

Feeding behaviour in rabbits

François LEBAS¹ and Thierry GIDENNE²

¹ Cuniculture, 87a Chemin de Lassère, 31450 Corronsac, France (E-mail: lebas@cuniculture.info)

² INRA, Centre de Toulouse, Station de Recherches Cunicoles,
BP 27, 31326 Castanet-Tolosan, France (E-mail: gidenne@toulouse.inra.fr)

Introduction

The rabbit is a monogastric herbivore, belonging to the *Lagomorpha* order (*Leporidae* family: rabbits and hares, Grassé and Dekeuser, 1955). Thus, it is not a rodent although one of its main feeding behaviour features is to gnaw. The information about the feeding behaviour have been mainly obtained on the domestic rabbit, either raised for meat or fur production, or as a laboratory animal. It basically involved rabbits receiving *ad libitum* a balanced complete pelleted feed, supplemented or not with dry forages or straw, but most generally without a real food free choice. One of the most original features of the rabbit feeding behaviour is the caecotrophy, which involved an excretion and an immediate consumption of specific faeces named soft faeces or "caecotrophes". Consequently, daily intake behaviour of the rabbit is constituted of two kinds of meals: feeds and caecotrophes.

We choose first to recall some basis of digestive anatomy and physiology, since it governs the feeding behaviour and allow us a better understanding. Regulation of the intake behaviour will be reviewed according to several factors: age, type of feed, environment etc. The last part will be devoted to feeding behaviour of the wild rabbit and of domestic rabbits in situation of free choice.

1 Anatomy of the alimentary tract, bases of digestive physiology and caecotrophy.

The digestive system of the rabbit is adapted to a herbivorous diet, including specific adaptations, from teeth to an enlarged hindgut for fermentation, and the separation of caecal digesta particles allowing for caecotrophy.

1.1 Anatomy

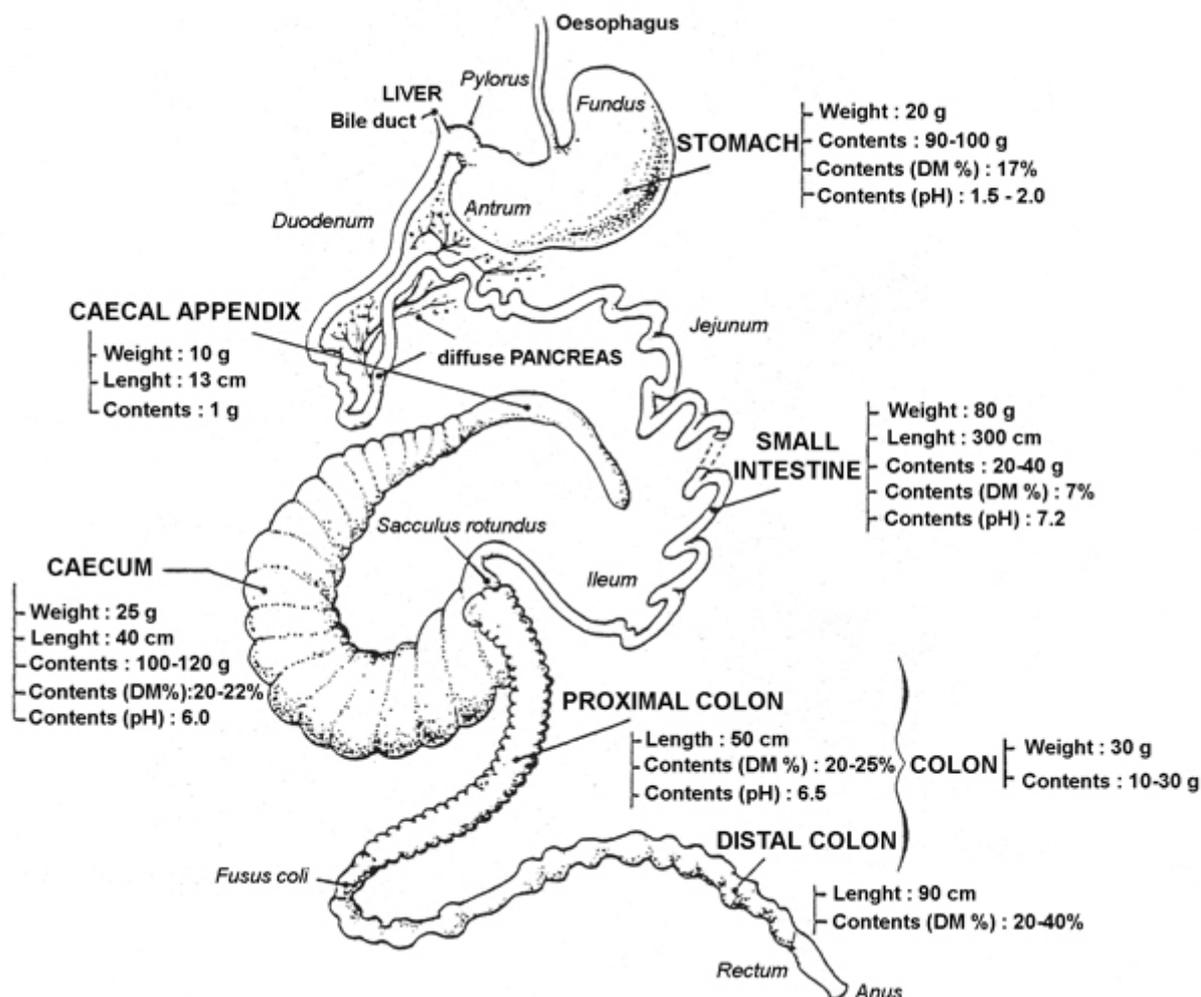
In an adult rabbit (4 to 4.5 kg) or semi-adult (2.5 to 3 kg), the total length of the alimentary tract is 4.5 to 5 m. The general organisation of the digestive tract is presented in the figure 1 together with the main characteristics of each segment.

1.1.1 Mouth and Oesophagus

The rabbit's dental formula is $2/1 \ 0/0 \ 3/2 \ 3/3$. The 28 teeth grow continuously throughout the life (1 to 2.4 mm / week). All teeth of the upper jaw are mainly wore out by those of the lower jaw and vice versa, without any real relationship with feed's hardness. In practice, incisors cut raw feeds and molars shred them coarsely; altogether, mastication efficiency is poor. Mastication is of low importance when a rabbit eats pelleted diets, but more consequent when raw forages are eaten (120 mastication movements per min.). Salivary glands produce saliva with low amylase concentration (10-20 times lower than that of pancreatic juice). Time between feed intake and swallowing is only few seconds.

The oesophagus is short and acts exclusively to transport feed material from mouth to stomach. Regurgitation or vomiting is impossible.

Figure 1: The digestive tract of a rabbit. Numerical values are those observed in a 2.5 kg New Zealand White rabbit, fed *ad-libitum* a pelleted balanced diet (according to Lebas *et al.*, 1997).

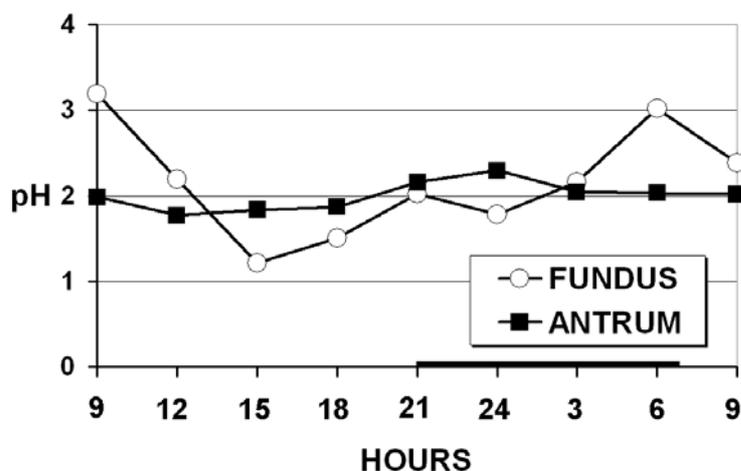


1.1.2 Stomach

After a quick transit through the oesophagus, feeds arrived in the simple stomach, which stores about 90 to 120 g of a rather pasty mixture of feedstuffs. Its dry matter content varies from 16% to 23%.

In the stomach, the blind part (great curve) is named fundus and the opposite part is the antrum, *i.e.* the opening to the small intestine through the pylorus. The latter has a powerful sphincter, which regulates the entrance into the duodenum (first part of the small intestine). During some period of the day, soft faeces (see further chapter) are stored mainly in the fundus while feeds are stored in the pyloric part of the stomach. At some other moments of the day only a homogenous paste can be seen in the stomach, but at no time a liquid phase can be observed. Glands included in the stomach wall secrete hydrochloric acid, pepsin and some minerals (Ca, K, Mg and Na). Stomach pH, always acidic, varies along the day mainly in the fundus (in relation with soft faeces storage) (figure 2), the average pH is 1.5 to 2.0.

Figure 2: Nycthemeral variations of the pH in the 2 mains parts of the stomach in 10 weeks old rabbits (according to Gidenne and Lebas, 1984)



1.1.3 Small intestine

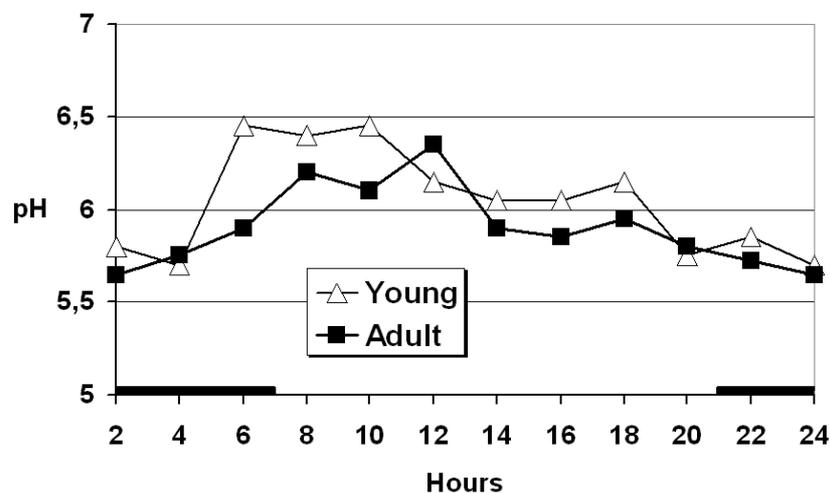
The small intestine is about 3 m long and 0.8 to 1 cm in diameter. It is classically divided in 3 parts: duodenum, jejunum and ileum. The biliary duct opens immediately after pylorus but the pancreatic duct opens 40 cm farther away in duodenum.

The contents are liquid, especially in the upper part (<10% DM). Their pH is slightly basic in the upper part (pH 7.2-7.5) and more acidic in the end of ileum (pH 6.2 - 6.5). Normally there are small segments, about 10 cm long, which are empty. Small intestine end in the caecum basis through the ileo-caecal valve or *sacculus rotundus*, the wall of which being mainly made of lymphoid tissue.

1.1.4 Caecum

This second storage segment contains about 40% of the whole digestive content, and is about 40 to 45 cm long with an average diameter of 3 or 4 cm. It contains 100 to 120 g of a uniform pasty mix, with a dry matter content of about 20-24%. The pH varies around 6.0 but can be only 5.6 during the night and 6.4 in the morning (figure 3).

Figure 3: Nycthemeral variations of pH of the caecal contents, in 6 weeks old and adults rabbits (18 weeks old), according to Bellier *et al.* (1995).



All along the caecum the organ wall enters partially in direction of the caecum lumen according a spiral (22-25 spires) increasing then the possibilities of contact between the inner surface and the caecal contents. The caecal appendix placed at the end of the caecum is 10 to 12 cm long and has a much smaller diameter. Its wall is are composed of lymphoid tissues.

1.1.5 Colon

At the caecum basis begins the colon, 1.5 m long. The first 50 cm are named proximal or haustrated colon (beginning with 3 and ending with 1 haustrations line). They end with the short **fusus coli** (1-2 cm) the only part of the intestine with red muscle. After this zone begins the distal colon, 1.0 m long, ending with the rectum and the anus. The proximal colon has a diameter of about 2-3 cm and the distal one a diameter of 1 cm.

1.1.6 General development of the digestive tract

Digestive tract is relatively more developed in a young than in an adult rabbit. In a breed like the New Zealand White, the most commonly studied rabbit, the definitive dimension of the digestive tract is observed when rabbits are 12-14 weeks old and weight 2.6-2.7 kg alive *i.e.* only 60-70% of the adult weight. In addition, development of the end part of the digestive tract (caecum and colon) is clearly later than that of the upper part (stomach and small intestine).

1.2 Digestive physiology

1.2.1 A classical digestion process in the upper part of the digestive tract

Feed eaten by the rabbit quickly reaches the stomach. There it finds an acid environment and remains in the stomach for a few hours (2 to 4), undergoing little chemical change. Thus the rabbit stomach could be considered as a short-term storage compartment. The contents of the stomach are gradually "injected" into the small intestine in short bursts, by strong stomach contractions. As the contents enter the small intestine they are diluted by the flow of bile, the first intestinal secretions and finally by the pancreatic juice.

After enzymatic action from these last two secretions the feeds elements that can easily be broken down are freed and pass through the intestinal wall to be carried by the blood to the cells after collection by the portal vein system and a passage through liver.

The particles that are not broken down after a total stay of about 1-2 hours in the small intestine enter the caecum. There they stay from 2 to 18 hours (meanly 6-12h), while they are attacked by bacterial enzymes. Thus caecum is the second storage compartment of the digestive tract, but a more long term one. Elements which can be broken down by this new attack (producing mainly volatile fatty acids and ammonia) are freed and most of them pass through the wall of the digestive tract and into the bloodstream or are metabolised by some other bacteria.

The contents of the caecum are then evacuated into the colon. Approximately half consists of both large and small food particles not already broken down, mixed with partially degraded intestinal secretions, while the other half consists of bacteria that have developed in the caecum, fed on matter arriving from the small intestine.

1.2.2 The dual functioning of the colon and the caecotrophy

So far, the functioning of the rabbit's digestive tract is virtually the same as that of other monogastric animals. The uniqueness of rabbit species (and of *Lagomorpha* in general) lies in the dual function of the proximal colon.

If the caecum contents enter the colon in the early part of the morning they undergo few biochemical changes. The colon wall secretes mucus, which gradually envelops the pellets formed by the wall contractions. These pellets gather in elongated clusters and are called soft pellets (more scientifically, caecotrophes).

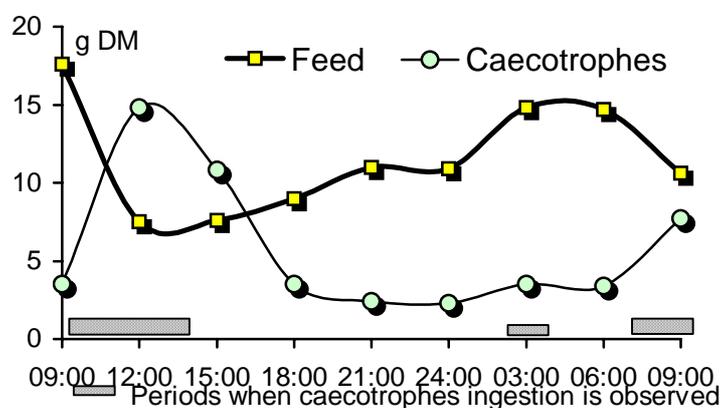
If the caecal contents enter the colon at another time of day the activity of the proximal colon is entirely different. Successive waves of contractions in alternating directions begin to act; the first to evacuate the contents normally and the second to push them back into the caecum. Under the varying pressure and rhythm of these contractions the contents are squeezed like a sponge. Most of the liquid part, containing soluble products and small particles of less than 0.1 mm, accumulates along the colon's wall in the haustrae and is forced back into the caecum (Björnhag, 1972). The solid part, containing mainly large particles over 0.3 mm long, remains in the middle of the colon's lumen and is pushed in direction of the rectum in form of hard pellets. The later are then immediately expelled. In fact, as a result of this dual action, the colon produces two types of excrements: hard and soft. Table 1 shows the chemical composition of these pellets.

Table 1 : Average composition of rabbit's hard and soft pellets (according to Proto, 1980) Means and dispersion correspond to a study with 10 feedstuffs including complete pelleted feeds, green and dry forages.

	Hard pellets		Caecotrophes	
	Average	Extremes	Average	Extremes
• Dry matter (%) as % DM	53.3	48-66	27.1	18-37
• Proteins	13.1	9-25	29.5	21-37
• Crude fiber	37.8	22-54	22.0	14-33
• Lipids	2.6	1.3-5.3	2.4	1.0-4.6
• Minerals	8.9	3-14	10.8	6-18

When produced, hard faeces are rapidly expelled, but soft pellets are temporarily stored in the distal colon. Inside of a stereotyped action of grooming they are recovered by the rabbit directly upon being expelled from the anus in the early morning (Faure, 1963). To do this the rabbit twists itself round, 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 are large numbers of these pellets inside the stomach, where they may represent three quarters of the total contents (Gidenne, 1987a – figure 4). The intriguing presence of these soft pellet in the stomach was at the origin of the

Figure 4 : Daily variation of the stomach content (9weeks old rabbits, daily feed intake =130 g)



first correct description of caecotrophy by Morot in 1882, *i.e.*, production of 2 types of faeces and systematic ingestion of one of the 2 types (the soft ones). This makes caecotrophy

different from the coprophagy classically practiced by rats or pigs, were only one type of faeces is produced and partially eaten.

After a stay in stomach during 4-6 hours (longer than that of normal feed) and breaking up the external aggregative structure, the soft pellets contents follow the same digestive process as normal feed. Considering the fact that some parts of the initial intake may be recycled once, twice and even three or four times, and depending on the type of feed, the rabbit's digestive process lasts from 18 to 30 hours in all, averaging 20 hours.

The soft pellets consist of fewly modified caecal contents, *i.e.* half of imperfectly broken-down food residues + what is left of the intestinal secretions and half of bacteria. The latter contains an appreciable amount of high-value proteins and water-soluble vitamins. The practice of caecotrophy therefore has a real nutritional value. In normally fed rabbits caecotrophy provides 15 to 20% of the total daily nitrogen entering the stomach. It provides also all C and B group vitamins necessary for the rabbit.

The composition of the soft pellets (caecotrophes) is more or less influenced by feed composition (Proto *et al.*, 1968). In the same manner, the dry matter quantity expelled daily may be under dependence of the feed composition. For example the quantity of soft pellets produced daily is positively correlated with the diet's fibre content (Gidenne, 1987b; Pinheiro, 2002). Nevertheless, the soft faeces quantity is generally underestimated because in most studies the estimation is made with rabbits wearing a collar around the neck (to prevent caecotrophes ingestion) a device which is stressful and source of a high variability of results (Carabaño *et al.*, 2000). As a matter of fact, Gidenne (1987a) with a technique based on feed markers, estimates the dry matter (DM) quantity daily recycled in form of soft pellets as 26% of the feed DM intake, when in other studies done in similar conditions but with collars the proportion is 12% to 16% only.

The higher the crude fibre content of the feed and/or the coarser the particles, the faster it passes through the digestive tract. From the feeding behaviour point of view, this acceleration of the speed of digestive transit with the increase of fibrous materials in the diet, makes possible a higher daily ingestion of forages than that of concentrates.

On the other hand, this particular functioning requires roughage. If the feed contains few large particles and/or it is highly digestible, most of the caecal contents are pushed back to the caecum and lose elements which nourish the "normal" bacteria living in the caecum. This would appear to increase the risk of undesirable bacteria developing in this unbalanced environment (very few available carbohydrates but rich in nitrogenous compounds). Some of these unexpected bacteria might be harmful. It is thus advisable to include a minimum of roughage in the feed providing enough undigested raw particles in the colon during hard faeces production and then enabling the rabbit's digestive process to be completed fairly rapidly.

Regulation of caecotrophy is under dependence of flora integrity and of feed intake rhythm. The soft pellets ingestion is observed 8-12 hours after the distribution of feed in case of feed restriction or after the main period of ingestion in rabbits fed *ad libitum* (Laplace, 1978). For the latter, the ingestion rhythm is under direct influence of lighting and as a consequence the caecotrophy rhythm too. The caecotrophy regulation is also under internal regulation since, for example, ablation of adrenals suppress the dual functioning of the colon and injections of cortisol in adenalectomized rabbits restore it. Finally, the caecotrophy compartment appears in the young (domestic or wild) with the first significant intake of solid food, *i.e.* between 22 and 26 days (Orengo and Gidenne, 2005).

2 Feeding behaviour in the domestic rabbit

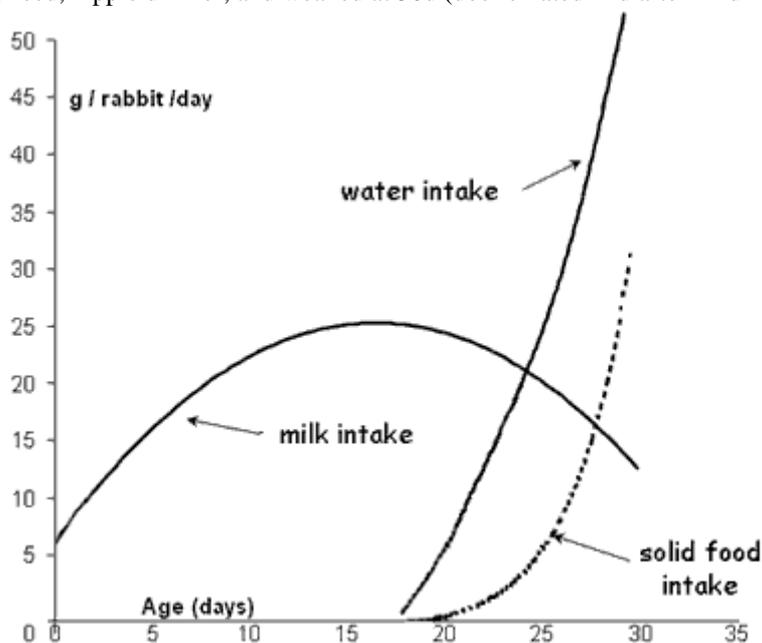
2.1 From birth to weaning

The feeding pattern of the newborn rabbits is imposed by the dam. A doe in fact feeds her young only once every 24 hours (Cross, 1952; Zarrow *et al.*, 1965). However, recent studies suggested that some does (10-15%) would nurse their young twice a day (more frequently in the second week of lactation: mean number of nursings = 1.3 per 24h - Hoy and Selzer, 2002). Suckling lasts only 2-3 minutes for a litter of 8 to 11 kits. The first suckling (colostrum) normally occurred during the parturition for the first kits born, and within the first hour after birth for the others. This first milk intake is essential to ensure the kits survival (Coureaud *et al.* 2000). The newborn rabbits does not appropriate one nipple (contrary to piglet), but is able to pass from one to another nipple frequently even within one suckling (Hudson *et al.*, 2000). Five to six days old kits can drink up to 25% of their live-weight in milk in one nursing session. The nipple searching behaviour is very stereotyped and controlled by a pheromonal signal (Schaal *et al.*, 2003).

If there is not enough milk the young try to feed every time the doe enters the nest box, but she will hold back her milk. On the contrary if for example 2 suckling does are proposed daily (one every 12 hours) the young are able to suckle twice, leading to a higher growth rate (Gyarmati *et al.*, 2000).

During the first post-natal week of life (between 4 and 6 days of age) the young also consumes hard faeces deposited by the doe in the nest, thus stimulating the caecal flora maturation (Kovacs *et al.*, 2004).

Figure 5 : Milk, water and dry feed intake of the young rabbit (adapted from Szendrő *et al.*, 1999; and Fortun-Lamothe & Gidenne, 2000) Mean values, for a kit in a litters of 7-9 , with pelleted dry feed, nipple drinker, and weaned at 30d (doe remated 11d after kindling).



From one to three weeks of age, the young increases its milk intake from 10 to 30g of milk/day (or suckling) (figure 5), and then the does milk production is decreasing (more sharply if pregnant). A young rabbit, reared in a litter of 7-9 kits, therefore consumes about 360 to 450g of milk between birth and 25d old (vs 100 to 150g from 26 to 32d). Individual milk intake pattern are relatively variable and dependant partly of the live-weight of the kit (Fortun-Lamothe and Gidenne, 2000). The dry feed intake begins significantly when the

young is able to move easily to access a feeder (with pelleted feed) and a drinker, *i.e.* around 17-20 days old (figure 5). Then, the daily food intake increases 25 fold from 20 till 35 days of age (Gidenne and Fortun-Lamothe, 2002). However, large variations among litters have been observed for the time of the beginning of the dry feed intake. For example, an increase in the competition for milk, dependant of the litter size, stimulates the dry feed intake of the young (Fortun-Lamothe and Gidenne, 2000). Reversely, offering a second milking to the young (using a second doe) delayed the dry feed intake (Gyarmati *et al.*, 2000). Besides, the young rabbits prefer to eat at the mother feeder rather to a young specific feeder (Fortun-Lamothe and Gidenne, 2003), probably by imitation of the feeding behaviour of their mother.

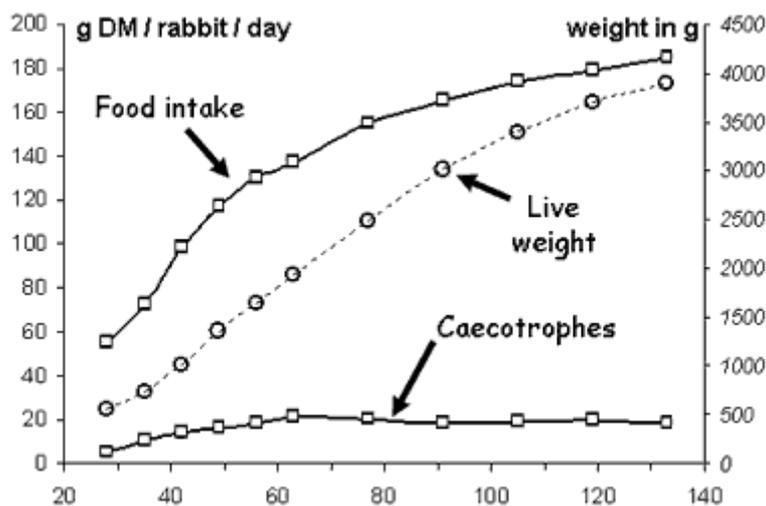
Age at weaning is obviously an efficient factor to modulate the dry feed intake. For instance, in wild condition the young rabbit could be weaned at about 3½ weeks of age, when the doe is pregnant and preparing a new nest for her next litter, and thus is forced to consume rapidly dry food.

The 25-30 days of age period is particular, since the intake of solid feed and water will exceed the milk intake. During this period the changes in feeding behaviour are remarkable: the young rabbit goes from a single milk meal per day to a large number of more or less alternating solid and liquid meals distributed irregularly throughout the day (25 to 30 meals/24h). Additionally, as previously mentioned, the caecotrophy behaviour starts at about 22 to 26 days of age, when a significant dry feed intake occurs that leads to a caecal and a colon filling and to the dual motility pattern of the proximal colon. Until weaning kits have 4 types of intake : milk, solid food, caecotrophes and water. However, the individual feeding behaviour of the young remained largely unknown (regulation factors, number of meals, etc...), since no method is presently available to assess the intake level of young reared collectively (till weaning).

2.2 Feeding behaviour of the growing and adult rabbit.

From weaning (classically between 4 and 5 weeks old) the daily feed intake of the domestic rabbit (fed a complete pelleted feed) increases correlatively to the metabolic live-weight (figure 6) and levelled up at about 4-5 months of age. Taking as a reference animal an adult fed

Figure 6: Dry matter intake from pelleted feed, caecotrophes, and live-weight from weaning (28d) till adulthood. Data from domestic rabbit, fed *ad-lib.* a pelleted feed (Gidenne and Lebas, 1987), data of caecotrophes excretion obtained on rabbits wearing a collar.



ad libitum (140-150 g DM/day, for example, for a 4 kg New Zealand White): at 4 weeks a young rabbit eats a quarter of the amount an adult eats, but its liveweight is only 14% of the adult's one. At 8 weeks the relative proportions are 62 and 42%; at 16 weeks they are 100 to

110 and 87%. Between the weaning (4-5 weeks) and 8 weeks of age, the weight gain reached its highest level (table 2) while the feed conversion is the most efficient. Then, the feed intake increases less rapidly than the growth speed, and is maximum at around 12-14 weeks of age for current commercial so called hybrid lines of domestic rabbit. It is a little bit lower after this age and then stable in the adult.

Table 2 : Feeding behaviour of the domestic rabbit after weaning . Average feed intake and growth rate of rabbits (current commercial lines), fed ad-libitum a pelleted diet (89% DM), and having free access to drinkable water.

	Periods of age (weeks)	
	5-7 weeks	7-10 weeks
Solid feed (pellets, 89% DM)		
Solid feed intake (g/d)	100-120	140-170
Weight gain (g/d)	45-50	35-45
Feed conversion ratio	2.2-2.4	3.4-3.8

A rabbit regulates its feed intake according to energy need, as for other mammals. Chemostatic mechanisms are involved, by means of the nervous system and blood levels of compounds used in energy metabolism. However, in monogastric animals the glycemia plays a key role in food intake regulation, while in ruminants the levels of volatile fatty acids in blood have a major role. Since rabbit is a monogastric herbivore, it is not clear which is the main blood component regulating feed intake, but it is likely to be the blood glucose level. Voluntary intake, proportional to metabolic live-weight ($LW^{0.75}$), is about 900-1000 kJ DE/d/kg $LW^{0.75}$ (DE: digestible energy), and the chemostatic regulation appears only with a dietary DE concentration higher than 9-9.5 MJ/kg (Parigi-Bini and Xiccato, 1998). Below this level, a physical-type regulation is prevalent and linked to gut fill.

The intake of soft faeces increases only till 2 months of age and then remained steady (figure 6). Expressed as fresh matter, the soft faeces intake evolved from 10 g/day (1 month old) to 55 g/day (2 months), thus representing 15 to 35% of the feed intake (Gidenne and Lebas, 1987).

The rabbit fractionates its voluntary solid intake in numerous meals: about 40 at 6 weeks of age, and a slightly lower number at adulthood (table 3). This meal fractionation is probably linked to the relatively weak storage capacity of the stomach (cf. section 1.1.2), particularly when compared to ruminants or even carnivorous or omnivorous ones (such dog or pig).

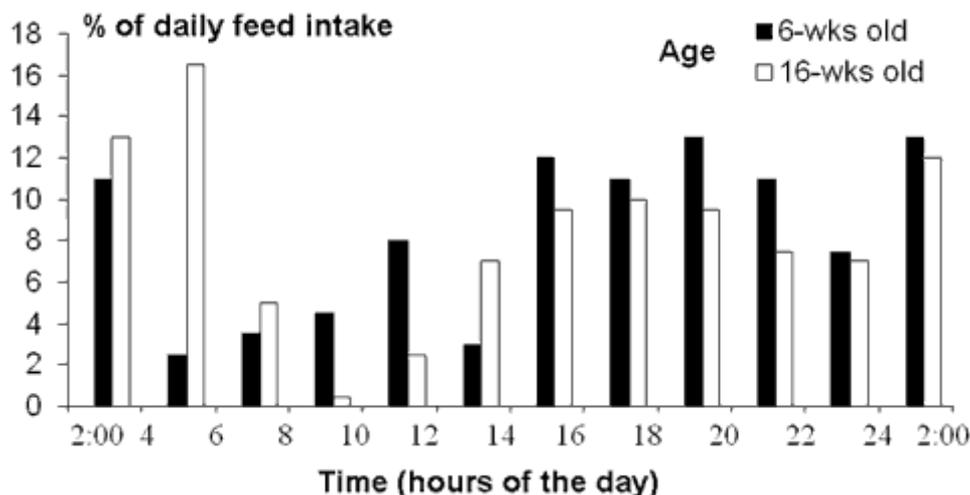
Table 3 : Feeding and drinking behaviour of the domestic rabbit from 6 to 18 weeks old. Mean values from 9 New Zealand White rabbits, fed ad-libitum a pelleted diet (89% DM), and having a free access to drinkable water (Prud'hon *et al.*, 1975).

Age in weeks	6	12	18
Solid feed (pellets, 89% DM)			
- Solid feed intake (g/d)	98	194	160
- No. of meals per day	39	40	34
- Average quantity per meal (g)	2.6	4.9	4.9
Drinking water			
- Water intake (g/d)	153	320	297
- No. of drinks per day	31	29	36
- Average weight of 1 drink (g)	5.1	11.5	9.1
Water to feed ratio	1.56	1.65	1.86

For 6 weeks old rabbits, fed with a pelleted diet, the time spent on feeding every 24 hours exceed slightly 3 hours. Then, it drops rapidly to less than 2 hours. If a ground non pelleted diet is proposed to rabbits, the time spent to eat is doubled (Lebas, 1973). The number of liquid meals evolved in parallel to that of feed, and the time spent to drink is lower than that spent to eat. Furthermore, at any age, feed containing over 70% water, such as green forage, will provide rabbits with sufficient water at temperatures under 20°C and in this case rabbits may not drink at all. In growing rabbit fed with pellets, the normal ratio between water and dry matter is about 1.6-1.8. In the adult or the breeding doe it is increased up to 2.0-2.1.

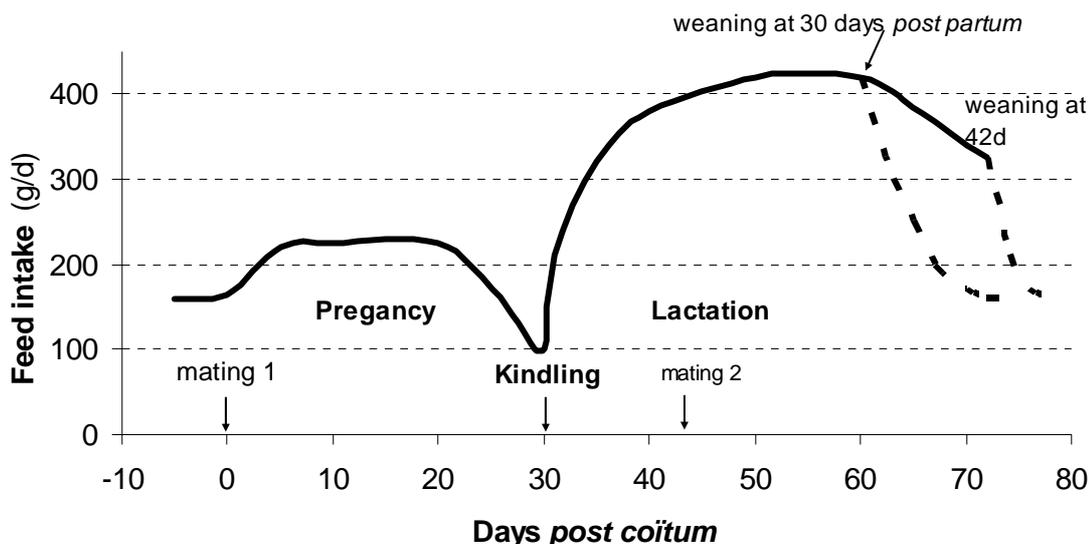
The hourly solid intake varies over a 24 hour period, as shown in Figure 7. Over 60% of the solid feed (excluding soft faeces meals) is consumed in the dark period for a domestic rabbit submitted to a 12L/12D light schedule. The nycthemeral changes of liquid meals is strictly parallel to that of solid meals for the domestic rabbit fed pellets (Prudh'on *et al.*, 1975), but no correlation can be established between time or intervals of solid and water meals. With ageing, 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 is no longer without eating, since it has more than 20 meals of dry feed a day, and it also has meals of caecotrophes (early morning). Moreover, Hirakawa (2001) pointed out that leporids (including rabbits) also consumed a part of their own hard faeces that are masticated contrary to soft faeces that are swallowed. Meals of soft faeces (and sometime hard) increase in proportion when food availability is insufficient for rabbits.

Figure 7: Circadian pattern of feed intake in growing or adult rabbit. Mean values of 2 hours feed intake for domestic rabbits (n=6) fed *ad-libitum* a pelleted feed (daily feed intake = 80 and 189 g/d respectively for 6 and 16 wks old) and raised under a 7:00-19:00 light schedule (Bellier *et al.*, 1995).



Obviously, the feed intake level is modulated by the physiological status of the animal. For instance, a doe's voluntary intake varies greatly during the reproduction cycle (Figure 8). The intake during the final days of pregnancy drops off markedly. Some does refuse solid food just before kindling. Water intake, however, never stops completely. After kindling, the feed intake increases very rapidly and can exceed 100 g dry matter/kg liveweight a day. Water intake is also increased at that time: up to 200-250 g a day per kg of liveweight. When a doe is both pregnant and lactating, she eats amounts similar to that observed for a doe that is only lactating.

Figure 8 : Average daily feed intake of a rabbit doe during gestation and lactation . Data from Lebas (1975), domestic rabbit fed a balanced pelleted feed (89% DM)



3 External factors modulating the feeding behaviour of the domestic rabbit

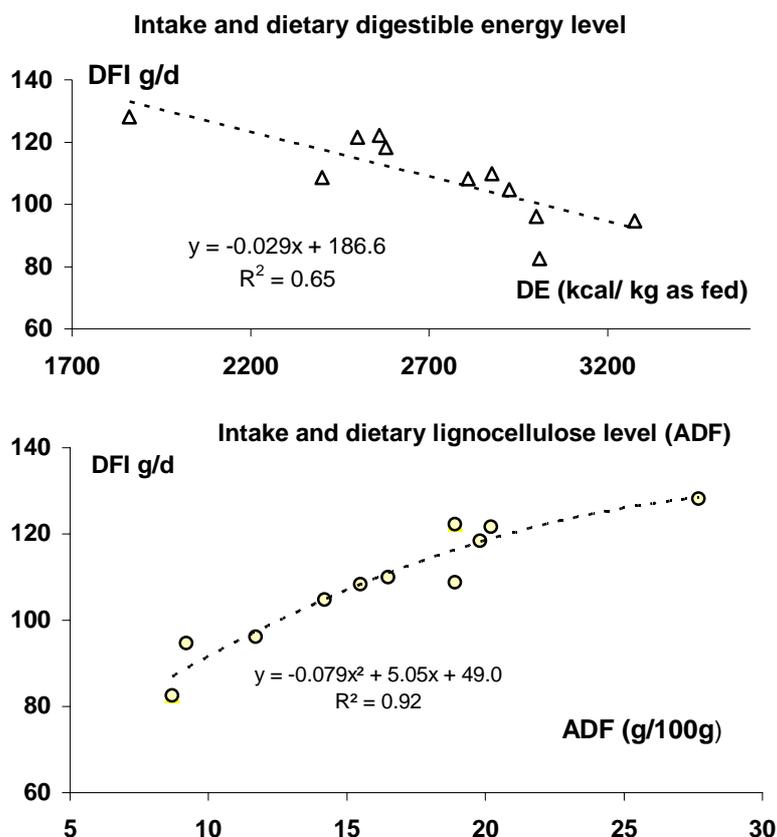
3.1 Feed composition and presentation form

One of the main dietary components implicated in feed intake regulation, after weaning, is the digestible energy (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 9 and 12 MJ/kg, or when the dietary fibre level is between 10 and 25% ADF (Acid Detergent Fibre). The intake level is thus well correlated with the dietary fibre level, compared to the dietary DE content (figure 9). However, the incorporation of fat in the diets, while maintaining the dietary fibre level, increases the dietary DE level, but leads to a slight reduction of the intake. Reversely, before weaning, the young seemed not to regulate its feed intake according to the DE level (Gidenne and Fortun-Lamothe, 2002), since litters consumed preferentially a diet with a higher DE content.

Other nutrients in the diets are able to modify the food intake, such protein and aminoacids (Tomé, 2004). For example, an excess in methionine reduced by at least 10% the feed intake of the growing rabbit (Colin *et al.*, 1973; Gidenne *et al.*, 2002)

The diet presentation is an important factor modulating the 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 seemed to disturb the circadian cycle of feed intake (Lebas and Laplace, 1977). Pellet size and quality (hardness, durability) are also able to affect the feeding behaviour (Maertens and Villamide, 1998). A reduction in pellet diameter, that also increases the hardness, reduces the feed intake of the young (Gidenne *et al.*, 2003) or of growing rabbit (Maertens, 1994) and although time budget for feeding was increased.

Figure 9: Feed intake in weaned domestic rabbit, in relation with diet's digestible energy and ADF content.



3.2 Environmental factors affecting the feeding behaviour of the rabbit

The rabbit's energy expenditure depends on ambient temperature. Feed intake to cope with energy needs is therefore linked to temperature. Studies on growing rabbits showed that at temperatures between 5°C and 30°C intake of pelleted feed dropped from 180 to 120 g/day and water intake rose from 330 to 390 g/day (Table 4). A closer analysis of feeding behaviour

Table 4 :Feeding behaviour of growing rabbits according to ambient temperatures. Data from Eberhart (1980)

Ambient temperature	5°C	18°C	30°C
Relative humidity	80%	70%	60%
Pelleted feed eaten (g/day)	182	158	123
Water drunk(g/day)	328	271	386
Water/feed ratio	1.80	1.71	3.14
Average weight gain (g/day)	35.1	37.4	25.4

shows that as temperature rises the number of solid meals eaten in 24 hours drops. From 37 solid feeds at 10°C the number drops to only 27 at 30°C (young New Zealand White rabbits). The amount eaten at each meal drops with high temperatures (5.7 g/meal from 10°C to 20°C down to 4.4 g at 30°C) but the water intake goes up, from 11.4 to 16.2 g/meal between 10°C and 30°C.

The feeding and drinking behaviour were also studied for the doe and their litters according to the climatic conditions, as reviewed by Cervera and Fernandez-Carmona (1998).

If drinking water is not provided and if the only feed available is dry with a moisture content of less than 14%, dry matter intake drops to nil within 24 hours. 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, though its weight may drop 20-30% in less than a week (Cizek, 1961) Rabbits with access to drinking water but no solid feed can survive for 3 to 4 weeks. Within a few days they will drink 4-6 times as much water as normal. Sodium chloride in the water (0.45%) reduces this high intake, but potassium chloride has no effect (sodium loss through urination). The rabbit is therefore very resistant to hunger and relatively resistant to thirst; but any reduction in the water supply, in terms of water requirements, causes a proportional reduction in dry matter intake, with a consequent drop in performance.

Other environmental factors have also been studied in the domestic, such the light schedule or the housing systems. In absence of light (24h/24 dark), the apparent feed intake of fattening rabbits is increased when compared to rabbits submitted to a 8h/24 or 16h/24 light program, but feed efficiency was decreased (Lebas, 1977). In these conditions of absence of light, rabbits organised their feeding pattern in a regular 23.5-23.8 hours program, with about 5-6 hours devoted to soft faeces ingestion and the remaining part of the cycle to feed intake. In continuous lighting, the feeding pattern is organized in an about 25 hours program. (Jilge, 1982; Reyne and Goussopoulos, 1984). For breeding does, reduction of the total lighting duration to only 4 hours during a 24 hours cycle by introduction 2 folds a 4 hours period of dark during the normal 12h of lighting in a 12L/12D program (intermittent lighting) does not modify the average daily feed intake despite an increase of the milk production leading to a better feed efficiency for milk production (Virag *et al.*, 2000).

As previously mentioned, type of caging also influences the daily feed intake and the feeding pattern of rabbits. For instance, the feed intake is affected by the density of rabbits in the cage. Increasing the density above the classical 16-18 rabbits / m², which seems to lead to a higher competition for feeders among the animals, leads to a reduction of feed intake (Aubret and Duperray, 1993). But 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 to cage housing of groups of 4 rabbits, pen housing of groups of 30 rabbits (same density of 15.5 /m²), allows more movements to the rabbits and reduces the daily feed intake (Maertens et Van Herck, 2000). Nevertheless, at the same density, rabbits caged by 2 or by 6 have the same daily feed intake, but in cages of 2, rabbits spent a lower proportion of their time budget for feed consumption: 5.8% vs 9.9% of the 10 hours of the lighting period during which they were observed (Mirabito *et al.*, 1999). Finally according to the feeding pattern, the number of places at feeder (1 to 6) for a group of 10 rabbits does not influence the individual daily feed intake of *ad libitum* fed rabbits (Lebas, 1975). Nevertheless, the feeder's length become of some importance when rabbits are submitted to feed restriction (Rashwan and Soad, 1996).

4 Feeding behaviour in situation of choice

All studies at basis of the above explained results were conducted with domestic rabbits, generally fed with complete and more or less balanced diets. In the wild or in situation of free choice for caged rabbits, an other dimension must be added to the feeding behaviour: how rabbits select the feeds?

4.1 Feeding behaviour of wild rabbits in open situation (grazing rabbits)

First of all the feed resources available for wild rabbits are most generally constituted by a great range of plant material. Rabbit clearly prefer graminaceous plants (*Festuca* sp.,

Brachypodium sp. or *Digitaria* sp.) and graze only few dicotyledons if sufficient grasses are available (Williams *et al.*, 1974). Within the dicotyledons rabbits graze specially some leguminous plants and some compositae. But it could be underlined that grazing pressure on carrots (*Daucus carotta*) is very light, this plant being out of those preferred by rabbits (CTGREF, 1978).

Proportion of dicotyledonous species and even mouses may increase during some seasons depending on the availability of plants (Bhadresa, 1977). In winter time and early spring, grazing of cultivated cereals by rabbits may completely compromise the crop, specially up to a distance of 30-100 m of the warren (Biadi and Guenezan, 1992). When rabbits can choice between winter cereals cultivated with or without mineral fertilisation (phosphorus and/or nitrogen) they clearly prefer the cereals without artificial fertilisation (Spence and Smith, 1965).

Grazing rabbits may be very selective and for example choice one part of the plant or the type of plant with the highest nitrogen concentration (Seidenstrücker, 2000). Similarly, wild rabbits have grazed more intensively one variety of spring barley than 4 others in a test performed in Ireland, probably in relation with plant's composition. But differences in sugar content of varieties did not fully explain this varietal selection by grazing rabbits (Bell and Watson, 1993).

The great winter appetite of rabbits for buds and young stems of some woody plants must be underlined. Grazing of very young trees or of shoots may completely compromise regeneration of some forests (CTGREF, 1980), or more specifically the regeneration of different shrubs like juniper (RSPB, 2004) or common broom (Sabourdy, 1971). In winter time rabbits like to eat bark of some cultivated trees (not only young stems), specially that of apple trees and in some extent that of cherry and peach trees. Barks of pear, plum or apricot trees are generally less attacked (CTGREF, 1980). In forests, rabbits clearly prefer broad-leaved trees but may also attack bark of conifers (mainly spruce and some types of pines), but on the contrary when very young trees are available rabbits prefer to eat apical or lateral sprouts of spruces or firs instead of that of oaks (CTGREF, 1978).

So basic reasons of the choices remain unclear, even if they are constant. It could only be said that it is under regulation of hypothalamus since hypothalamic lesions modify clearly the choice pattern of rabbits (Balinska, 1966). Modified feeding pattern is also observed in vagotomized rabbits (Sanderson *et al.*, 1975).

Many experiments were conducted specially in Australia and New Zealand to study the wild rabbits compartment when different more or less manufactured baits are proposed (the final objective being the eradication of imported wild rabbits). Many variations were observed depending on the type of bait, but also of season. For example pollard+bran pellets (5/1 in weight) are well consumed throughout the year. In contrast, the acceptability of carrots or oats varies seasonally. Addition of salt (1% or 5% NaCl) or of lucerne meal (15%) to the pollard+bran pellets significantly reduces the baits consumption (Ross and Bell, 1979).

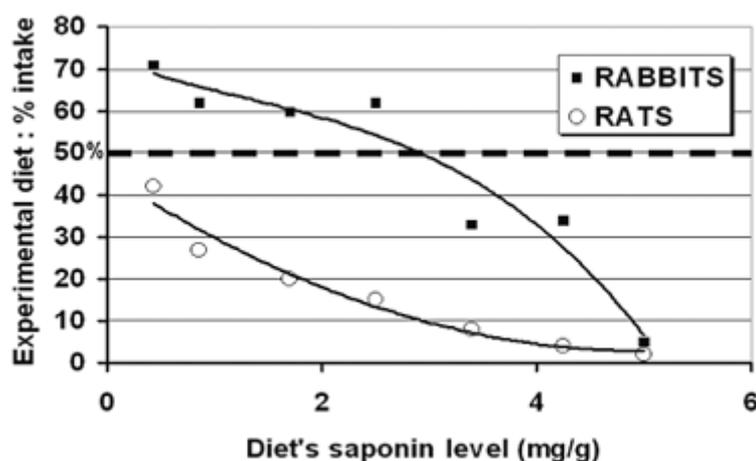
4.2 Free choice for domestic caged rabbit

When a choice is proposed between a control diet and the same diet + an appetiser, rabbits generally prefer the diet with the appetiser. But when the same 2 diets are offered alone to rabbits, the daily feed intake is exactly the same and the growth performance too (Fekete and Lebas, 1983). It means that the pleasant smell of the proposed food is not essential for the feed intake regulation. This was also proved with a repellent diet (addition of formalin)

clearly rejected in the free choice test but consumed in the same quantity in the long term single food test (Lebas, 1992).

In the same way Cheeke *et al.* (1977) have demonstrated that rabbits like a certain bitterness of their feed. For example they prefer alfalfa with saponin, a bitter component, up to 3 mg/g of the diet, whereas rats always prefer the control diet without saponin in the range of 0.4 to 5 mg/g (figure 10). But when single feeds with different levels of saponin are offered to rabbits (saponin from 1.8 to 6.4 mg/g of complete diet), the feed intake and growth rate are independent of the saponin level (Auxilia *et al.*, 1983)

Figure 10 : Relative feed intake of a lucerne based diet with various levels of saponin in rats and rabbits in situation of free choice between this diet and a control diet without saponin (according to Cheeke *et al.*, 1977)



On the contrary, when a toxic is present such as aflatoxins, rabbits refuse completely to consume the diet or consume it in very low quantities (Morand-Fehr *et al.*, 1968; Morisse *et al.*, 1981; Saubois and Nepote, 1994). This regulation may be considered as pertinent to protect the animal against food injuries.

When a concentrate (low fibre diet compound diet) and a fibrous material are proposed as free choice to rabbits, they prefer the concentrate. The fibrous material is consumed in only small quantities and the growth rate may be reduced (Lebas *et al.*, 1997). The consequence is also an immediate increase of the sanitary risk for rabbits with digestive disorders by lack of fibre (Gidenne, 2003). This is the consequence of the specific search of rabbit for energetic sources (scarce in the wild), the dominant regulation system of feed intake in rabbits.

Effectively when 2 energetic concentrates are proposed with free choice as it was done by Gidenne (1985) with a complete diet and fresh green bananas, the growth rate is equivalent to that of the control and the digestible energy daily intake identical. Nevertheless it must be underlined that in this study the proportion of bananas in the dry matter intake decreased from 40% at weaning (5 weeks) to 28% at the end of the experiment 7 weeks later.

In an other way, 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, prefer clearly the solution with the missing amino acid (Lebas and Greppi, 1980)

To add a last constituent to this chapter on free choice, it could be reminded that in free choice situation, a simple variation of humidity of one component may change the equilibrium in the rabbit's choice. For example when dehydrated lucerne and normally dried maize grains (11% DM) are offered *ad libitum* to rabbit the result of the choice is 65% lucerne/35% maize. But if the dry matter content of the maize grains is increased up to 14-15%, the proportion of maize

becomes 45-50% (Lebas, 2002). In this case the choice reason of rabbits seems motivated more by the immediate palatability of the feeds than by their nutritive value.

As it was described above regulation of intake in free choice situation is delicate to predict. Thus in most practical situations of rabbit production the utilisation of a complete balanced diet is advisable.

5. Conclusion

The rabbit feeding behaviour is very particular compared to other mammals, with special features, such the caecotrophy, associated to a particular digestive physiology, intermediate between the monogastric and the herbivore. As herbivorous, the feeding strategy of the rabbit is almost opposite to that of ruminants. The feeding strategy of the latter consists to retain the food particles in the rumen till they reach a sufficiently low size. Thus for ruminants, diet's bulkiness is of great importance in the feed intake regulation. The rabbit has adopted a reverse strategy characterised by a preferential retention of fine digesta particles in the fermentative segment (caecum and proximal colon), with a quick removal of the coarse particles (such low digested fibres) in hard faeces. This is associated to numerous meals distributed during most of the 24h cycle, thus favouring a quick digesta rate of passage, the digestion of the most digestible fibre fractions and a possibility for feed intake to increase with fibre concentration in feedstuffs.

Therefore, the rabbit is adapted to various feeding environments, from desert to temperate or even cold climates, and is able to consume with benefit a very wide variety of feeds, from seeds to herbaceous plants.

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