water and hay. A well-fed rabbit masticates its food extensively, whereas this practice does not occur to any great extent when the rabbit is hungry. This forms a good practical guide to regulating food quantities.

Good-quality hay should form the basis of any rabbit feeding programme and is essential not only for appropriate nutrition (Meredith, 2000), but also for maintaining behavioural norms (Mulder et al., 1992) and good physiology (e.g. tooth wear).

### 17.2.2 Feeding guide

It is generally agreed that the energy requirement of the pet rabbit can be estimated with the following equation:

\[
\text{Maintenance energy in Kcal ME} = \text{body weight}^{0.75} \times 100
\]

ME, metabolizable energy

Typically a multiplier of 1.35 is used for early gestation; of 2 for late gestation and growth; and 3 for lactation. However, considerable between-animal variation should be expected (Tobin, 1996).

A guide to typical daily feed intakes for adults at maintenance is around 0.030–0.035 of body weight.

Practically, adult animals at maintenance need to be controlled-fed, based initially on the ideal weight for the breed and then on body condition. A suitable body condition scoring method and advice on how to estimate the body condition score of the rabbit can be found at [http://www.pfma.org.uk/pet-ownership/pet-size-o-meter.htm](http://www.pfma.org.uk/pet-ownership/pet-size-o-meter.htm). Adjustments to feeding rates should be in the order of ±10% every 14 days. It is probably better to alter the amount of non-forage food as rabbits are efficient utilizers of diet and the obese animal may maintain weight even on high-fibre foods (as opposed to forage).

After weaning, reduced rations should be given for a few days followed by feeding to condition. Growing young rabbits should be fed to appetite until 10 weeks of age and then at maintenance amounts.
Responsible manufacturing would imply that suitable daily feeding guidance is provided on-pack. This should be based on the above equation for requirements and the appropriate energy value for the feed. Diets containing 10.5 MJ kg\(^{-1}\) are the norm and may be fed up to 25 g kg\(^{-1}\) body weight along with free-choice good-quality hay. However, due to variations between rabbits these values should only be used as a guide and owners are encouraged to feed to condition.

Fresh foods can be fed to appetite in adults, again making sure that excessive weight gain does not occur. A good approach is to provide only as much as will be consumed by the next meal. Hay or similar fresh long fibre must be supplied on a free-choice basis. Roots, if fed, should be given as lumps rather than slices or small pieces. It is worth remembering that an average adult rabbit can eat an amount of root equivalent to the size of a tennis ball.

If feeding extensively on a home-grown diet, one meal of grains and one of greens or roots should be provided each day, with dust-free hay and water offered on a free-choice basis. Roots, if fed, should be given as lumps rather than slices or small pieces. It is worth remembering that an average adult rabbit can eat an amount of root equivalent to the size of a tennis ball.

Any changes to the dietary composition should be made gradually, over a 7- to 10-day period. Sugary treats, bread and other table scraps are inappropriate feeds for rabbits.

**17.2.3 Housing**

Rabbits should be housed in hutches or pens sited in a quiet part of the garden or yard. Small wooden hutches are preferable, with some protection from the weather in winter. The housing should have a darkened area for sleep and an open area for exercise and feeding. The exercise area should be large enough for the rabbit to stretch out fully and run, as opposed to just hopping. Exercise is important for the overall physiological and psychological health of the rabbit. If the hutch is within an out-building then it is important to avoid drafts, yet to provide adequate ventilation and light.

The ‘house rabbit’ is now widely popular. Established in the USA in the 1980s, the loose-housed, house-trained indoor rabbit makes an affectionate and intelligent companion. Indeed, there is some evidence to suggest that because of the social nature of rabbits, the behaviour patterns of house rabbits are more natural than those kept in a hutch. In addition, such methods of keeping encourage exercise. Even with the house rabbit, however, penning may be beneficial on certain occasions.

**17.2.4 Feeding equipment**

Feed containers should be heavy in construction as rabbits are prone to throwing them about. Earthenware or galvanized steel, the latter hung on the door, seem to be the most effective. The best designs accommodate a turned-in lip to prevent the rabbit from scratching out the feed. Containers must be <75 mm deep or the rabbit will find access a problem. The inclusion of a fine wire sieve in the bottom to remove dust from feed pellets can be beneficial if feed replacement occurs only once daily.

Water is frequently provided via nipple or automatic drinkers in commercial situations and such arrangements are ideal. For the domestic situation, however, heavy earthenware pots or bottle drinkers are more practical. If a pot is provided within the cage or pen then precautions to prevent fouling by the rabbit are essential. A bottle drinker in a frame outside the pen and a small trough inside or a 6 mm diameter drinking tube overcome such problems with ease.

The provision of free-choice roughage in the form of quality meadow hay is essential. The best method of supply is in a hay rack, which not only saves space but also keeps the hay fresh and free from fouling. In pens with a wire mesh roof, the hay can be put on top of the pen and rabbits will happily pull it through.
Within the 50 or more breeds of domestic rabbit there are four basic fur types: (i) normal with fur length 30 mm in length; (ii) rex 12 mm; (iii) satin; and (iv) the one wool-producing Angora, which has 120-mm-long, fine fur. Typical pet breeds weigh in the range of 1–5 kg, although larger breeds >10 kg as mature adults are occasionally selected (Sandford, 1986).

The rabbit is a true non-ruminant herbivore grazer. Its dentition differs from that of the rodent, with which it is sometimes mistakenly categorized, having two pairs of upper incisor teeth whereas rats and mice have only one. The upper and lower teeth, which continually grow, meet and grind each other down with use. Herbivores by their nature consume high-fibre plant-based diets, which present their own unique problems in terms of digestive efficiency.

Herbivores in general have developed in different ways to produce a digestive reservoir, which permits an increase in the efficiency of utilization of their fibrous diets (Cheeke, 1988). The rabbit has a very large non-compartmentalized and non-distensible stomach. In the adult this has a very low pH <2.0, exerting an antimicrobial effect. The weanling rabbit does not exhibit this low stomach pH and is thus more prone to bacterial infestation and upset (Meredith, 2008).

The stomach, which empties into a relatively narrow-diameter small intestine, comprises about 15% of the volume of the gastrointestinal tract. It functions largely as a food reservoir and is usually never empty. The cardiac sphincter is well developed and anatomically arranged to prevent vomiting. The pylorus is very muscular.

The rabbit also possesses a well-developed, coiled, thin-walled caecum. This is the largest organ of the gastrointestinal tract, having ten times the capacity of the stomach, and provides substantial microbial digestion. The colon is characterized by sacculations (haustra) and bands. The horse utilizes the caecum and colon for insoluble fibre (lignocellulose) fermentation. The rabbit, however, rapidly eliminates insoluble fibre from the gut, using this fraction of the diet primarily as a motility modifier rather than a nutrient.

Relying on the bulk in the stomach to effect intestinal passage of digesta, this high voluntary feed intake, some four times higher pro rata than that of a 250 kg steer (Santomá et al., 1989) is associated with a low gut retention time of 17.1 hours in the rabbit compared with, for example, cattle at 68.8 hours. The high voluntary feed intake, together with the re-utilization of gut content by reingestion of caecal material (referred to as caecotrophy), supports the rabbit’s high nutrient requirement per unit of body weight and improves feed utilization. This approach allows the rabbit to consume a large amount of roughage while avoiding being weighed down by the storage of bulk fibre, which is a good approach considering the small size and high metabolic rate of the rabbit. The rabbit exhibits frequent feeding, with estimates ranging from 30 times per day of 2–8 g intake over 4–6 min per occasion (Prud’hon et al., 1975), up to 4–6 hours in total.

The nature of the dietary fibre component, pectic constituent concentration, degree of lignification of neutral detergent fibre (NDF) and particle size best characterize the influence of the source of fibre (García et al., 2000) on the rabbit.

Designing a safe and efficacious diet for the rabbit must thus give considerable consideration to the fibre profile of the daily ration. Unfortunately, ‘fibre’ measurement is still a developing science and many measurement methods that would be helpful in rabbit diet design are not routinely available in commercial laboratories. It is therefore beholden upon the nutritionist to factor a margin of safety into the dietary fibre and forage to the health (gut, teeth) and well-being (behaviour) of the rabbit, even when a complete diet is appropriately designed and subsequently stated on-pack, it is always considered good practice to encourage the pet rabbit owner to offer good quality long fibre in the form of hay and to feed to condition.
A note on-pack to this effect could be considered as critical as the one stating that the rabbit must always have access to fresh, clean drinking water.

Diseases of the rabbit linked to inappropriate dietary fibre intake are gastric trichobezoars, chronic soft stools (sticky-bottom syndrome), diarrhoea, gut motility stasis, obesity and dental problems.

17.3.1 Caecotrophy

At 3–8 h after feeding the rabbit produces a soft, mucus-coated faecal pellet that is swallowed whole, without chewing, directly from the anus. The arrival of the pellet at the anus induces a reflex action to consume the pellet. The normal faecal pellet is harder and is passed both during the day and night. A 2.5–3.0 kg typically rabbit passes 150 faecal pellets day⁻¹.

The soft faecal pellet results from the separation of digesta on the basis of solubility and particle size in the hind gut. Peristaltic action removes larger particles (>0.5 mm) of predominately ligno-cellulose through to the colon, which are subsequently excreted as hard pellets. Antiperistalsis moves the smaller particles (0.1–0.2 mm) and soluble components into the caecum, where fermentation occurs (Bjornhag, 1987). Once consumed soft faeces remain in the stomach of the rabbit for 6–8 h, where they are protected from digestive attack by the mucosal cover. Microorganisms within the soft faecal pellets continue fermentation with the production of lactic acid. These pellets provide microbial protein, which accounts for between 0.15 and 0.25 of total amino acid and between 0.09 and 0.15 of the digestible energy (DE) requirement of the rabbit (Lebas, 1989). In addition, the pellets provide all of the B-group and K vitamins and a certain amount of volatile fatty acids (VFAs).

17.3.2 Digestive efficiency

Rabbits digest fibre poorly (mean coefficient of total tract digestibility of lignin 0.10–0.15, cellulose 0.15–0.18, hemicellulose 0.25–0.33; Gidenne, 2003) because of selective separation and rapid excretion. However, rabbits require generous amounts of fibre to ensure intestinal motility and minimize disease. In crude fibre (CF) terms, a diet with <140 g kg⁻¹ CF will almost always result in digestive upsets, while a diet with >250 g kg⁻¹ CF may result in increased incidences of caecal impaction and mucoid enteritis (Fraser, 1991).

Fibre influences the digestibility of the diet and alters the analysis of caecal contents. A diet devoid of fibre results in a coefficient of apparent digestibility of organic matter of 0.90; this declines in a linear fashion to 0.40 when the diet contains 350 g kg⁻¹ CF. Increasing the CF of the diet increases the CF of the caecal contents and decreases the protein content (Carabaño et al., 1988). The enzyme profile of the digestive system of the rabbit is similar to that of other non-ruminants and thus the digestive efficiency of non-cell-wall constituents is comparable.

17.4 Raw Materials

17.4.1 General considerations

As with any pet animal, the key to feeding lies in the provision of a well-balanced diet. The range of feeds upon which the rabbit can survive is wide and varied. This means that the pet rabbit owner can tailor the feeding from purchased compounds to entirely home-made diets from the garden to meet the budget and individual circumstances. The creation of an entirely home-grown complete diet does, however, demand a knowledge of both the requirements of the rabbit and the nutrient content, risks and benefits of the plants in the garden. Conversely, the many commercially available compound feeds now offer a simple and convenient alternative package, with only the additional requirement of water to provide complete and balanced nutrition. Such diets have steadily increased in presence and popularity since their introduction in...
the 1950s. Some compound diets will require the addition of hay to supply a complete diet. In general, the recommendation that hay should be supplied on a free-choice basis as a rule of good husbandry of the pet rabbit should be included in the feeding instructions.


Table 17.1 gives a typical schedule for the feeding of ‘classic’ home-made diets based on cereals, bran and forages, fed fresh in the summer and dried in the winter and supplemented with hay, beet and carrots.

17.4.2 Raw material groups

The raw materials used to feed the rabbit can be grouped into succulents (greens and roots), roughages, concentrates (grains and proteins) and compounds. The last is not strictly a raw material group, but general considerations will be covered.

Succulents

If feeding roots and greens, it should be remembered that their nutritional value will vary with season, age at harvest, soil type, weather and storage, and that this will inevitably affect the nutrient supply to the rabbit and possibly the overall balance of the diet. There are many green foods suitable for the pet rabbit and a few general principles apply to them all:

- Greens and roots should ideally be fed fresh.
- If they have to be stored prior to feeding then they should not be left in a heap as they quickly ferment and this can be fatal to young rabbits.
- Introduce greens and roots gradually. Any new food should be introduced in this way, not only to minimize digestive upsets but also to avoid excessive feed selection and therefore perceived palatability. A sudden change of diet may lead to inappetence and the animal may starve itself rather than eat the new diet. Force-feeding by starvation to achieve diet acceptance is not effective in the rabbit.
- Fresh cut grass is favoured. However, lawn mowings should not be used as these will begin to inappropriately ferment almost before the rabbit can consume them.
- Wilted greens are acceptable, provided they are not yellow in colour or mouldy in any way.
- Plants to avoid include those with bulbous roots, Lobelia, lupins, potato leaves and tomato haulm.
- Rabbits will not in themselves reject poisonous plants. A further peculiarity of the rabbit is that it is unable to vomit and therefore cannot expel unwanted material or poisons if consumed.

GREENS. Kale chicory, kohlrabi, carrot leaves, endive, spring greens, spinach and watercress are very acceptable to rabbits, although the leaves of the cabbage (Brassica) family should only be fed in small quantities to minimize the intake of the glucosinolate goitrogens, which impair the uptake of iodine by the thyroid. Leafy vegetables are rich sources of minerals and vitamins.

Hedge or cow parsley (Anthriscus sylvestris), dandelion (Taraxacum officinale), coltsfoot (Tussilago farfara), sow thistle (Sonchus), plantain (Plantago) and knapweed (Centaurea species, especially C. nigra) are similarly useful succulents. However, if fed to excess the dandelion may result in a condition known as ‘red-water’, which is a kidney complaint.

Lettuce should be fed in strict moderation as its milky juice, lactucarium, is soporific and similar in action to opium. Wild varieties are somewhat worse than cultivated in their effects.

Rhubarb, clover and lucerne may be fed in small amounts. All are prone to inducing bloat.

Elder keeps flies away, but is not recommended as a food.

Some plants are thought to act medicinally. For example, shepherd’s purse (a white-flowered, hairy cornfield weed with a triangle
Table 17.1. An illustration of the availability of succulent foods each month to the pet rabbit feeder throughout the year (adapted from data in Sandford, 1973).

<table>
<thead>
<tr>
<th></th>
<th>Jan</th>
<th>Feb</th>
<th>Mar</th>
<th>Apr</th>
<th>May</th>
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<th>Oct</th>
<th>Nov</th>
<th>Dec</th>
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<tbody>
<tr>
<td>Carrots</td>
<td>Carrots</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>Chicory</td>
<td>Chicory</td>
<td>Chicory</td>
<td>Chicory</td>
<td>Chicory</td>
<td>Carrots</td>
<td>Carrots</td>
<td>Carrots</td>
</tr>
<tr>
<td>Cabbage and kale</td>
<td>Kale (thousand head)</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>Oats, clover and lucerne</td>
<td>Oats, clover and lucerne</td>
<td>Oats, clover and lucerne</td>
<td>Oats, clover and lucerne</td>
<td>Oats, clover and lucerne</td>
<td>Cabbage and kale (marrow stem)</td>
<td>Cabbage and kale</td>
<td>Cabbage and kale</td>
</tr>
<tr>
<td>Swede</td>
<td>Swede</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>Green maize</td>
<td>Green maize</td>
<td>Swede</td>
<td>Swede</td>
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<tr>
<td>Mangolds</td>
<td>Mangolds</td>
<td>Mangolds</td>
<td>Mangolds</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>Kohlrabi</td>
<td>Kohlrabi</td>
<td>Kohlrabi</td>
<td>Kohlrabi</td>
<td>Kohlrabi</td>
</tr>
<tr>
<td>Fodder and sugarbeet</td>
<td>Fodder and sugarbeet</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>Fodder and sugarbeet</td>
<td>Fodder and sugarbeet</td>
<td>Fodder and sugarbeet</td>
</tr>
<tr>
<td>Cereals</td>
<td>Cereals</td>
<td>Cereals</td>
<td>Cereals</td>
<td>Cereals</td>
<td>Cereals</td>
<td>Cereals</td>
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<td>Cereals</td>
<td>Cereals</td>
<td>Cereals</td>
<td>Cereals</td>
</tr>
<tr>
<td>Hay</td>
<td>Hay</td>
<td>Hay</td>
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<td>Hay</td>
<td>Hay</td>
<td>Hay</td>
<td>Hay</td>
<td>Hay</td>
<td>Hay</td>
<td>Hay</td>
<td>Hay</td>
<td>Hay</td>
</tr>
</tbody>
</table>
of cordate pods) and blackberry, raspberry and strawberry leaves are all considered beneficial in cases of scouring in the rabbit.

The most useful and successful green-feed is grass and the products of grass (hay and dried grass pellets). Traditionally, young grass has been used to improve growth and the general plane of nutrition. Similarly, lucerne (alfalfa), a modest protein source that is rich in fibre, calcium, carotene and vitamin E, is a common material in rabbit diets.

**ROOTS.** Carrots, swedes, turnips, parsnips and fresh sugarbeet (dried beet, although low in sugar, will require soaking before use) are all useful feeds. They are high in moisture (750–950 g kg\(^{-1}\)) and low in protein, starch and fibre and a poor source of vitamins. Most of the dry matter (DM) fraction is in the form of sugars; thus, they should be limited to a small proportion of the total feed. They should never be fed frozen or thawed, mouldy or rotten.

Potatoes are somewhat higher in DM than other roots and are primarily a starch source; cooking to a mash has the advantage of reducing the non-protein nitrogen alkaloid (solanidine) and substantially reduces the risk of gastrointestinal disturbances.

The Jerusalem artichoke is a good food all year round, with the leaves and stems as a summer food and the roots in the winter. The plant is related to the sunflower and its roots are similar in nutrient content to potatoes. One of the advantages is that the root is impervious to frost and can therefore be left in the ground all year round. When harvested it must be washed prior to feeding.

Beetroot is considered to be a good appetite stimulant.

**Roughages**

Good hay – as explained in the previous section – is the best, with meadow hay before flowering being the best. True clover hay may be too coarse and of doubtful value, although a proportion of clover in the meadow is considered beneficial. Good hay smells sweet with no sense of mustiness and a faint tang of tobacco. Hay should be stored prior to use; new-season hay (i.e. cut within the last 3–4 months) will often result in scouring in rabbits. Lucerne hay and pea haulm are also currently popular and are favoured by rabbits; however, lucerne is higher than grass hay in protein and calcium and, while appropriate during the growth period, should be limited or avoided in the adult. Hay from well-grown stinging nettles and dried carefully makes a pleasant change and is protein-rich, though rabbits will not eat fresh nettles (Netherway, 1979).

Straw, although traditionally used for bedding, is consumed by rabbits and is a useful ingredient in mixed feeds and compound diets in the form of alkali-treated (sodium hydroxide) straw pellets.

**Concentrates**

**GRAINS.** Oats are generally considered to be the best grain. The order of preference is oats, barley, maize and then wheat. Little or no information on rye, triticale and others is found in the literature for pet rabbits. Whole plump oats are preferable to crushed oats as, with the latter, the rabbit will pick out the kernel and leave husk. Rolling the oat so as to just crack the skin is an alternative preparation for use in flake mixes. Wheat has a tendency to be pasty and is not generally fed alone. Wheat bran is a very popular and useful raw material and was traditionally fed in quantity to domestic rabbits in the early part of the last century (Netherway, 1979). It was the only foodstuff of all rationed materials to be allowed to the rabbit breeder during post Second World War rationing in the UK (Sandford, 1986). Low-starch wheat feed is a similarly useful material. Maize, although excellent, may be relatively expensive compared to other cereals in certain countries.

Cereals in general are good energy sources, typically containing 80–120 g kg\(^{-1}\) protein. The primary deficiencies in cereals are in lysine, vitamins A and D and calcium. The phosphorus content, although frequently twice the level of calcium, is of limited availability as approximately 0.5 is in the phytate form.
PROTEINS. Both beans and peas are useful, with peas being preferred. Only old-season beans should be used as new-season crops tend to heat when ground. Both are rich in protein (200 g kg\(^{-1}\)) with a high lysine content which complements the cereals, although they are similar to cereals in terms of being low in calcium and high in phosphorus.

Many legumes contain antinutritional factors such as trypsin inhibitors, tannins and phytohaemagglutinins. While heat treatment can reduce these factors, the inclusion of such materials in the diet should be limited. Beans of the genus *Phaseolus* (kidney, navy and butter beans) are toxic when fed raw and should not be used.

For commercial feeds both the Mediterranean carob and African locust bean are very palatable and popular favourites. Sunflower seeds are also popular and visually attractive in flake mixes. Oil cakes (peanut, sunflower, sesame and soya), usually in decorticated form, can form an important part of a mixed feed, but should never be fed alone. Linseed, which has traditionally been used in a mash as a laxative and to achieve a ‘bloom’ on the coat, is now recognized as an important source of n-3 fatty acids as well as protein.

Animal proteins are unnecessary for the pet rabbit. Although they have been considered important in farmed situations, they are now illegal for use in rabbit diets throughout the European Union.

**Compounds**

The design of a pelleted diet allows for a wide range of raw materials to be selected for their nutritional qualities rather than visual appeal. This also means that less reliance needs to be placed on any single ingredient in the diet, producing a more consistent approach to meeting the nutrient requirements of the rabbit. Furthermore, the inclusion of supplements to balance the diet together with vitamins and trace minerals in a palatable form is easy. Diets do not necessarily need to be complicated in their raw material composition, as confirmed by Cheeke (1988) who used a combination of only five ingredients, although relying heavily on lucerne, oats and a mineral and vitamin supplement. There are, however, some general restrictions on the inclusion of certain raw materials that should be taken into account in the design of the complete compound feed (Table 17.2).

Pellet hardness and the homogeneity of the mix are critical to the construction of the diet. Dusty pellets are poorly accepted by the rabbit and a non-uniform mix of components will exacerbate selective feeding and result in dietary imbalance. A wide range of technologies is employed in the production of prepared compound feeds for rabbits, which include conventional pelleted diets and mixes combining either steamed or micronized flakes of cereal, pulses and legumes, together with pellets or extrusions. Many diets are now solely based on either soft or crisp extruded complete diets. All of these formats are proven to be acceptable to the rabbit. Flaked mixes can be coated with oil, molasses or glucose syrup to aid palatability and reduce dust. The amounts of these coatings do not, if applied appropriately to a well-designed diet, provide either excess calories in the case of fat or excess total sugar (>6%) in the case of molasses or glucose syrups. The basic techniques for the processing of such diets have been reviewed by Tobin (1996).

In addition to conventional ingredients, purified fibre sources are now available for compound feeds. These include refined lignins, celluloses and materials with prebiotic properties such as mannans and fructo-oligosaccharides.

Compound feeds that are designed for *ad-libitum* feeding should contain sufficient energy (>9.3 MJ DE kg\(^{-1}\)) to allow the rabbit to regulate its intake based on energy consumption. Very high or very low (<9.0 MJ DE kg\(^{-1}\)) energy diets require a twice-daily restricted feeding regime, which will be explained in the feeding instructions. Restricted feeding can be used to reduce growth rates below the theoretical maximum genetic potential by up to one-third (Schultz *et al.*, 1988). This may be desirable in pets, where growth rate is relatively unimportant.
Pelleted feeds are best produced to a finished size of 3–4 mm in diameter by 10 mm in length. It is important not to exceed 5 mm in diameter as this has been shown to increase wastage of the diet, while a pellet that is much shorter than 10 mm is not well accepted by the rabbit (Lebas, 1987). It is possible to feed compounds as meals, providing the grist is large enough and product essentially dust-free. However, this imposes certain constraints on the method of water supply, which is likely to be a problem for a pet (Lebas, 1987).

### Table 17.2. A guide to typical raw material constraints in compounds for pet rabbits (based on data from Santomá et al. 1989; Maertens, 1992; and industry experience).

<table>
<thead>
<tr>
<th>Ingredient</th>
<th>Suggested maximum inclusion (g kg⁻¹)</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>Barley</td>
<td>300</td>
<td>–</td>
</tr>
<tr>
<td>Wheat</td>
<td>250</td>
<td>All wheat products 300 g kg⁻¹</td>
</tr>
<tr>
<td>Oats</td>
<td>350</td>
<td>May be lower for processing reasons</td>
</tr>
<tr>
<td>Maize</td>
<td>250</td>
<td>–</td>
</tr>
<tr>
<td>Wheat feed</td>
<td>300</td>
<td>All wheat products 300 g kg⁻¹</td>
</tr>
<tr>
<td>Bran</td>
<td>250</td>
<td>May be lower for processing reasons</td>
</tr>
<tr>
<td>Oat feed</td>
<td>250</td>
<td>May be lower for processing reasons</td>
</tr>
<tr>
<td>Dried distillers’ grains</td>
<td>100</td>
<td>Some sources may contain high copper levels, thus restricting use to 50 g kg⁻¹</td>
</tr>
<tr>
<td>Peas</td>
<td>100</td>
<td>50 g kg⁻¹ more common</td>
</tr>
<tr>
<td>Field beans</td>
<td>50</td>
<td>Old crop to avoid heating on grinding</td>
</tr>
<tr>
<td>Sunflower extractions</td>
<td>1000</td>
<td>Commercially, a 300 g kg⁻¹ limit is more practical</td>
</tr>
<tr>
<td>Soya (dehulled)</td>
<td>200</td>
<td>Some believe this should have no upper limit</td>
</tr>
<tr>
<td>Full-fat soya</td>
<td>250</td>
<td>Typically no more than 125 g kg⁻¹ is used</td>
</tr>
<tr>
<td>Citrus pulp</td>
<td>75</td>
<td>–</td>
</tr>
<tr>
<td>Grass nuts</td>
<td>1000</td>
<td>No limit on grass inclusion, either as dried grass or hay</td>
</tr>
<tr>
<td>Lucerne</td>
<td>300</td>
<td>Ensiled lucerne may result in decreased food intake</td>
</tr>
<tr>
<td>Sugarbeet</td>
<td>200</td>
<td>May consider lower value if molasses is included in the process</td>
</tr>
<tr>
<td>Soya hulls</td>
<td>250</td>
<td>–</td>
</tr>
<tr>
<td>Molasses</td>
<td>50</td>
<td>Consider contribution from sugarbeet</td>
</tr>
<tr>
<td>Wheat straw</td>
<td>150</td>
<td>Either plain or sodium hydroxide-treated. Up to 250 g kg⁻¹ has been used successfully</td>
</tr>
<tr>
<td>Maize gluten feed</td>
<td>200</td>
<td>Maize gluten-60 to no upper limit</td>
</tr>
<tr>
<td>Locust beans</td>
<td>1000</td>
<td>Carob has similar inclusions</td>
</tr>
<tr>
<td>Grape seed</td>
<td>100</td>
<td>May depress feed intake at higher inclusion rates</td>
</tr>
</tbody>
</table>

17.4.3 Water

Water is perhaps the most often neglected raw material (or, perhaps more correctly, nutrient). A fresh supply of clean, high-quality drinking water should always available. The popular belief that rabbits that are fed fresh greens do not need water is not entirely without foundation (Schwabe, 1995), but should not be considered as a safe practice for the domestic pet rabbit. A loss of 0.10 body water results in death. In the summer, rabbits in a hutch may lose up to 28 g h⁻¹ in direct sunlight and 3.5 g h⁻¹ in shade (Sandford, 1986). In winter, it is often wise to provide warm water to encourage intake and prevent digestive upsets.

The various estimates provided in the literature for the water intake of the rabbit vary widely. Netherway (1979) reported that a 4–5 kg rabbit on dry diet will drink 0.25 l 24 h⁻¹, whereas Sandford (1986) suggested a range of between 0.42 and 0.57 l 24 h⁻¹ for rabbits on a dry diet. A similar doe with a
litter of seven or eight kits at 3 weeks of age will drink 0.5–0.625 l 24 h⁻¹, while the litter on their own in a hutch will drink up to 1.5 l 24 h⁻¹. A good basis for maintenance would be 120 ml kg⁻¹ body weight.

17.5 Nutrient Requirements

The suggested values presented below are based on a review of the literature, commercial diet design practice and general experience.

17.5.1 Protein

While there are a number of excellent reviews on the protein requirements of the rabbit (NRC, 1977; Lebas, 1989), scant consideration has been given to the effect of varying protein quality on the pet rabbit. The fact that commercial rabbits have successfully been reared on diets based on simple mixtures of plant proteins suggests that both protein quantity and quality are of little importance to the pet. There are, however, suggestions that excess dietary protein results in scouring (NRC, 1966; Lebas, 1989).

The protein digestibility capacity of the rabbit is maximized early in life, at around 4 weeks of age (Lebas et al., 1971). In the adult rabbit the ability to digest protein appears to be related to the dietary protein source, with protein concentrates, cereals and forages having a coefficient of apparent digestibility of 0.80, 0.67, 0.55, respectively. The fermentation within and contents of the caecum are critical to the supply of protein to the rabbit, as only 0.35 of total protein digestion occurs in the small intestine (Gidenne, 1988).

Ammonia is the main end product of nitrogen catabolism as well as the main nitrogenous source for the microbial population in the caecum. Ammonia is between 6.0 and 8.5 mg 100 ml⁻¹ caecal contents with normal diets (Carabaño et al., 1988). If caecal ammonia concentrations are limiting for microbial growth, as in very low-protein diets, then urea supplementation is effective; urea is metabolized and absorbed before reaching the caecum, resulting in increased urinary nitrogen (Santomá et al., 1989). Consequently, as caecotrophy provides approximately 0.18 of the total protein intake for the rabbit, although varying with dietary constituents, excessively low-protein diets are to be avoided. Consideration of the protein quality of the rest of the diet is probably important even for the pet rabbit, but more in terms of health and tissue repair than for production considerations.

The contribution of the soft faeces increases protein digestibility in the rabbit by a factor between 1.05 and 1.2 (Fraga and de Blas, 1977). This may explain the better utilization of protein from forages in rabbits than in other non-ruminant species.

In terms of specific amino acids, lysine is considered the first limiting, followed by methionine (Santomá et al., 1989). Colin (1975) suggested that cystine can meet the total methionine plus cystine requirement. Given the typical raw material base of the pet rabbit diet, a shortfall in sulphur amino acids is likely to be the first concern. The NRC (1977) and Lebas (1987) suggested that the rabbit requires ten essential amino acids, while Cheeke (1987) suggested that glycine should be also considered essential.

It is concluded from a review of the literature, based on adult maintenance recommendations, that a protein content for the domestic pet rabbit should be in the range 120–160 g kg⁻¹. The minimum amino acid constraints on this should be 5–6 g kg⁻¹ for lysine and 5–7 g kg⁻¹ for methionine plus cystine. Arginine should be in the region of 8–9 g kg⁻¹, but this is unlikely to require constraining in typical formulations and some have argued that the rabbit is capable of some arginine synthesis (Santomá et al., 1989).

17.5.2 Fibre

Fibre is critical to the rabbit for health and well-being. Many chemical compounds are included in the broad definition of fibre.
Their relative proportions in the diet will affect the way in which the rabbit responds to the diet. The nature of the fibre is important both in terms of its chemical (soluble versus insoluble fibre) and physical (long unground fibre versus short ground fibre) characteristics. Reviews of the nature and characterization of fibre have been published (Van Soest and McQueen, 1973; Sunvold and Fahey, 1994; Fahey, 1995).

Cell wall constituents (indigestible fibre; lignocellulose, estimated by acid detergent fibre (ADF) analysis) are important in providing bulk to the diet. This is reflected by the high CF values of complete diets. Too little indigestible dietary fibre (IDF) increases mortality as a result of a malfunctioning of the digestive system and the proliferation of certain undesirable microflora and pathogenic bacteria (Gidenne, 1987), particularly in growing rabbits (Perez et al., 1994; Chao and Li, 2007). Carabaño et al. (1988) demonstrated that this was the result of an increase in retention time with diets containing low levels of IDF by using a diet with <120 g CF kg−1. Increases in the caecal content and a reduction in the rate of caecal content turnover was observed.

The presence of adequate IDF in the diet of the rabbit maintains intestinal transit times, whereas the presence of an appropriate amount of soluble fibre (hemicellulose, estimated by NDF plus pectins minus ADF) is important for satisfactory fermentation in the caecum. Gidenne et al. (1986) demonstrated that the production of a diet based on beet pulp, higher in soluble fibre, increased retention time in the rabbit when compared with an iso-CF diet based on lucerne. Grape residue has the reverse effect (Santomá et al., 1989). Thus, for the complete compound rabbit diet, it is important to consider the relative proportions of digestible fibre and starch to IDF or long fibre when using beet, sunflower hulls, rice bran, olive pulp and grape cake. One approach is to include a minimum amount of conventional raw materials such as lucerne, straw and wheat bran and exclude the CF contribution from beet and other digestible sources, or fix a minimum IDF nutrient constraint.

Because fibre influences transit time, and transit time is rapid in the rabbit, the energy supply from CF is less than for other species. In conventional diets this may be 0.05 of the DE. Consequently fibre digestion is relatively poor in the rabbit, although coefficients of apparent digestibility in the region of 0.55–0.7 have been reported, which may be explained by the extent of the lignification of cell wall material in the diet (Lebas, 1989).

The degree of grinding of the fibre fraction of the diet, including the IDF fraction, is an important consideration in the design of the complete compound rabbit diet as it can exert similar physical effects on intestinal motility as those resulting from insufficient IDF (Pairet et al., 1986; Bouyssou et al., 1988). The finer the grinding, the greater the digesta retention time and caecal content (Lebas and Laplace, 1977; Candau et al., 1986), with resulting digestive upsets. Screen sizes of 1 mm induce such digestive upsets, especially if the diet is marginal in IDF content (Pairet et al., 1986; Auvergne et al., 1987). However, diets ground on 2–7 mm screens do not produce such problems (Lebas et al., 1986; Lebas and Franck, 1986). There is general agreement that screen sizes for complete compound feeds would be 2 mm.

The fine fibre material and soluble components of the diet that enter the caecum are fermented mainly to VFAs between 34.5 and 351 µmol g DM, predominantly acetic (0.73), butyric (0.17) and propionic (0.08) acids. Energy is the limiting factor for the caecal microbial population. The VFAs produced may contribute between 0.12 and 0.40 of the DE of the adult rabbit (Hoover and Heitman, 1972; Marty and Vernay, 1984). Thus, maintaining caecal fermentation and gut health is critical to diet design. To promote a beneficial microbial caecal population and enhance the production of butyrate with its associated immune-stimulation properties, the inclusion of a fructose oligosaccharide is now popular in pet rabbit formulations (P. Bruneau, Lichfield, 1998, personal communication). This has the added advantage that the shift in VFA proportions enhances intestinal motility,
thereby reducing the importance of a minimum inclusion of IDF.

As with all diet designs, a balance of fibre type to other nutrients is important and this is perhaps more so in the case of the small pet rabbit. For example, with the Netherland Dwarf it is possible that a high-fibre diet with a concomitantly low DE of <8.1 MJ kg\(^{-1}\) (as-fed) may result in insufficient intake to provide sufficient energy for maintenance, although this problem may not arise for larger breeds (>3.5 kg, e.g. Mini Lop and New Zealand White).

If the diet is designed so that the CF levels are <100–120 g kg\(^{-1}\) then a decrease in intestinal transit time occurs. This increases the caecal volume, resulting in a decrease in the carbohydrate supply for energy. This increases (in relative terms) the proportion of energy from protein sources. At the other extreme an increase in the fibre content of the diet, such that insufficient DE can be consumed, also results in a concomitant rise in the proportion of energy derived from protein and has the effect of promoting proteolytic bacteria and ammonia production. This inevitably leads to digestive problems. If, however the increase in fibre (150–160 g kg\(^{-1}\)) is associated with a reduction in the protein to DE ratio then digestive upsets will be avoided.

A similar increase in caecal content and caecal impaction as occurs with an increase in the fibre protein to DE ratio can also occur with an excess mineral load in the diet, such as when a clay binder is used in excess to enhance pellet quality (Grobner et al., 1985). De Blas et al. (1986) suggested that sufficient IDF is provided with 100–110 g CF kg\(^{-1}\). However, to achieve 90 g kg\(^{-1}\) IDF it is suggested that 130–140 g CF kg\(^{-1}\) diet is necessary in many formulations. Exceeding a maximum CF of 160 g kg\(^{-1}\) can lead to increased mortality in young rabbits (Lebas, 1989).

Given that rabbits thrive on diets of hay and grass, it may be considered appropriate to formulate a fibre intake similar to these materials. However, to exercise this approach a better measurement of the fibre fraction of the diet is required. This has been reviewed by Gidenne (2003).

- Total dietary fibre: this represents all water-soluble non-starch polysaccharides.
- Water-insoluble cell wall content: this represents the pectic substances of hemicellulose, cellulose and lignin.
- NDF: equates to most of the hemicellulose and lignin, and all of the cellulose.
- ADF: equates to cellulose and most of the lignin. Consequently, NDF minus ADF represents the hemicellulose content of the diet.
- Acid detergent lignin: nearly all lignins.
- CF: this is the term declared on pack and represents 20–90% of the lignin and 30–100% of cellulose, depending upon the plant ingredient being analysed.

For a complete diet, CF ranges as wide as 140–250 g kg\(^{-1}\) fibre may be found. It is suggested that a minimum of 140–160 g kg\(^{-1}\) CF should be adopted, or preferably a more detailed assessment of the fibre fraction should be used with a minimum of 170–200 g ADF kg\(^{-1}\), NDF in the region of 300–400 g kg\(^{-1}\) and a ratio of (NDF + pectins) – ADF to ADF of ≤1.3. Alternatively, for a complementary feed a minimum source of IDF should be supplied through the addition of traditional materials such as hay or straw to the daily ration of compound feed.

### 17.5.3 Fat

It is generally thought that plant materials meet the essential fatty acid requirements of the rabbit, which can be achieved with a diet containing 25 g fat kg\(^{-1}\). For the pet rabbit, where weight constraint is important, the major role of fat in the diet is for the supply of essential fatty acids. An adequate supply of fat is often found within the normal raw materials used in diet formulations. However, Cheeke (1974) reported that rabbits prefer diets coated with 50 g kg\(^{-1}\)
maize oil over those without fat addition. It is therefore suggested that, if added, the fat content should not exceed 50 g kg\(^{-1}\).

17.5.4 Starch and energy

While starch is well-digested even at high levels (>600 g kg\(^{-1}\) of barley in the diet), starch levels >150 g kg\(^{-1}\) at the caecum will lead to undesirable fermentation patterns. The sensitivity to high-starch diets is controversial and appears to be much more apparent in the young weanling rabbit than in the adult. As discussed by Lebas (1989), if the relationship between starch and fibre is independent, a minimum fibre and maximum starch constraint (<140 g kg\(^{-1}\) in the young rabbit and 180–200 g kg\(^{-1}\) in the adult) is a sensible formulation consideration. There is evidence to suggest that the presentation of starch in terms of flakes, ground or cereal type is immaterial to the total amount (Santomá \emph{et al.}, 1985; Seroux, 1986). However, if the initial starch in the dietary ingredients is processed in such a manner (e.g., extrusion) as to be readily digested and absorbed as simple sugar in the small intestine then this may not present a problem in the final diet.

While many of the equations used to predict the DE of diets overestimate the DE content of diets with high levels of digestible fibre and underestimate those with added fat, for the conventional pet rabbit diet it is suggested that the following equation provides a reasonable practical predictor of DE:

\[
\text{DE} = (-1801 + 7.10\text{CP} + 12.01\text{EE} + 5.59\text{NFE}) \times 0.004184
\]

Where DE is MJ kg\(^{-1}\); CP is crude protein; EE is ether extract; NFC is organic matter minus crude protein, ether extract and NDF; and NDF is neutral detergent fibre, assayed with a heat-stable amylase and expressed exclusive of residual ash.

The literature provides some estimates of the DE of raw materials for rabbits. A selection is summarized in Table 17.3, together with data for NDF and ADF. It is interesting to note the similarity between these values and those generally used for pigs, even for forages.

In conclusion, the DE of the diet should be in the region of 9–10.5 MJ DE kg\(^{-1}\). Based on typical values of coefficients of apparent digestibility for concentrates at 0.8, cereals and brans at 0.65–0.70 and forages at 0.45–0.65, the energy concentration of the diet per unit of digestible protein (DP) can be estimated at 98 kJ g DP\(^{-1}\). Thus, for a typical diet of 102–110 g DP kg\(^{-1}\), an energy level of 10.0–10.5 MJ DE kg\(^{-1}\) would be considered suitable.

17.5.5 Vitamins and minerals

\textbf{Vitamins}

As indicated, the B-group vitamin requirements of the pet rabbit are supplied in sufficient quantity from soft faeces (NRC, 1977; Harris \emph{et al.}, 1983). For complete compound feeds it is usual to supplement this to a limited extent, together with up to 2 mg kg\(^{-1}\) vitamin K.

While fresh green foods may contain large amounts of carotene, the precursor of vitamin A, much of this is lost upon drying, storage and processing. It is thus advisable to supplement complete diets with vitamin A in the range of 5000–12,000 IU kg\(^{-1}\) (Roche, 1998). There is also some evidence to indicate that breeding rabbits benefit from an additional 30 mg carotene kg\(^{-1}\) diet, even when vitamin A is in plentiful supply (Tobin, 1996).

Vitamin E is usually provided at 40–70 mg kg\(^{-1}\). Rabbits are sensitive to its deficiency, developing muscular dystrophy and myocardial dysfunction and showing an increased incidence of coccidiosis.
Minerals

The rabbit appears to be unable to regulate its uptake of calcium from the intestinal tract and the concentration of calcium in the complete diet must therefore be close to the requirement. However, it is important to consider the extent to which low-calcium fresh foods may be fed as part of the diet, leading to a reduction in plasma calcium and a possible excess of phosphorus. While rabbits tolerate wide calcium to phosphorus ratios, inverse ratios soon lead to problems.

Such imbalances of calcium to phosphorus have been implicated in dental problems in pet rabbits (Harcourt-Brown, 1996). However, Bucher (1994) indicated that the nature of the feed ingredients also exerts effects on incisor growth and attrition. The provision of too much calcium in the diet may lead to an increased incidence of urolithiasis. The deposition of calcium salts in the urine occurs due to the alkalinity of the urine, which is often enhanced by high levels of potassium from grass or lucerne consumption, contributing to the base excess. It is thus suggested that dietary calcium should be in the region of 5–10 g kg$^{-1}$. To minimize the risk of the deposition of excess calcium in soft tissues the vitamin D content of the diet should be in the region of 800–1200 IU kg$^{-1}$. While the rabbit may be tolerant of a wide range of calcium to phosphorus ratios, it is desirable to maintain the ratio between 1:1 and 2:1 in favour of calcium.

There is no reason to believe that the requirements for other minerals and trace elements are different from those indicated by the NRC (1977). However, 50 mg of supplementary zinc kg$^{-1}$ should be considered to overcome the potential low bioavailability of zinc raw material in the diet when large amounts of phytate are present. There may be a benefit to the addition of the supplementary zinc in the form of a chelate or polysaccharide complex as there are indications that these sources are not involved in such interactions (Lowe and Wiseman, 1997).

### 17.5.6 Suggested diet specifications

On the basis of the foregoing discussion and the author’s experience, the specifications given in Table 17.4 are suggested for diets suitable for the pet rabbit.

### 17.5.7 Nutritional ailments

When faced with an unwell pet, it is important to differentiate between symptoms and disease. Many so-called diseases, for
example scouring (diarrhoea), are not in themselves a disease but are actually a symptom of a disease. As far as the complete or complementary diet manufacture is concerned, nutritional deficiencies and metabolic disorders may predispose to these conditions. It is worth bearing in mind that there is nothing so potent for producing ill health as improperly constituted food or an inappropriate feeding strategy.

In many cases it is not the design of the food that is at fault, but the way in which the diet is presented to, fed to or selected by the pet rabbit. Therefore, the feeding instructions and guide as to how to best utilize the food in the day-to-day feeding programme of the pet rabbit are as important in the design and manufacture of pet rabbit diets as the nutrient and raw material specifications. Death from malnutrition is rare, but excess bulk in the diet of young rabbits can result in starvation. This may arise when insufficient complete diet relative to hay is provided.

Similarly, selective feeding of flake-mix-type diets has been reported to lead to deficiencies or excess of certain nutrients.

### 17.6 Conclusions

Diets for the pet rabbit can be produced from a wide selection of materials, ranging from those grown in the garden to complete commercial diets. The creation of entirely home-produced diets must be treated with caution unless there is extensive knowledge of both the requirements of the rabbit and the nutrient content of the ingredients. The science of nutrition and diet formulation requires education and considerable experience, and a haphazard approach is not usually successful. Furthermore, even the best designed and manufactured diets are only successful in providing appropriate nutrition to the pet rabbit if they are fed according to the instructions provided with them. The nutritionist is

---

**Table 17.4. Suggested nutrient constraints for pet rabbit diets.**

<table>
<thead>
<tr>
<th>Component and nutrient</th>
<th>Range</th>
<th>Nutrient (mg kg⁻¹)</th>
<th>Typical range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Protein</td>
<td>120–160</td>
<td>Vitamin A (IU kg⁻¹)d</td>
<td>5,000–12,000</td>
</tr>
<tr>
<td>Crude fibrea</td>
<td>140–200</td>
<td>Vitamin D (IU kg⁻¹)</td>
<td>800–1,200</td>
</tr>
<tr>
<td>ADF</td>
<td>170–n/a</td>
<td>Vitamin E</td>
<td>40–70</td>
</tr>
<tr>
<td>Starchb</td>
<td>0–140</td>
<td>Copper</td>
<td>5–10</td>
</tr>
<tr>
<td>Fat</td>
<td>20–50</td>
<td>Vitamin B₁</td>
<td>1–10</td>
</tr>
<tr>
<td>Digestible energy (MJ kg⁻¹)</td>
<td>9–10.5</td>
<td>Vitamin B₂</td>
<td>3–10</td>
</tr>
<tr>
<td>Lysine</td>
<td>5–n/a</td>
<td>Vitamin B₆</td>
<td>2–15</td>
</tr>
<tr>
<td>Methionine and cystine</td>
<td>5–n/a</td>
<td>Vitamin B₁₂</td>
<td>0.01–0.02</td>
</tr>
<tr>
<td>Calciumc</td>
<td>5–10</td>
<td>Folic acid</td>
<td>0.2–1.0</td>
</tr>
<tr>
<td>Phosphorusd</td>
<td>5–8</td>
<td>Pantothenic acid</td>
<td>3–20</td>
</tr>
<tr>
<td>Magnesium</td>
<td>3</td>
<td>Niacin</td>
<td>30–60</td>
</tr>
<tr>
<td>Zinc</td>
<td>50–100</td>
<td>Biotin</td>
<td>0.05–0.20</td>
</tr>
<tr>
<td>Potassium</td>
<td>6–7</td>
<td>Choline</td>
<td>300–1,500</td>
</tr>
<tr>
<td>Sodium chloride</td>
<td>5–10</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

ADF, acid detergent fibre; n/a, not applicable.

aA more appropriate estimate for minimum fibre inclusion is 310 g kg⁻¹ neutral detergent fibre (NDF) and 190 g kg⁻¹ ADF for the young rabbit and 270 g kg⁻¹ NDF and 170 g kg⁻¹ ADF for the adult (Gidenne, 2003).

bThe starch maximum only applies to diets for the very young rabbit. For the young adult pet, a 140–200 g kg⁻¹ maximum constraint for the mature adult may be considered, providing the fibre constraints are exceeded.

cThese levels allow for the fact that the pet rabbit may be used for breeding. Adult maintenance can be satisfied with levels in the region of 4 g phosphorus kg⁻¹ and 6 g calcium kg⁻¹. Also note that >10 g kg⁻¹ may be unpalatable to the rabbit (NRC, 1977).

dIt may be necessary to include higher levels of certain vitamins to allow for losses during manufacture. These will be specific to the raw materials and production processes used and must be taken into account when designing the supplementary additions.
duty-bound to provide the best guidance possible in this area and the pet rabbit owner would be wise to follow instructions carefully and pay due care and attention to the finer points of management, including feeding to maintain an appropriate body weight.

The importance of fibre to the rabbit cannot be overstated. Dietary minimums should always be comfortably met and the pet owner should be clearly encouraged to feed additional fibre, even when complete diets that meet the daily nutritional needs are fed.

References


Roche (1998) Roche Vitamin Supplementation Guidelines for Domestic Animals. Roche, Paramus, New Jersey, USA.


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