The Nutrition of the Rabbit

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Contents

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Preface

In the last 20 years, rabbit production has become an increasingly intensive system, such that productivity is now equivalent to that obtained in other intensively farmed species.

The importance of nutrition has increased significantly as feed costs, pathological conditions associated with energy and nutrient deficiencies, and considerations of product quality have become limiting factors to economic output from a unit.

The rabbit is unique. It requires a high daily nutrient and energy intake but, because it is a herbivore, it also needs a diet with a high concentration of fibre to ensure optimum performance and, in addition, to minimize the incidence of digestive disorders.

Diets of rabbits are closer to those of dairy cows than to other intensive meat producers such as pigs or poultry. This means use of a wider range of raw materials (forages, but also those with high concentration of energy and nutrients) and greater complexity in both formulation of optimum diets and the overall feed manufacturing process.

Furthermore, the unusual digestive physiology includes several characteristics such as the mechanism of particle separation at the ileo-caecal junction and the recycling of soft faeces through caecotrophy, both of which have specific nutritional and pathological implications.

The objective of this book has been to update the wealth of scientific information on rabbit feeding and nutrition. The chapters have been written by distinguished research workers from around the world who are recognized specialists in their field. The contents cover the physiological basis of nutrition, nutrient requirements, feeding value and management, feed manufacturing, interaction of nutrition with environment, pathology and carcass quality. The final two chapters have been devoted to Angora and pet rabbits.

Abbreviations

ADL	acid detergent lignin
AFB_1	aflatoxin B_1
ANF	antinutritive factors
ASESCU	Asociacion Española Cunicultura Cientifica
CCW	caecal contents weight
CF	crude fibre
CP	crude protein
CPD	crude protein digestibility
CT	computerized tomography
CV	coefficient of variation
DDP	dietary digestible protein
DE	digestible energy
DF	dietary fibre
DM	dry matter
d.p.	degree of polymerization
DP	digestible protein
DWG	daily weight gain
EAA	essential amino acids
EBG	empty body gain
EE	ether extract
EEd	ether extract digestibility
EFA	essential fatty acids
EGRAN	European Group on Rabbit Nutrition
FA	fatty acids
FCR	feed conversion ratio
FE	faecal energy
GasE	intestinal fermentation energy associated with gas production
GE	gross energy
HE	heat energy
HI	heat increment
ICPD	ileal digestibility coefficient of crude protein
IDF	indigestible dietary fibre
INRA	Institut Nationale de la Recherche Agronomique
LA	linoleic acid
LCT	lower critical temperature
LW	live weight
ME	metabolizable energy
MEI	metabolizable energy intake
MEn	metabolizable energy corrected to N equilibrium
MRT	mean retention time
N-ADF	N bound to acid detergent fibre
NDF	neutral detergent fibre
NE	net energy
NEFA	non-esterified fatty acids
NMR	nuclear magnetic resonance
NSP	non-starch polysaccharide
PCW	plant cell walls
PTH	parathyroid hormone
PUFA	polyunsaturated fatty acids
RE	retained energy
SAA	sulphur amino acids
SFA	saturated fatty acids
THI	temperature–humidity index
TNZ	thermoneutral zone
Tobec	total body electrical conductivity
TT	transit time
UCT	upper critical temperature
UE	urine energy
UFA	unsaturated fatty acids
UN	urinary N
VFA	volatile fatty acids
VFI	voluntary feed intake

1. The Digestive System of the Rabbit

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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. 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 a milk-base feeding to the sole dependence on solid feed without milk or its by-products. It is intended in this chapter: (i) to give 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) to explain how these characteristics change from the time of weaning until attainment of maturity.

The digestive system of the rabbit

The first important compartment of the digestive system of the rabbit is the stomach, which 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 caecotrophs. 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 vs. cardiac–pyloric region), the presence or absence of soft faeces (Griffiths and Davies, 1963), the time from the feed intake (Alexander and

 The Nutrition of the Rabbit (eds C. de Blas and J. Wiseman)

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 rabbits older than 5 weeks. 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). The caecum is characterized by having a weak muscular layer and contents with a dry matter of 200 g kg^{-1}. The pH of the caecal contents is slightly acid (5.6–6.2) (Candau *et al*., 1986; Carabaño *et al*., 1988). 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 the formation of haustra between them, while 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).

Age-related changes in the morphology and function of the digestive system of the rabbit

The different segments of the digestive system of the rabbit grow at different rates until reaching maturity. The capacity for milk intake increases threefold from the time of birth until the peak of milk production (12–35 g milk day^{-1}). Caecum and colon develop faster than the rest of the body from 3 to 7 weeks of age whereas the relative size of intestine and stomach decreases from 3 to 11 weeks of age (Fig. 1.1; Lebas and Laplace, 1972). The fast growth of the caecum during this period is more evident if the caecal contents are included. Caecum and caecal contents reach a peak of about 0.06 of total body weight 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).

Very marked changes also occur in the activity of the different digestive enzymes. In the 4-week-old rabbit, the activity of 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). As the activity of gastric lipase decreases, pancreatic lipase activity increases, both when expressed as specific activity (μmol of substrate degraded per unit of time and mg of protein) or as total activity (μmol of substrate degraded per unit of time for the whole organ) after 14 days of age. Prior to this age, the specific activity is constant or increases slightly (Lebas *et al*., 1971; Corring *et al*., 1972).

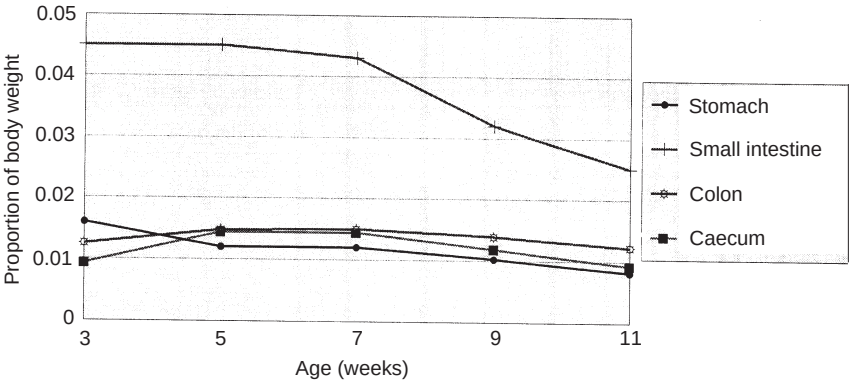

Fig. 1.1. Development of different segments of the digestive system of the rabbit from 3 to 11 weeks (Lebas and Laplace, 1972).

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). In the case of the pancreatic enzymes trypsin and chymotrypsin, their total activity increases markedly after 32 and 21 days of age, respectively (Corring *et al*., 1972). However, the specific activities of these two enzymes decrease during the period 1–43 days of age (Lebas *et al*., 1971).

The other main enzyme activity at the pancreatic level is amylase. The age-related changes in the activity of this enzyme are similar to those of the pancreatic lipase, with marked increases both in specific and total activities after 14 days of age and a slight decrease in specific activity from 1 to 14 days of age (Lebas *et al*., 1971; Corring *et al*., 1972). The carbohydrase activity of the pancreas is complemented by the activities of disaccharidases located mainly in the small intestine. Lactase activity decreases with age whereas that of invertase and maltase increases (Marounek *et al*., 1995). 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 activities provided by the intestinal microflora.

Role of the intestinal flora in the digestion and absorption of nutrients by the rabbit

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). The *Bacteroides*

population comprises 10^9–10^{10} bacteria g^{-1} and 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} (Bonnafous and Raynaud, 1970; Gouet and Fonty, 1979; Forsythe and Parker, 1985; Penney *et al*., 1986; Cortez *et al*., 1992).

The presence of cellulolytic bacteria in the caecum of the rabbit has already been indicated by Hall (1952) and Davies (1965). Later, Emaldi *et al.* (1979) studied the enzymatic activities of this 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 and pectinolytic, has been indicated in studies conducted by Forsythe and Parker (1985) and Marounek *et al.* (1995). Forsythe and Parker (1985) estimate populations of 10^8 and 10^9 xylanolytic and pectinolytic bacteria, 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.*, 1996). 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 be stabilized, whereas those of colibacilli decrease as the numbers of cellulolytic bacteria increase (Padilha *et al.*, 1995). However, milk intake may delay the colonization by cellulolytic flora but does not seem to affect the evolution of the population of colibacilli (Padilha *et al*., 1996). As a consequence of the age-related changes in the microbial population, production of volatile fatty acids (VFA) 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 5–6 h (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, VFA are produced in the proportion of 60–80 moles of acetate, 8–20 moles of butyrate, and 3–10 moles of propionate per 100 moles of VFA (Gidenne, 1996). However, this proportion changes with the time of the day, as described in the caecotrophy section of this chapter, 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), VFA 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 requirement from VFA produced by fermentation in the hindgut (Parker, 1976; Marty and Vernay, 1984).

Caecotrophy

Patterns of daily feed intake and soft faeces excretion

Soft faeces are excreted according to a circadian rhythm which is the opposite of 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). Figure 1.2 shows the pattern of 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 them 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 (Fig. 1.2). Feed intake increases from 15.00 to 18.00 h and then remains high until 24.00 h. 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 h and 06.00 h.

The age of the rabbits, their physiological status or 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 vs. 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 maternal behaviour of does through the morning rather than to physiological status. All the experiments described above were carried out with *ad libitum*

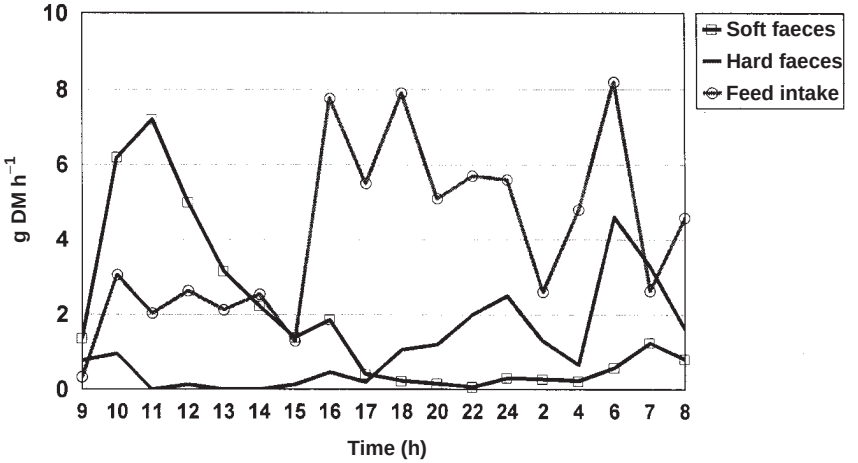

Fig. 1.2. Soft and hard faeces excretion and dry matter intake throughout the day (Carabaño and Merino, 1996).

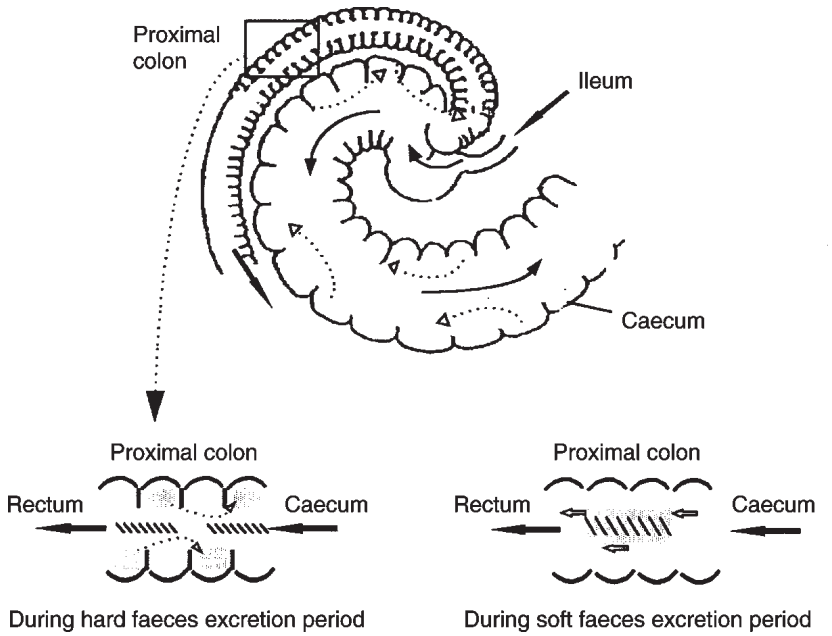

Fig. 1.3. Movement of digesta in the rabbit ileo-caeco-colic segment. Courtesy of T. Gidenne. ▭ liquids and fine particles; \\\\\\ large particles (>300 μm); ➔ peristaltic digesta movement; ⇨ antiperistaltic digesta movement.

access to feed. When the feeding regime is changed from *ad libitum* to a restricted access to feed the rhythm of excretion is profoundly altered, whatever the length of the light period. In these situations, the time for 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) recommend distributing the feed once per day late in the afternoon. In other situations (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.

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. As is shown in Fig. 1.3, during hard faeces excretion, water-soluble substances and fine particles (smaller than 0.3 mm diameter) (including microorganisms) are brought back to the caecum by means of antiperistaltic movements and retrograde flow. Coarse particles (larger than 0.3 mm diameter) pass to the distal part of the colon. In contrast, the motility of both the caecal base and proximal colon decreases during the formation of soft faeces (Ruckebush and Hörnicke, 1977). Endogenous prostaglandins play an important role in the motor function involved in soft faeces formation. The infusion of both PGE_2 and $PGF_{2\alpha}$ produces an inhibition of proximal colon movements, a stimulation of 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 VFA 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 typically involved in feed intake regulation, such as lateral hypothalamus and the hypothalamic ventromedian 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, 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 mechanoreceptors in the rectum have been proposed as factors involved in reingestion of soft faeces. However, results obtained from rabbits deprived of olfactory bulbs and supporting an artificial anus which bypasses the rectum show that rabbits are still able to recognize and reingest soft faeces (Gallouin, 1984).

Nutritional implications

Caecotrophy in rabbits does not occur as a response to a nutritional imbalance, but represents a specialized digestive strategy. Caecotrophy in rabbits begins at 3 weeks of age, when rabbits begin to consume solid food. In postweaned rabbits (4 weeks old), soft faeces production linearly increases with age, showing a maximum at 63–77 days old (25 g dry matter (DM) day^{-1}). This period corresponds to the maximum growth requirements and to the greatest increment in feed intake. From 77 to 133 days old (2.5 vs. 3.9 kg, respectively) growth rate decreases, feed intake slightly increases and soft faeces excretion is stabilized (20 g DM day^{-1}) (Gidenne and Lebas, 1987). Similar figures (21.8 g DM day^{-1}) have been reported for adult females during pregnancy. However, lactating does showed greater soft faeces production (34 g DM day^{-1}) related to the higher feed intake (Lorente *et al*., 1988). In these situations caecotrophy represents from 0.09 to 0.15 of total DM intake (feed intake + soft faeces). The importance of caecotrophy also varies with the nutritive characteristics of diet as will be discussed in the following chapters.

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 1.1). Soft faeces contain greater proportions of protein, minerals and vitamins than hard faeces. In contrast with this, hard faeces are enriched 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, either in growing rabbits or lactating does. Protein of soft faeces is high in essential amino acids such as lysine, sulphur amino acids or threonine (Proto, 1976; Spreadbury, 1978; C. de Blas, personal communication) which represents from 0.10 to 0.23 of total intake. 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 0.60 (Spreadbury, 1978; García *et al*., 1995). Microbial activity is also responsible for the high content of K and B vitamins in soft faeces.

Table 1.1. Average chemical composition of caecal contents and soft and hard faeces.

	Caecum	Soft faeces	Hard faeces	Ref.
Dry matter (g kg^{-1})	200	340	470	3,4,5,6,7
Crude protein (g kg^{-1} DM)	280	300	170	3,4,5,6,7
Crude fibre (g kg^{-1} DM)	170	180	300	3,4,5,6,7
MgO (g kg^{-1} DM)		12.8	8.7	2
CaO (g kg^{-1} DM)		13.5	18.0	2
Fe_2O_3 (g kg^{-1} DM)		2.6	2.5	2
Inorganic P (g kg^{-1} DM)		10.4	6.0	2
Organic P (g kg^{-1} DM)		5.0	3.5	2
Cl^- (mmol kg^{-1} DM)		55	33	2
Na^+ (mmol kg^{-1} DM)		105	38	2
K^+ (mmol kg^{-1} DM)		260	84	2
Bacteria (10^{10} g^{-1} DM)		142	31	2
Nicotinic acid (mg kg^{-1})		139	40	1
Riboflavin (mg kg^{-1})		30	9	1
Panthotenic acid (mg kg^{-1})		52	8	1
Cianocobalamine (mg kg^{-1})		3	1	1

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).

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.

Methodological implications of caecotrophy on physiological research work

The marked circadian rhythms of caecotrophy and feed intake imply changes both in the 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 the experimental procedures to obtain reliable digestibility data. The lack of homogeneity in the sampling procedure between different studies leads to difficulties in making comparisons and considerable misunderstanding. The diurnal variations of the main physiological parameters will now be summarized.

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 up to 20% and 30%, respectively, can be observed (Fraga *et al*., 1984; Gidenne and Lebas, 1987).

Differences in the origin of stomach contents are explained by the diurnal changes in 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. Protein content of precaecal digesta is the chemical parameter more affected by sampling time, showing greater values (from 50 to 100%) 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.

Ileal digestibility

The use of cannulated animals to determine ileal digestibility requires the use of markers to estimate the ileal flow of DM and the need to obtain an ileal sample which is representative of that present throughout the day. Merino (1994) observed in cannulated animals a diurnal variation in the crude protein (CP) content of ileal digesta, showing greater values during the soft faeces excretion period than during the hard faeces excretion period (180 vs. 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). These results suggest that it is essential to take samples throughout the day to estimate the average composition of ileal digesta. No diurnal changes were detected in the marker concentration or fibre content of ileal digesta.

Fermentation patterns

The results obtained by Fioramonti and Ruckebusch (1976) and Gidenne and Bellier (1992) in adult animals showed that VFA concentration in caecal contents depends on time of feeding, rising to a maximum 5 h after feeding. In weaned (4 weeks old) or growing rabbits (9 weeks old) 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 were observed during hard faeces excretion. In consequence, it is preferable to take the caecal samples during the hard faeces excretion period.

Transit time

Giving a marker as simple doses is the most frequent procedure used in transit time studies. The question is at what time must the doses 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, in consequence, the opportunity to detect it.

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.

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 (type of marker, time and route of administration of the marker, mathematical calculations, etc.), the animal (age, physiological status, caecotrophy allowed or not), and feeding variables (feed intake, particle size and fibre concentration of the diet). It has been reported

that the marker ytterbium was retained for 3 h longer than chromium (Gidenne and Ruckebush, 1989) and that liquid-phase markers are retained 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 contents from 220 to 400 g kg^{-1} decreased 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).

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