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 Lagomorph order (Leporidae family: rabbits and hares; Grassé and Dekeuser, 1955) and, consequently, expresses one main specificity: 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. Caecotrophy behaviour starts around 21–25 days of age, when a significant solid feed intake occurs, leading to both caecal and colon filling (Gidenne *et al.*, 2002a; Orengo and Gidenne, 2007) and to an increased microbiota activity. Hard faecal pellets are excreted (and rejected), but soft faecal pellets are totally 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 in the fundus, where they may comprise three-quarters of the total stomachal contents. Presence of soft faecal pellets in the stomach was first correctly described by Morot (1882) who identified 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 and partially consumed.

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 single milky meal a day (until 14 days old), to several solid meals a day.

Milk intake

Initial nursing occurs during parturition. The mother induces suckling 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.

After birth, the doe generally visits the nest to suckle her young only once a day (1.12 per 24 h: Hoy and Selzer, 2002) and for a short time (3–5 min: Zarrow *et al.*, 1965; González-Mariscal, 2007). However, some does (wild or domestic) nurse their young twice a day (Hoy and Selzer, 2002). 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 offers few nutritional benefits: the weight of kits at 21 days increased only by 5% (Echegaray-Torres *et al.*, 2004) and was not influenced by suckling frequency (Tudela and Balmisse, 2003). Under conventional 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: 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). But does from breeds or lines selected for prolificacy may have up to 12 nipples (Fleischhauer *et al.*, 1985; De Rochambeau *et al.*, 1988; Szendrö *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 (Kovács *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 decreases 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

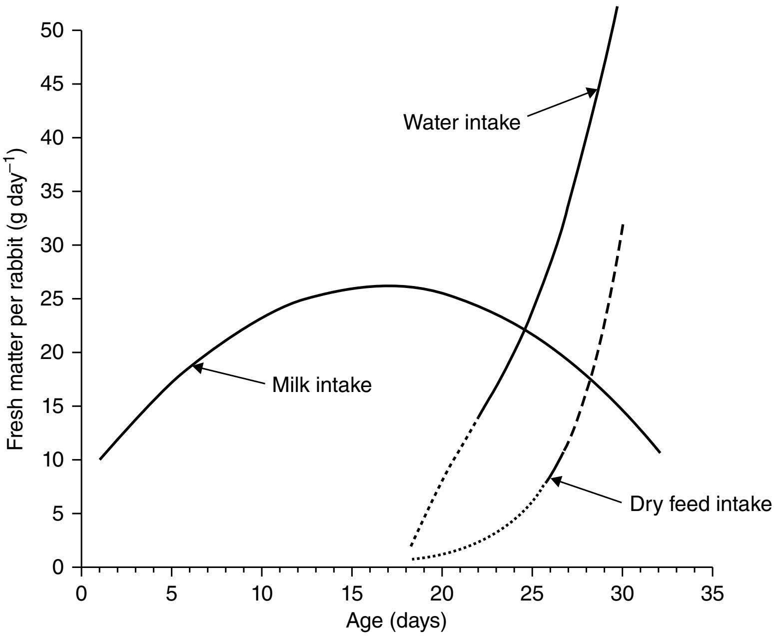

Fig. 13.1. Milk, water and dry feed intake of the young rabbit before weaning in a conventional farming system. Values are means for litters of seven to nine kits reared in a conventional system (pelleted feed, nipple drinking, weaning at 30 days, does mated 11 days after kindling). (Adapted from Szendrö *et al*., 1999; Fortun-Lamothe and Gidenne, 2000.)

age. In commercial systems, weaning is generally carried out between 28 and 35 days of age, even if milk production has not completely stopped.

At nursing, maternal faecal excretion in the nest has been observed, and coprophagous behaviour of the pups has been described and partly quantified (Kovács *et al*., 2006; Moncomble *et al*., 2004). This faecal excretion in the nest is highly variable among the does (Gidenne *et al*., 2013) and with time: maximal between 2 and 9 days of lactation (1–3 faeces day^{-1}), then decreased and disappeared after 14 days of lactation. The consumption of maternal faeces by the pups began at 9 days old (1 faeces per litter day^{-1}), then increased from 9 to 14 days (1.5 faeces per litter day^{-1}). This coprophagic behaviour could be prolonged (till 21 days) and amplified if 'foreign' faeces are supplied in the nest (3 faeces per litter day^{-1}) corresponding to a total 3–4 g of fresh matter consumed per kit. Ingestion of these faeces is involved in caecal microbiota implantation (Combes *et al*., 2014), since the impairment of coprophagy delayed the caecal bacterial community implantation and enhanced mortality in the pups.

It seems also possible to stimulate the solid intake of the kits as early as 8 days of age by supplying specific creep feed in the nest: 1.6 g DM per kit from 8 to 17 days old (Paës *et al*., 2018). An earlier caecal microbiota implantation is expected by such creep feeding, and thus an enhancement of the kit health status. Similarly, the onset of solid pelleted feed intake (out of the nest) before weaning induces a sharp change of caecal microbial community structure and decreased phylogenetic diversity (Read *et al*., 2019).

Solid food intake and evolution of nutrient and energy supply

Young rabbits begin to eat significant quantities of solid food offered outside the nest at around 16–18 days of age, when they are able to leave the nest and move easily to access a feeder (with pelleted feed) and drinker.

Initially, the young eat very small quantities of pelleted feed (<2 g day^{-1} per rabbit before 20 days of age), increasing 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.

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), suggesting 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 intake changes sharply 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, while lipids come mainly from milk until weaning. Carbohydrates intake is almost null (<0.3 g day^{-1}) until 17 days of age, and 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. The availability of milk is a key regulating factor of solid feed intake 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 feed ingestion is delayed

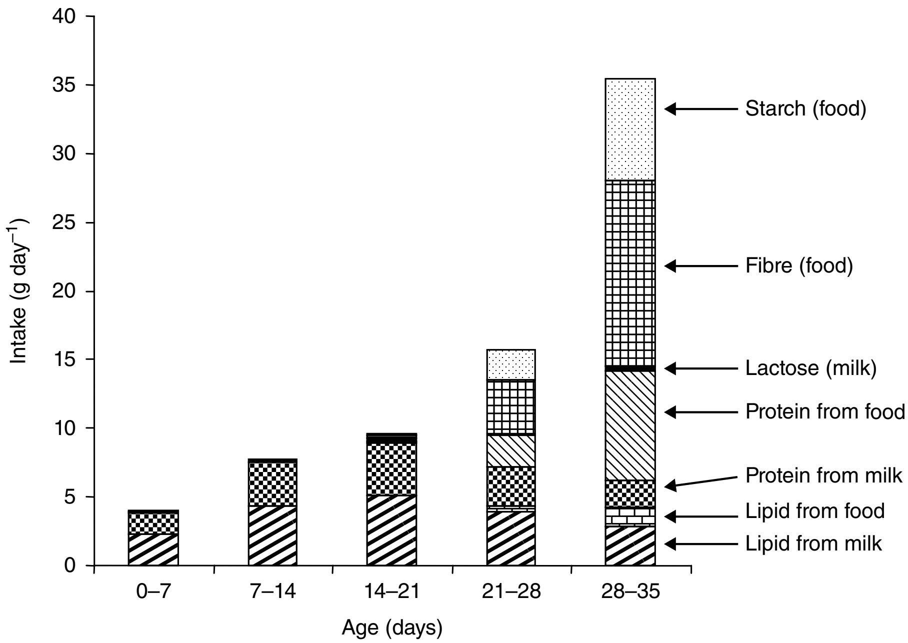

Fig. 13.2. Changes in nutrient intake of young rabbits between birth (day 0) and weaning (day 35) in conventional farming system.

by 2–4 days (Fortun-Lamothe and Gidenne, 2000) and the litter intake 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 solid feed intake (Gallois *et al*., 2005; Xiccato *et al*., 2005).

The influence of pelleted feed nutritional composition on feeding behaviour before weaning is poorly understood, since the results on the control of intake before weaning through the nutrient or energy supply are not consistent, and because the intake variability among littermates is very high (up to 45%). 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 as 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. The individual feeding behaviour of kits (e.g. regulation factors, number of meals) remains largely unknown, and methods are needed to bring further knowledge on this question.

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. The relative proportions of feed intake vs LW in young rabbits compared to New Zealand White adult animals fed *ad libitum* a pelleted feed (140–150 g dry matter DM day^{-1}, 4 kg) is (i) 0.25 for feed intake against only 0.14 for LW at 4 weeks; (ii) 0.62 and 0.42 at 8 weeks; and (iii) 1.00–1.10 and 0.87 at 16 weeks, 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

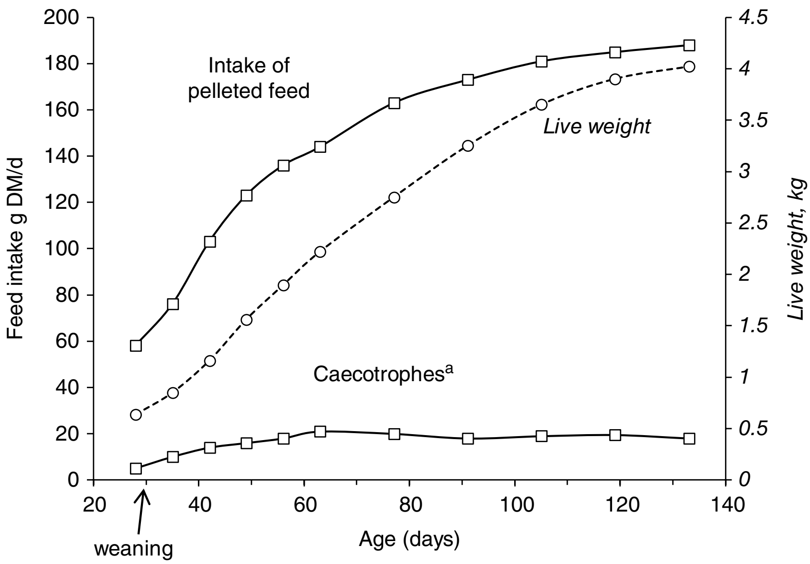

Fig. 13.3. Intake from feed and caecotrophes, and rabbit growth from weaning (28 days) until adulthood. Data are from the domestic rabbit, fed *ad libitum* a pelleted feed (Gidenne and Lebas, 1987). [a]Data on caecotrophe excretion were obtained from rabbits wearing a collar.

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}) *ad libitum* and with free access to drinkable water.

	Age (weeks)	
	5–7	7–10
Solid feed intake (g day^{-1})	100–120	140–170
Weight gain (g day^{-1})	45–50	35–45
Feed conversion	2.2–2.4	3.4–3.8

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 (890 g dry matter kg^{-1}) *ad libitum* and with free access to drinkable water (Prud'hon *et al.*, 1975b).

	Age in weeks		
	6	12	18
Solid feed (pellets, 890 g dry matter kg^{-1})			
Solid feed intake (g day^{-1})	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 day^{-1})	153	320	297
No. of drinks per day	31	28.5	36
Average weight of one drink (g)	5.1	11.5	9.1

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 (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. Belenguer *et al.* (2008) developed methods based on microbial marker analysis that are less intrusive for the animal but much more complex to manage.

If fed freely, 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.

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. According to Horton *et al.* (1974) and Jolivet *et al.* (1983), intake is usually spread over two main periods: (i) one at the end of the dark interval (or early in the day); and

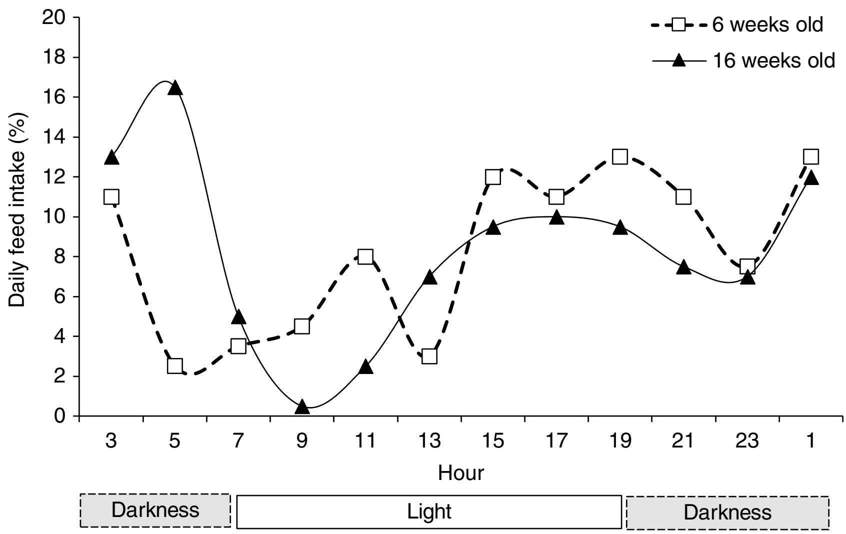

Fig. 13.4. Circadian pattern of feed intake in the growing or adult rabbit. Mean values for domestic rabbits (n = 6) fed a pelleted feed *ad libitum* (daily feed intake of 80 and 189 g day^{-1}, respectively, for 6- and 16-week-old rabbits) and bred under a 7:00–19:00 light schedule (Bellier *et al.*, 1995).

(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 consumes caecotrophes (early in the light period). Besides, Hirakawa (2001) reported that leporids (including rabbits) might 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 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

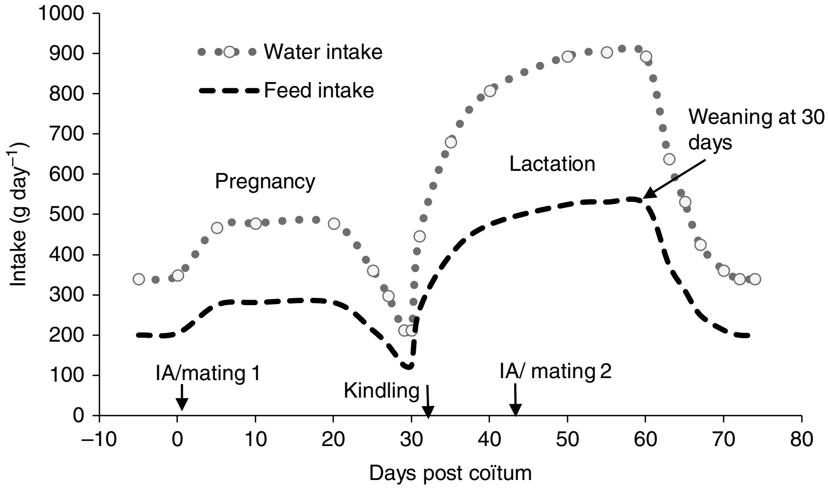

Fig. 13.5. Intake behaviour of a reproducing female during gestation and lactation. Data for rabbit female (hybrid genotype) in conventional farming system (IA, artificial insemination; 11 days after kindling; pelleted diets and nipple drinking).

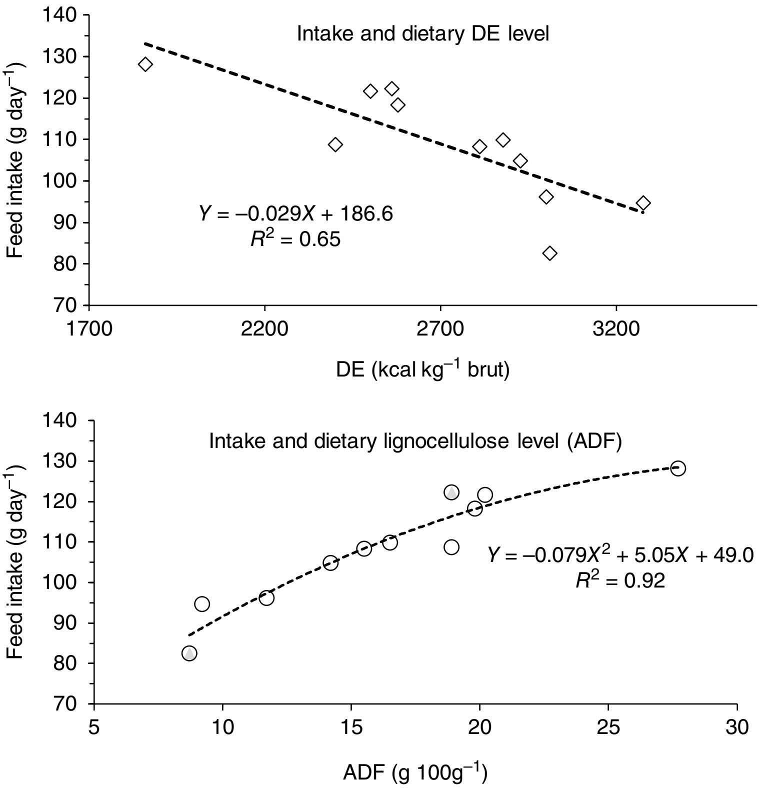

Fig. 13.6. Feed intake prediction for the growing rabbit, after weaning (between 4 and 11 weeks of age) in conventional farming system (pelleted feed). ADF, acid detergent fibre; DE, digestible energy (Gidenne, 2000).

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.

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).

Table 13.3. Feeding behaviour of the growing rabbit according to ambient temperature (data from Eberhart, 1980).

	Ambient temperature		
	5°C	18°C	30°C
Relative humidity (%)	80	70	60
Pelleted feed eaten (g day^{-1})	182	158	123
Water intake (g day^{-1})	328	271	386
Water to feed ratio	1.80	1.71	3.14
Average weight gain (g day^{-1})	35. 1	37.4	25.4

With only 6 h of hot temperatures (29–32°C) within each day, the feed intake increased by 11% for 7-week-old fatteners (Selim *et al*., 2004). 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 performance. 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).

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; Reyne 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 housing 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 could increase the competition for feeders among the animals and reduce feed intake (Aubret and Duperray, 1993).

When comparing cage with 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 vs 0.099 for a 10-h light period: 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 and pelleted 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 wild rabbit is classed as a folivore (i.e. a leaf eater) and its feed resources invariably include a wide range of plant material. Rabbits try to optimize the digestibility and protein content of the green forage by selecting leaves and shoots of ground vegetation (Rodel, 2005). Larger (older) shoots and stems with a higher content of low-digested fibre (lignocellulose) are discarded if the animals have a choice. It has been shown that the protein content of the selected forage (which is highest in spring with about 19–20% protein) is about three times greater than the total protein content of harvested food plants (Rogers *et al.*, 1994). The domestic rabbit also prefers plant material with a high proportion of leaves and with higher protein content. For instance, in organic rabbit farming, when the herbage allowance is high (spring), the fresh intake of grass could double for a legume compared with a graminaceous pasture (Legendre *et al.*, 2019). A legume pasture (e.g. sainfoin) grazed without grain complement could lead to a growth of about 25 g day^{-1} (compared to 15 g day^{-1} for grass), sufficient to meet a final LW of 2.8 kg at 100 days old (Roinsard *et al.*, 2017). The intake of fresh grass can be very high when pasture is appetent. For instance, on a sainfoin pasture the intake averages 300 g day^{-1} (Martin *et al.*, 2016; Legendre *et al.*, 2019), but can reach 700 g for an 8-week-old rabbit (2 kg LW). On a dry matter basis, the herbage intake averages 60 g DM kg^{-1} metabolic weight as observed for other species (sheep or cow). Recently, a mathematical model was developed to simulate the herbage intake and predict the rabbit growth at pasture (Joly *et al.*, 2018) according to climatic conditions and grass availability.

In the wild, rabbits prefer graminaceous plants (*Festuca*, *Brachypodium* or *Digitaria* species) and graze 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, suggesting 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 (Cooke, 2014) since they are competing with domestic ruminant for pasture, and 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 appetizer, 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.

When growing rabbits were offered fresh green bananas and a pelleted diet in complement (free choice), the DE intake was similar as well as the growth rate compared to rabbits fed only the pelleted diet (Gidenne, 1986), suggesting a good adjustment of the DE intake. 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 sulfur amino acids) and drinking water with or without the missing amino acid in solution clearly prefer the

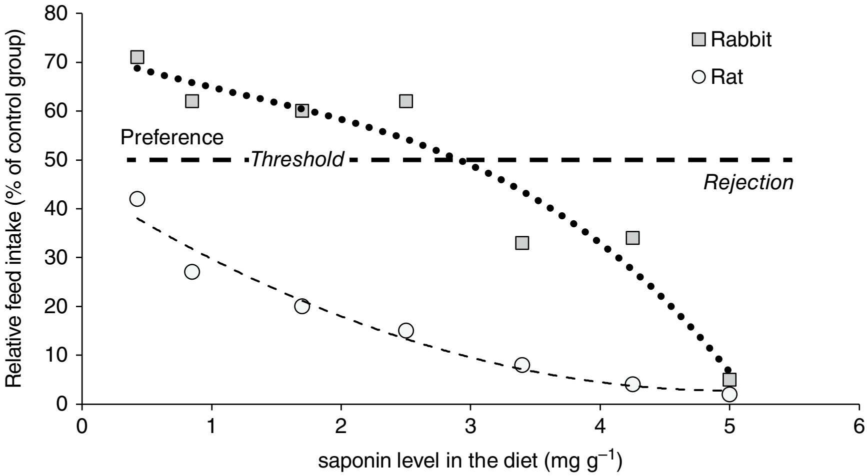

Fig. 13.7. Relative feed intake of a lucerne-based diet with various levels of saponin in rats and rabbits in a situation of free choice between this diet and a control diet without saponin (Cheeke *et al.*, 1977).

solution with the missing amino acid (Lebas and Greppi, 1980).

Finally, 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 time necessary to consume the whole meal is dependent of the quantity distributed. For instance, an adult rabbit consumes an 80% (versus free intake) daily allocation within 10 h. For growing 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 identical 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 significantly 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 different studies conducted (Fig. 13.8). For example, feed restriction to 8 h day^{-1} was associated, 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 feeders (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 quantitative 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 regularly 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 consume 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 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 *ad libitum* (Szendrö *et al*., 1988).

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 *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}.

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 libitum* 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 as caecotrophy associated with a particular digestive physiology,

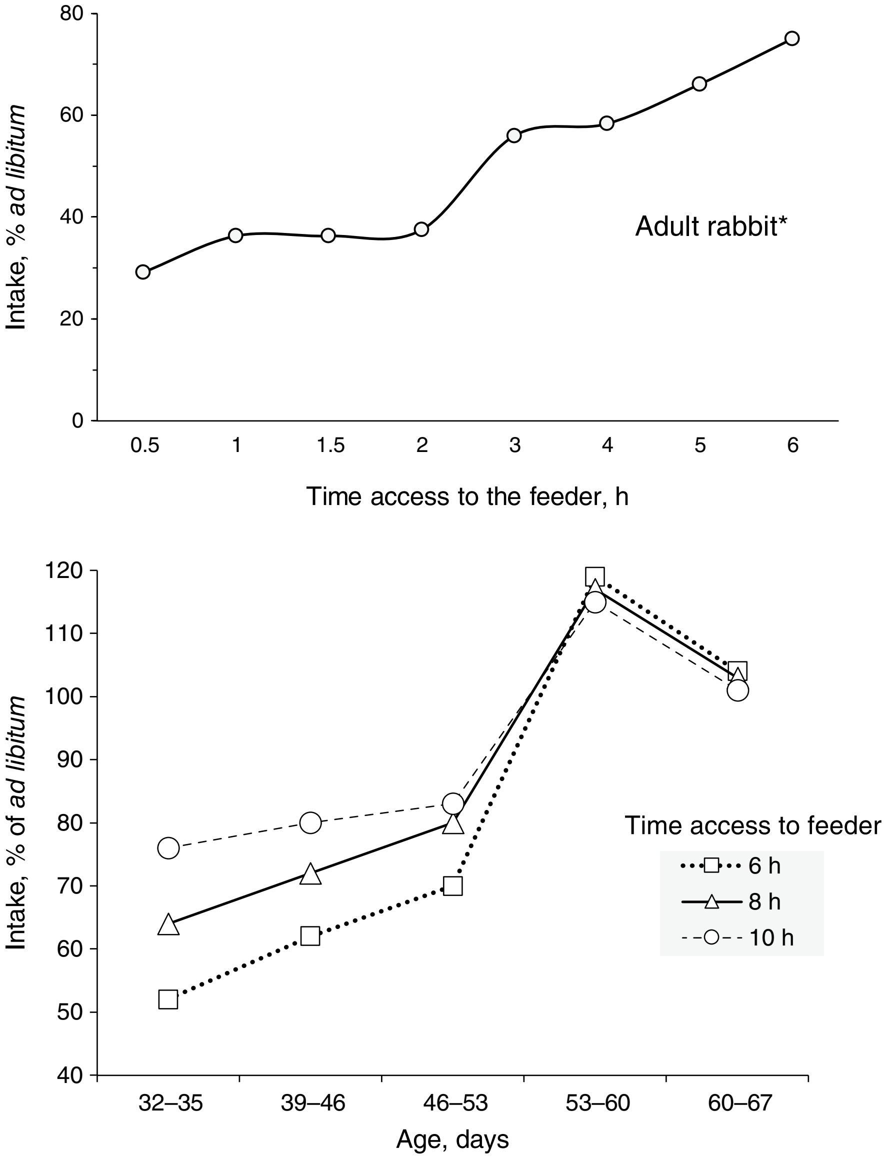

Fig. 13.8. Pelleted feed intake according to duration of access to the feeder in adult or growing rabbit. Adult rabbit (3.5 kg LW) adapted for 7 days to the restricted access to feeder (Tag El Den *et al*., 1988). Growing rabbit (hybrid line) housed collectively and restricted from weaning (32 days) to 53 days old (Foubert *et al*., 2007).

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 of 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

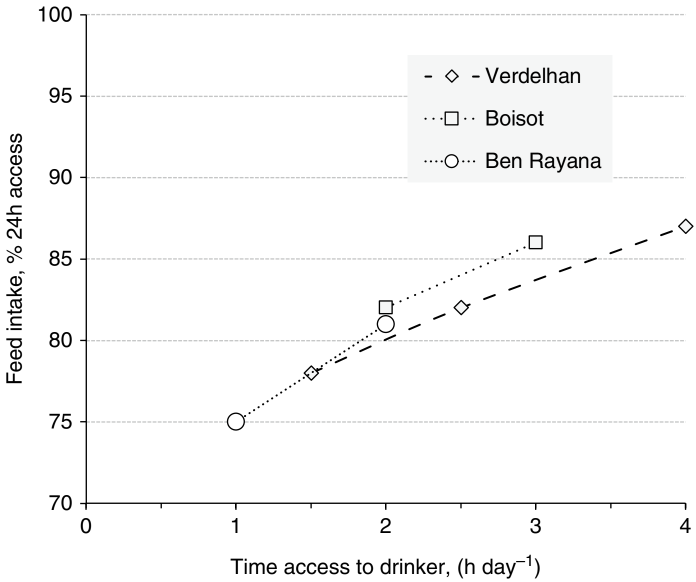

Fig. 13.9. Feed intake according to the duration of access to the drinker in the growing rabbit (hybrid line) housed collectively, from weaning (5 weeks) to 9 weeks old. Results are expressed as percentage of the control rabbits, watered and fed *ad libitum* a pelleted diet. (Data from Boisot *et al*., 2004; Verdelhan *et al*., 2004; Ben Rayana *et al*., 2008.)

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.

Feeding and watering conditions	*Ad libitum* control	Water available for 1 h day^{-1}	Quantitative feed restriction (theoretical 0.65)
Feed intake	136 g day^{-1} = 1.00	0.78	0.66
Water intake	228 g day^{-1} = 1.00	0.56	1.36
Water to feed ratio	1.7	1.2	3.5

meals, thus favouring a quick digesta rate of passage and digestion of the most digestible fibre fractions, and finally, at pasture the relative grass intake capacity is similar in rabbits and ruminants.

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.

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