

## Coprophagy in leporids and other mammalian herbivores

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### ABSTRACT

Leporids have long been known to reingest soft faeces. However, it was recently found that they regularly reingest hard faeces, too. During the daytime, both soft and hard faeces are defecated and all of the faeces are reingested. Excreted at night are the hard faeces, which are normally discarded but reingested in starvation. The separation mechanism in the proximal colon, which diverts fine particles into the caecum and thus only passes large food particles, produces hard faeces. When the mechanism ceases acting, fermented caecal materials are excreted as soft faeces. The reingestion of soft faeces, rich in vitamins and microbial proteins, is physiologically imperative. Hard faeces are basically a refuse, but their thorough mastication at reingestion reduces poorly digestible large particles to fine ones good for fermentation. The regular reingestion of daytime hard faeces thus promotes food digestibility. The temporary use of night-time hard faeces allows leporids to do without food for some time. It thus gives leporids behavioural flexibility and thereby an ecological advantage. Reingestion is also known in other small- to medium-sized herbivores, which are all caecal fermenters. Morphological differentiation between faeces is reported only in larger species, but all ingested faeces are found to be richer in nutrients than discarded ones. Thus a separation mechanism is probably present in all reingesting species. Reingestion activity is deeply related to other behavioural and physiological traits of small mammalian herbivores, hence its study is important to understanding of their ecology and biology. Leporids are the largest of the reingesting species except for the semi-aquatic Coypu, and reingestion by leporids is certainly the most sophisticated. This development of a reingestion-involved digestive system has probably brought them to their present niche, as terrestrial medium-sized generalist mammalian herbivores, and consequently made their characteristic hide-and-run lifeforms by exposing them to a strong predation pressure.

*Keywords:* coprophagy, reingestion, leporid, herbivore

### INTRODUCTION

The term ‘coprophagy’ literally means faeces-eating, where ‘faeces’ could conceivably be of various kinds: faeces of other species or of the conspecifics; those of other individuals (allopiphagy) or its own (autocoprophagy); those once deposited or taken directly from the anus. This review focuses on the last type of coprophagy, characteristic of small- to medium-sized herbivorous mammals: the ingestion of their own faeces taken directly from the anus. This coprophagy has been called ‘refection’ by some authors, but I will use the plain descriptive term ‘reingestion’ following Watson (1954). Reingestion is not merely a recycling of undigested materials, but has a specific digestive function.

A good and well-known example is caecotrophy (reingestion of soft faeces or caecotrophs) by leporids. Leporids produce two types of faeces (soft and hard faeces). Soft faeces originate from the fermented materials in the caecum, rich in vitamins and microbial proteins. All soft faeces are ingested at excretion directly from the anus, hence not normally exposed to

our observation. The reingested soft faeces are digested in the stomach and small intestine (Cork, 1994). If prevented from reingesting soft faeces, the Domestic Rabbit (*Oryctolagus cuniculus*) on a normal diet develops malnutrition (Morot, 1882; Olsen & Madsen, 1944). Ingestion of soft faeces is thus an indispensable part of the digestion process.

Besides leporids, the habit of reingestion is reported from pikas, a primate, a marsupial and many rodent species. Although in most of these species reingested faeces are morphologically indistinct, they are reported to be richer in nutrient content than discarded faeces. This indicates that the reingestion in these species also has a specific digestive function.

Recently, I found a new aspect of coprophagy in leporids: regular reingestion of hard faeces, which is the type commonly observed being deposited in the field. This finding led me to this review, which has three purposes. One is to give the latest, and possibly most comprehensive, picture of reingestion in leporids, integrating recent findings with many past studies and clarifying the ecological significance of hard faeces reingestion. Some confusion and misunderstandings in past studies and the current literature are also addressed. The second purpose is to summarize available information on reingestion in other small mammalian herbivores and to show the importance of studying reingestion to understanding their biology and ecology. The third is to consider the development of the reingestion habit in herbivores and its implications for evolution in leporids.

## **COPROPHAGY IN LEPORIDS**

### **Discovery of the reingestion habit in leporids**

The fact that leporids reingest their own faeces first became widely accepted thanks to the rediscovery and confirmation of Morot's (1882) study by Madsen (1939) and Taylor (1939). They showed that the Domestic Rabbit produces hard and soft types of faeces and reingests all soft faeces without mastication by taking them directly from the anus. The soft faeces, which in effect had not been known until that time, were subsequently suggested as being derived from caecal contents because of the similarity in nutrient composition (Eden, 1940b; Kulwich, Struglia & Pearson, 1953; Huang, Ulrich & McCay, 1954; Thacker & Brandt, 1955). Later, soft faeces were found in the stomachs or colons of many other wild leporid species (five *Lepus* and three *Sylvilagus* species, *Oryctolagus cuniculus* and *Pentalagus furnessi*) (Southern, 1940; Watson & Taylor, 1955; Hamilton, 1955; Spencer, 1955; Geis, 1957; Lechleitner, 1957; Layne, 1958; Bookhout, 1959; Hewson, 1962; Saitoh, 1978; T. Sakoh, personal communication) and reingestion behaviour was directly observed (Kirkpatrick, 1956). As a result, it became understood that caecotrophy (reingestion of soft faeces) was a normal physiological digestive process widely practised in leporids.

### **Mechanism that separately produces soft and hard faeces**

The mechanism that separately produces hard and soft faeces was studied in the Domestic Rabbit in the 1970s and 1980s. The presence of the separation mechanism at the proximal colon was first suggested by Björnhag (1972) and Pickard & Stevens (1972). Later, the details of the movements of the digestive tract and the digesta were studied by Ruckebusch & Hörnicke (1977), Björnhag (1981a), Ehrlein, Reich & Schwinger (1983), and Hörnicke *et al.* (1984). The techniques used in these studies were all different and the relationships between the details of their results are not necessarily clear. However, their results can be summed up as follows (see also Björnhag, 1994):

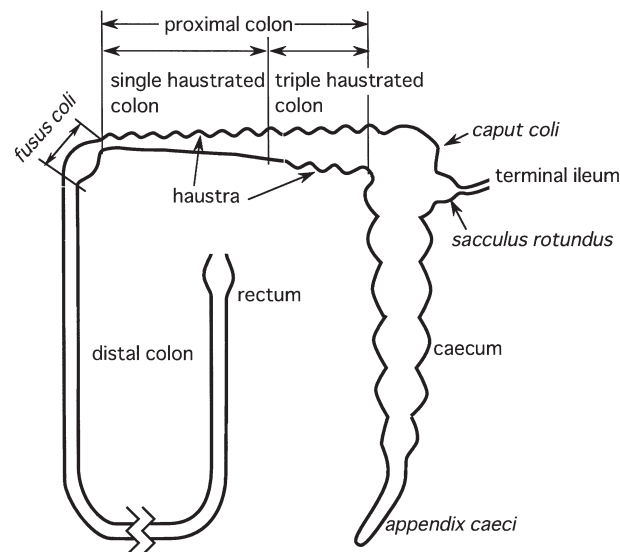
The digesta sent from the ileum to the caecum are driven back and forth in the caecum by peristalsis (once or twice per minute when forming hard faeces; the rhythm is halved when

forming soft faeces). Now and then, a large peristaltic movement sends a portion of the digesta to the proximal colon (Pickard & Stevens, 1972; Hörnicke *et al.*, 1984).

When forming hard faeces, the antiperistaltic movement of the haustra (a wall structure: three haustreae at the oral part, and a single haustra at the aboral part of the proximal colon: Fig. 1) is activated and diverts the fluid and fine food particles ( $< 100 \mu\text{m}$ ) of digesta back to the caecum (Björnhag, 1972, 1981a; Ruckebusch & Hörnicke, 1977; Ehrlein *et al.*, 1983). As a result, large particles ( $> 100 \mu\text{m}$ ) are accumulated in the digesta, which are formed into hard faeces around the fusus coli (Björnhag, 1972; Ehrlein *et al.*, 1983). Hard faeces are thus dry and composed mostly of poorly digestible large food particles.

When forming soft faeces, the movement of the haustreae is reduced and irregular mass peristaltic movement sends the digesta largely onward, where it is then formed into soft faeces around the fusus coli (Ruckebusch & Hörnicke, 1977; Ehrlein *et al.*, 1983). Soft faeces thus originate from the materials retained and fermented in the caecum while the separation mechanism is activated. The passage time from the aboral part of the proximal colon to the anus is slightly more than 2 hours irrespective of the faeces types (Leng, Clauss & Hörnicke, 1977).

The flow of digesta from the stomach to the ileum is continued throughout the day (Bouyssou, Kandau & Ruckebusch, 1986). Hence, the digesta is continuously provided from the ileum to the caecum when forming soft faeces as well as hard faeces. Thus, soft and hard faeces are produced entirely by the alternation of the separation mechanism at the proximal colon. The separation is a mechanical process depending on the size of food particles, and its basic function is to excrete poorly digestible large particles quickly in hard faeces but reflux and thus retain fine food particles and micro-organisms in the caecum for fermentation (Björnhag, 1994). Despite these studies, the naive misinterpretation that the difference of two types of faeces is due to the food having passed once or twice, as initially speculated by Madsen (1939), is still retained in some current literature (e.g. Gibb & Williams, 1990).



**Fig. 1.** Schematic view of the digestive tract in leporids from the end of the ileum to the rectum. (from Fig. 1 in H. Hirakawa (1995b) by permission of the Mammalogical Society of Japan.)

### Two types of soft faeces

Two distinctive types of soft faeces are observed among leporids: a spherical type coated with a tough mucous membrane (I will refer to this as a capsule type) and an amorphous type without such a surface membrane. The capsule type is common in *Oryctolagus*, *Sylvilagus* and *Pentalagus* (Watson, 1954; Meyers, 1955; Hamilton, 1955; Geis, 1957; Dexter, 1959; Heisinger, 1962; T. Sakoh, personal communication), and the amorphous type common in *Lepus* (Watson & Taylor, 1955; Lechleitner, 1957; Hewson, 1962; Flux, 1970; Pehrson, 1983; Hirakawa, 1994). However, the capsule type is sometimes found in *Lepus* (Lechleitner, 1957; Bookhout, 1959; Hewson, 1962; Saitoh, 1978) and the amorphous type in *Oryctolagus* and *Sylvilagus* (Taylor, 1940a; Watson, 1954; Spencer, 1955; Heisinger, 1962).

The surface membrane of rabbit soft faeces is formed at the latter part of the distal colon (Hirabayashi, 1961; Griffiths & Davies, 1963; Inaba, Suzuki & Hirabayashi, 1968). Composed of a vitamin B<sub>12</sub>-mucoprotein complex, the membrane is so tough that you can peel it off with forceps (Hirabayashi, 1961) and soft faeces that swell in water burst if punctured with a needle (Griffiths & Davies, 1963). Ingested without mastication, faeces of the capsule type stay intact in the stomach for several hours, during which microorganisms inside the faeces are actively decomposing carbohydrates and producing lactic acid (Griffiths & Davies, 1963). The acidity in the Domestic Rabbit stomach is known to be exceptionally high (pH 1.9) compared to that of other mammals (pH 4.3–6.0) (Cheeke, 1987). Hence, the tough mucous membrane of rabbit soft faeces plays a significant role in ensuring the microbial activity inside faeces continues even in the highly acidic environment of the stomach.

The amorphous soft faeces common to *Lepus* are also reingested without mastication, although sometimes brief mumbling jaw movements are observed (Hirakawa, 1994, 1997). However, because of their amorphous nature, they are mixed with other materials, hence hardly distinguishable in the stomach (Hewson, 1962; Hirakawa, 1995a). This implies that there is a large difference in the physiological function between the amorphous and capsule types of soft faeces. The acidity level of the *Lepus* stomach might be different from that of the Domestic Rabbit. Leporids are taxonomically divided into two large groups: *Lepus* vs. 10 other genera (Chapman & Flux, 1990) and it is interesting to note that the types of soft faeces correspond to these taxonomic groups.

### Rhythm of soft faeces reingestion in wild leporids

Most species of leporids are nocturnal: they actively forage during the night and rest during the day (Chapman & Flux, 1990). The reingestion rhythm in wild leporid species has been studied in almost all cases by the presence of soft faeces in the rectum and the stomach of carcasses killed at a known time of the day (Southern, 1942; Watson, 1954; Meyers, 1955; Watson & Taylor, 1955; Lechleitner, 1957; Toll, Baskett & Conaway, 1960; Heisinger, 1962; Hewson, 1962; Flux, 1970; Bothma, Steyn & Teer, 1982). Obviously, what these studies revealed was the rhythm of soft faeces reingestion, not the general rhythm of reingestion both for hard and soft faeces.

Considering the duration that the capsule-type soft faeces remain intact in the stomach, we can infer that caecotrophy occurs once a day from morning to early or mid-afternoon in every species studied (four *Lepus* and two *Sylvilagus* species, and *Oryctolagus cuniculus*), although it is known that a small portion of *Oryctolagus* populations practises caecotrophy in the middle of the night (Southern, 1942; Watson, 1954; Meyers, 1955). Heisinger (1965) showed that the rhythm of feeding and reingestion activities in the captive Eastern Cottontail (*Sylvilagus floridanus*) is regulated by photoperiod.

### Hard faeces reingestion and its rhythm

Although reingestion of hard faeces has been casually observed (Eden, 1940b; Southern, 1942; Hörnicke & Björnhag, 1980; Hirakawa, 1983), it had not been believed that they were normally reingested until their frequent reingestion was first reported in the Domestic Rabbit by Ebino, Shutoh & Takahashi (1993). Later, the regular reingestion of hard faeces was observed in the Japanese Hare (*Lepus brachyurus*) and the Mountain Hare (*L. timidus*) (Hirakawa, 1994, 1997).

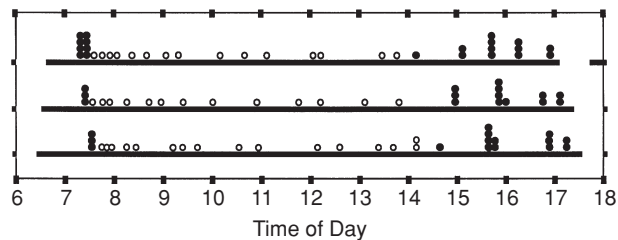
Hard faeces are well masticated at reingestion whereas soft faeces are not (mumbling jaw movements are sometimes observed after soft faeces reingestion, which Pehrson (1983) referred to as 'chewing' (Pehrson, personal communication), but these gentle and rather horizontal jaw movements are clearly different from the firm, rhythmical and vertical jaw movements observed after hard faeces reingestion, which I refer to as 'mastication'). Also, hard faeces are taken from the anus several times in succession, each followed by mastication, whereas soft faeces are taken in one batch (Fig. 2) (Hirakawa, 1994, 1997).

In the Japanese and the Mountain Hare, hard faeces are ingested for the first hour of resting in the morning, then soft faeces until the early afternoon, and then again hard faeces until dusk when hares leave the form to start night-time activity (Fig. 2) (Hirakawa, 1994, 1997). While feeding at night, the Japanese Hare excreted hard faeces, all of which were discarded; but if food is not available, hard faeces were reingested instead (Hirakawa, 1994).

The regular reingestion of hard faeces had not been reported before. However, there are descriptions indicating the occurrence of hard faeces reingestion in some other species (Drane, 1895; Watson, 1954; Lockley, 1964). Also, although other leporid species have the same rhythm of soft faeces reingestion as the Japanese and the Mountain Hare, yet hard faeces have not been observed to pile in forms or burrows where they rest in the daytime (e.g. Lockley, 1964). These strongly suggest that the reingestion of hard faeces is widely practised among leporids. Note that well-masticated hard faeces are not recognizable in the stomach (Hirakawa, 1995a), hence it is difficult to detect them by studying stomach contents.

### Activity and reingestion rhythm in the Domestic Rabbit

When exposed to regular photoperiods (e.g. 12 h light and 12 h dark) and allowed to feed ad lib., the Domestic Rabbit feeds during the dark phase and practises caecotrophy in the first half of the light phase (Jilge, 1974, 1976; Hörnicke & Batsch, 1977). The daily activity rhythm in the Domestic Rabbit is thus basically the same as other wild leporid species. Curiously, however, there are some individuals that have the second period of caecotrophy in the middle



**Fig. 2.** Reingestion activities of a Japanese Hare (*Lepus brachyurus*) during the daytime stay in the form. Each circle represents a single faeces-taking action; open circles for soft faeces and solid circles for hard faeces. The solid horizontal bars indicate the period of the hare staying in the form. The piles of circles indicate that faeces-taking action is repeated at a time.

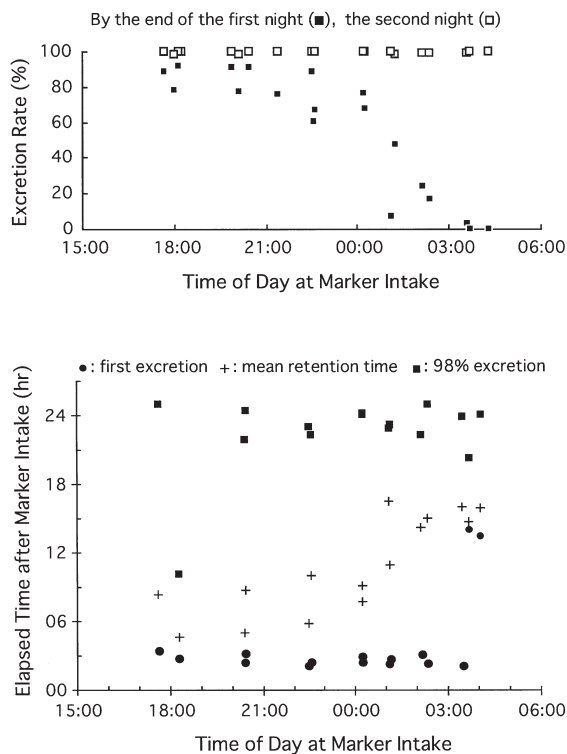
of the dark phase (Jilge, 1982), as is observed in the wild European Rabbit (Southern, 1942; Watson, 1954; Meyers, 1955).

Despite the aforementioned studies, understanding of the caecotrophy rhythm in the Domestic Rabbit has been in confusion, from the initial studies through to today. For example, Eden (1940b) called soft faeces 'night faeces' and Cheeke (1987) included this as one of the names for soft faeces. The cause of this confusion is probably the daily care routine, in that food is often provided first in the morning and in such an amount that none is left over to the next morning (Taylor, 1940a). Under this practice, the Domestic Rabbit probably becomes accustomed to start eating at the provision of food and continue eating until food is depleted. As a result, the feeding rhythm is reversed and soft faeces are excreted during the night after the food is depleted (for example, see Fig. 1 in Thacker & Brandt, 1955).

Ebino *et al.* (1993) reported frequent reingestion of hard faeces in the Domestic Rabbit, but did not clearly indicate the rhythm of reingestion.

### Passage and recycling of food particles

The passage rate of large food particles is quite fast in leporids (Olsen & Madsen, 1944; Hirakawa & Okada, 1995). In the Japanese Hare, large particles ingested early in the evening are almost completely eliminated by the end of that night (the minimum passage time is 2 hours and the mean retention time (MRT) is 4–5 hours) (Hirakawa & Okada, 1995). As ingested later on, however, they are increasingly eliminated in the daytime faeces (both in soft and hard faeces) and hence reingested. Of the reingested particles, those that still remain large after remastication are eventually discarded in hard faeces during the following night. The fate of large food particles thus varies depending on the time at ingestion (Fig. 3).



**Fig. 3.** Excretion of particulate markers in relation to the time at ingestion. The upper graph shows the excretion rates of particulate markers by the end of the first and second night. The lower graph shows their minimum passage time, mean retention time, and 98% excretion time. (Modified from Fig. 4 in Hirakawa & Okada 1995.)

Past passage-rate studies in the Domestic Rabbit seem to have three major problems (Hirakawa & Okada, 1995). One is ignorance of the feeding and reingestion rhythms. Many did not monitor those rhythms during experiments at all or, if they did, they did not specify the time of food (or marker) ingestion relative to the rhythm. Second, many did not recognize that the separation at the proximal colon was a size-dependent process, where the threshold was probably in the range of 0.1–0.3 mm (Björnhag, 1972). In addition, very large solid markers may be retained in the stomach for many hours (Pickard & Stevens, 1972) and some of the remarkably long passage times of solid markers observed in the past seem to be due to this effect (e.g. Bailey, 1968; Clemens & Stevens, 1980). The third is the ignorance of the presence of hard faeces reingestion. These problems indicate that the results of past passage-rate studies need to be carefully interpreted.

#### **Feeding, defecating, reingesting and digesta flow: a synthesis**

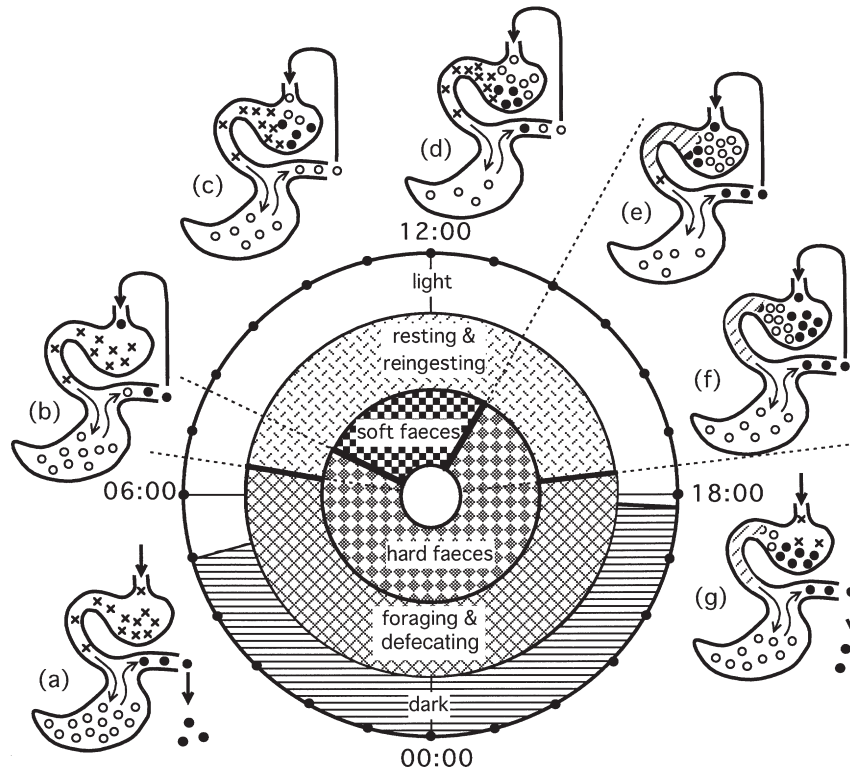
Because the passage rate of food is quite rapid, fresh food quickly fills the digestive tract after the onset of foraging activity in the evening. By morning, all the digesta in the digestive tract except a portion of caecal contents must be made up of the food freshly eaten in the night. While foraging in the night, the separation mechanism is activated so that the large food particles are quickly evacuated in hard faeces and the fine food particles are retained in the caecum (Fig. 4a).

The separation mechanism ceases and soft faeces formation begins at around the cessation of activity in the morning (Heisinger, 1962). But for a while, hard faeces remaining in the distal colon are excreted and reingested (hard faeces reingestion in the morning) (Fig. 4b). Then, soft faeces are excreted and reingested until the early afternoon (Fig. 4c). The digesta in the stomach, which is made up of food freshly eaten the previous night, continues to flow out from the stomach while forming soft faeces (Bouyssou *et al.*, 1986). However, the amount of stomach contents does not change much in the morning period (Watson, 1954; Flux, 1970; Gidenne, 1987). Hence, the inflow of reingested soft faeces to the stomach and the outflow from the stomach seem balanced.

At around noon, the separation mechanism is reactivated to form hard faeces (Fig. 4d). Hard faeces reach the anus in the early afternoon and are reingested (Fig. 4e). The material of the hard faeces obviously originates from the fresh food eaten in the previous night. Because the amount of stomach contents is decreasing in the afternoon (Watson, 1954; Flux, 1970; Gidenne, 1987), the outflow from the stomach seems more than the inflow of reingested hard faeces.

The amount of hard and soft faeces reingested during daytime is around 22–31 g (dry) in the Japanese Hare, while the maximum stomach content during daytime is 23 g (Hirakawa, 1995a). This means that the stomach contents in the evening when the night-time activity begins are almost entirely composed of the faeces reingested during the preceding daylight hours (Fig. 4f). Probably, most digesta left in the digestive tract in the morning is cycled once during the daytime through reingestion. On the other hand, large particles left in the digestive tract in the evening are almost all completely discarded in the subsequent night (Fig. 4g).

The fate of reingested faeces is inferred as follows. Most components of soft faeces (fine particles including micro-organisms) are digested and absorbed in the stomach and small intestine. If some reach the caecum, they are again retained in the caecum and excreted as soft faeces to be reingested. Hence, once broken into fine particles, they should stay in the digestive tract until eventually digested and absorbed. Consequently, fine but indigestible materials are recycled many times until they are eventually discarded. For example, it took 5 weeks for ingested copper sulphate to be completely eliminated (Eden, 1940a). As for large



**Fig. 4.** Daily activity cycle in the Japanese Hare (*Lepus brachyurus*). The circular diagram illustrates the phase relationships between photoperiod (outer circle), feeding and resting/reingesting and defecating (middle circle), and the excretion of hard and soft faeces in leporids (inner circle). The schemata (a–g) around the diagram show the types of digesta, their flow, and the formation and recycling of hard and soft faeces. × = fresh food; open circles = caecal materials and their resultant soft faeces; solid circles = hard faeces produced in the proximal colon. (Modified from Fig. 3 in H. Hirakawa (1994) with the permission of Cambridge University Press.)

particles in reingested hard faeces, if they become fine after remastication, they are incorporated into the fermentation process. If not, most of them are probably discarded nocturnally after the second passage following reingestion.

In summary, leporids feed all day long and defecate all day long. In the night-time, they feed on fresh food and ignore faeces; in the daytime, they excrete faeces and feed on them. During the day, digesta in the gut is almost completely cycled through reingestion, in which hard faeces are thoroughly remasticated. Particles remaining large after remastication are almost completely discarded in the following night.

#### Significance of hard faeces reingestion

If reingested large particles are masticated into fine particles, they would be incorporated into the fermentation process in the caecum and eventually digested and absorbed. Hard faeces reingestion thus has the effect of promoting food digestibility. During the daytime rest, it is more efficient to recycle hard faeces than merely to discard them. Stopping elimination, another conceivable option, is less desirable because it would require suspending the flow of digesta, thereby the sequential digestion process.



During foraging activity at night, it is more efficient to discard hard faeces than to recycle them. When better food is available, there is no point in reutilizing hard faeces. The separation mechanism that quickly evacuates low-quality food from the digestive tract helps leporids take in more fresh food and thereby makes efficient use of the limited digestive capacity.

Japanese hares kept in captivity (outdoor pen) never showed feeding activity from 07.00 hours to 11.30 hours throughout the year, but feeding was occasionally observed in the afternoon, especially in summer (Hirakawa, 1989). This suggests that the reingestion of soft faeces is imperative and obligatory whereas that of hard faeces is only facultative: if circumstances allow, leporids would probably prefer moving around to forage on fresh food than staying and reingesting hard faeces.

If food is not available during foraging activity at night, hard faeces are ingested as an emergency food. This reingestion of hard faeces implies more than the promotion of food digestibility. It helps leporids survive in an emergency situation, such as adverse weather conditions, without feeding for some time. When captured in the wild or exposed to a sudden food change in captivity, leporids often do without feeding for a few days (referred to as a 'hunger strike'). This phenomenon can only be reasonably understood by assuming hard faeces reingestion. Although hard faeces reingestion does not have a particular physiological digestive function, the faculty must give leporids a great ecological advantage.

The reingestion of hard faeces is equivalent to rumination in pregastric fermenters, in the sense that it is practised during the resting phase and that poorly digestible large particles are remasticated and ground into fine particles. In this sense, the term 'pseudo-rumination', which was proposed for soft faeces reingestion by Taylor (1940b) and used at times by subsequent authors, is more appropriate for hard faeces than soft faeces reingestion.

### **REINGESTION IN NON-LEPORID HERBIVORES**

Besides leporids, reingestion has been reported in pikas, a primate, a marsupial and many rodent species. Although there seem to be quite a few physiological studies on reingestion in laboratory animals like the Guinea Pig, the Golden Hamster, the Laboratory Mouse and Rat (e.g. Ebino, 1993), studies on the reingestion in wild species are limited. In this section, I first describe the reingestion activities in each species, then sort out possible patterns and finally suggest the importance of studying reingestion to understanding the biology and ecology of small mammalian herbivores. The body weights are from Walker (1964), MacDonald (1984) and Silva & Downing (1995).

Shrews, small carnivores, have been observed to lick the everted rectum and this behaviour has been referred to as 'refection' or 'coprophagy'. However, it is not appropriate to refer to it as such because it has not been ascertained what was actually licked, which in most cases is probably not faeces (Hirakawa & Haberl, 1998).

#### **Pikas**

Haga (1960) reported that the Northern Pika (*Ochotona hyperborea*) has two types of faeces: one is a deep green, spherical, hard but friable faex which is defecated mostly during the daytime; the other is a blackish-coloured soft faex, coated with a gelatinous and viscous substance. The latter faeces are deposited at night and left to dry until morning when they are eaten. In contrast, Kawamichi (1994) reported for the same species that soft faeces have no membrane and are either reingested directly from the anus or deposited in piles as a food stock for winter. Thus, there are inconsistencies between Haga's and Kawamichi's observations.

The Afghan Pika (*Ochotona rufescens*) is also reported to produce soft and hard faeces and reingest soft faeces (Matsuzawa, Nakata & Tsushima, 1981). Other pikas are also believed to practise reingestion of soft faeces.

### Primates

The Sportive Lemur (*Lepilemur mustelinus*), a nocturnal arboreal folivore (body weight: 0.5–1.0 kg), is probably the only primate species that is known to be a caecal fermenter and practises reingestion (Hladik *et al.*, 1971; Cork, 1994). Details are unknown.

### Marsupials

The Common Ringtail Possum (*Pseudocheirus peregrinus*) is the smallest folivorous marsupial (body weight: 0.5–0.7 kg) and the only marsupial species confirmed as practising reingestion (Chilcott, 1984). The Coppery Ringtail Possum (*Pseudochirops cupreus*) in New Guinea (body weight: 1.7–1.8 kg) may also practise reingestion (I. D. Hume, personal communication).

The habit of reingestion in the Common Ringtail Possum is quite similar to that in leporids: it forages in the night and practises reingestion in the daytime; it also has distinct hard and soft faeces. The only noticeable difference is that it thoroughly masticates soft faeces at reingestion. Soft faeces contain more water and proteins and less crude fibre than hard faeces. Fine particles are retained in the gut longer than large particles, suggesting the presence of a separation mechanism (Chilcott & Hume, 1985; Sakaguchi & Hume, 1990). However, because their proximal colon does not have a structure similar to that of leporids, Hume, Foley & Chilcott (1984) inferred that the separation mechanism was in the caecum.

In this connection, the Greater Glider (*Petauroides volans*) (body weight: 0.8–1.7 kg), another folivore in the same family, has a similar caecum structure, selectively retains fine particles but does not produce hard and soft faeces nor practises reingestion (Hume *et al.*, 1984; Foley & Hume, 1987). Similarly, the Koala (*Phascolarctos cinereus*) (body weight: 5–12 kg), another folivorous marsupial, has a caecum and proximal colon structurally similar to those of leporids, selectively retains fine particles, but still neither produces hard and soft faeces nor practises reingestion (Cork & Warner, 1983; Cork & Sanson, 1990).

### Rodents

Many rodent species are recognized as practising reingestion. However, the frequency varies greatly from species to species. Kenagy & Hoyt (1980) studied the reingestion behaviour in 13 rodent species from 10 genera, five families (Table 1). The behaviour was confirmed in all but the three Sciuridae. However, it was frequent only in the Chisel-Toothed Kangaroo Rat (*Dipodomys microps*) and the California Vole (*Microtus californicus*), both of which are strictly herbivorous. The Merriam's Kangaroo Rat (*D. merriami*), a granivore belonging to the same genus as the Chisel-Toothed Kangaroo Rat, rarely practised the behaviour.

The reingestion behaviour is similar in all the rodent species studied. They bend the head to bring the mouth to the anus, use incisors to pick up faeces from the anus, sometimes with the aid of forelegs, and ingest them after masticating well (no species are reported to do so without mastication). The reingested faeces are reported to be richer in nutrient content than non-reingested faeces, but a distinctive type of faeces for reingestion is not known except in two species of rodents (the Mountain Beaver, *Aplodontia rufa*, and the Coypu, *Myocastor coypus*). In some species, faeces are examined by manipulating within the mouth for several seconds before being ingested or rejected, indicating that faeces are selectively ingested (Kenagy & Hoyt, 1980; Oullette & Heisinger, 1980). If prevented from reingestion, animals

**Table 1.** Reingestion activities of 13 rodent species observed by Kenagy & Hoyt (1980)

Family	Species	Reingestion
Heteromyidae	<i>Perognathus formosus</i>	Rare
	<i>P. longimembris</i>	Rare
	<i>Dipodomys microps</i>	Frequent
	<i>D. merriami</i>	Rare
Geomyidae	<i>Thomomys bottae</i>	Rare
Muridae	<i>Peromyscus maniculatus</i>	Rare
	<i>P. crinitus</i>	Rare
	<i>Neotoma lepida</i>	Rare
	<i>Microtus californicus</i>	Frequent
Aplodontidae	<i>Aplodontia rufa</i>	Rare
Sciuridae	<i>Spermophilus saturatus</i>	Not observed
	<i>Ammospermophilus leucurus</i>	Not observed
	<i>Eutamias minimus</i>	Not observed

show a decrease in body weight or growth retardation (Barnes, 1962; Sharkey, 1971). Also, the frequency of reingestion varies depending on diet quality (Cranford & Johnson, 1989).

#### *Reingestion features in rodent species*

The Chisel-Toothed Kangaroo Rat, *Dipodomys microps*, (body weight: 50–60 g) practises reingestion mostly during daytime but feeds throughout the day and night. Faeces-examination behaviour is observed during the transition between reingestion and non-reingestion phases. Reingested faeces contain more water and protein but less ash than non-reingested faeces (Kenagy & Hoyt, 1980).

The California Vole (*Microtus californicus*) (body weight: 35–96 g) alternates the reingestion and non-reingestion phases several times a day and examines the faeces in phase transition. When shifting from reingesting to non-reingesting, it starts to examine faeces before ingestion, increasingly rejects faeces and eventually discards faeces without examination. In contrast, when shifting from non-reingesting to reingesting, it starts to pick up and examine faeces, increasingly accepts faeces and eventually ingest faeces without examination (Kenagy & Hoyt, 1980).

The Meadow Vole (*M. pennsylvanicus*) (body weight: 22–54 g) alternates the reingestion and non-reingestion phases several times a day. It reingests only while resting (Oullette & Heisinger, 1980). It examines faeces when shifting phases (Cranford & Johnson, 1989). A similar pattern is reported for the American Pine Vole (*M. pinetorum*) (Cranford & Johnson, 1989).

The Norway Lemming (*Lemmus lemmus*) (body weight: 45–50 g) practises reingestion many times a day and reingests all the faeces excreted at a time (1–4 pellets). About 30% of faeces excreted in a day are thus reingested (Björnhag & Sjöblom, 1977). The separation mechanism is at the spiral part of the proximal colon (Björnhag, 1981b, 1994; Sperber, Björnhag & Ridderstråle, 1983).

The Laboratory Rat (*Rattus norvegicus*) (body weight: 0.1–0.5 kg) practises feeding and reingestion during the night. Reingestion is mostly practised in the latter half of the night (Lutton & Chevallier, 1973). About 40% of the daily faeces are reingested (Lutton & Chevallier, 1973). Some faeces are richer in protein than others and the presence of the separation

mechanism at the proximal colon is suggested (Sperber *et al.*, 1983; Björnhag, 1994). If prevented from reingestion, the animal develops a nutrient deficiency (Barnes, 1962).

The Laboratory Mouse (*Mus domesticus*) shows great variation in the frequency of reingestion during growth. Reingestion is practised most frequently at 5–6 weeks old both in light and dark phases, but by 100 weeks old it is rarely used and then mostly in the light phase (Ebino, 1993).

The laboratory Guinea Pig (*Cavia porcellus*) (body weight: 0.3–0.9 kg) is highly dependent on the practice, and prevention from reingestion can result in death (Sharkey, 1971). The ingested faeces contain more nitrogen than the discarded faeces (Björnhag, 1981b; Holtenius & Björnhag, 1985), but they are not morphologically distinguishable (Sharkey, 1971). Short periods of reingestion are dispersed over the whole day (Björnhag, 1981b; Holtenius & Björnhag, 1985), but occur more often in the light phase (Hörnicker & Björnhag, 1980; Ebino, 1993). The separation mechanism is at the proximal colon (Hörnicker & Björnhag, 1980; Holtenius & Björnhag, 1985).

The Chinchilla (*Chinchilla lanigera*) (body weight: 0.36–0.48 kg) feeds in the night and reingests during the daytime like leporids. About 50% of the daily faeces are thus reingested. Daytime faeces contain significantly more nitrogen than night-time faeces (Björnhag & Sjöblom, 1977; Holtenius & Björnhag, 1985). However, they are not mutually distinguishable (Björnhag, 1981b). The separation mechanism is probably at the proximal colon because of its structural similarity to that of the Guinea Pig (Holtenius & Björnhag, 1985).

The Mountain Beaver (*Aplodontia rufa*) (body weight: 0.74–1.25 kg) alternates periods of rest and activity several times a day. On emerging from a rest, it defecates oblong hard pellets for 2–5 min by taking them from the anus to the mouth and tossing them to the faecal pile nearby. However, it interrupts at least once to masticate and ingest a pellet. The large intestine contains a few soft pellets each among many (10–23) hard pellets. Soft pellets are composed of light green, finely macerated material and are roughly four times as large as hard pellets (Ingles, 1961).

The Plains Pocket Gopher (*Geomys bursarius*) (body weight: 0.1–0.34 kg) and the Texas Pocket Gopher (*G. personatus*) take every pellet from the anus, examine and then either discard or thoroughly masticate and ingest it. Usually two to four pellets are excreted at a time with only one or two being eaten, often none. No distinctive faeces for reingestion were observed. Reingestion occurs not only in resting but in travelling and even in the middle of a meal. A similar reingestion is observed in the Mountain Pocket Gopher (*Thomomys monticola*) (Wilks, 1962).

The Coypu (*Myocastor coypus*) (body weight: 5–10 kg) feeds at night and reingests during the daytime like leporids. It also has distinct hard and soft faeces. Reingestion occurs from the morning to early afternoon (Gosling, 1979). The separation mechanism is suggested to be at the proximal colon (Snipes *et al.*, 1988). Because there is a period in the afternoon when no reingestion behaviour is observed and because hard faeces are discarded in a relatively large amount immediately after starting activity in the evening (Gosling, 1979), the Coypu probably does not practise hard faeces reingestion.

There are also reports of reingestion in the European Beaver (*Castor fiber*), the Naked Mole-Rat (*Heterocephalus glaber*), the European Souslik (*Citellus citellus*) (Hörnicker & Björnhag, 1980), the Laboratory Hamster (Ebino, 1993), the Water Vole (*Arvicola terrestris*) (Björnhag, 1994), and the Degu (*Octodon degus*) (E. Sakaguchi, personal communication). In summary, reingestion behaviour has been reported from 11 out of 29 families in Rodentia.

**DIVERSITY IN REINGESTION AND THEIR DEVELOPMENT**

As shown above, reingestion is widely practised among medium- to small-sized herbivorous mammals. On the one hand, a similar style of reingestion is observed in totally different taxa, and on the other hand, the behaviour is more frequent in herbivores than in granivores or frugivores of the same taxon (Kenagy & Hoyt, 1980). These indicate the development of reingestion is moulded not by phylogeny but by herbivory.

The styles of reingestion are quite diverse (Fig. 5). They are characterized by: (1) frequency of reingestion; (2) timing of reingestion in relation to defecating and feeding activities; (3) the presence or absence of faeces examination behaviour; (4) the presence or absence, the site and the structure of a separation mechanism; (5) differentiation of faeces (be it only nutritional or also morphological); and (6) presence or absence of mastication. Although the available information is too limited to sort out clear patterns, we can deduce several relationships among these traits.

For example, the faeces examination behaviour (voles, kangaroo rats and pocket gophers) implies the presence of nutritional differentiation in faeces and that their production is involuntary, which in turn implies the presence of a separation mechanism and the spontaneity of its rhythm. Ingesting only a few pellets from those excreted at a time after examination (pocket gophers and the Mountain Beaver) implies that the separation mechanism alternates with a short rhythm. In contrast, if reingestion and non-reingestion phases are separate and if faeces are examined in phase transition (voles and kangaroo rats), it means that the reingestion rhythm is regulated by the spontaneous rhythm of the separation mechanism. If the feeding is suppressed during reingestion period in this case (the Meadow and American Pine Voles), the feeding rhythm is also regulated by the spontaneous rhythm of the separation mechanism. Faeces examination behaviour has not been reported in the animals that have a regular reingestion period with suppressed feeding once a day (leporids, the Common Ringtail Possum, the Coypu, and the Chinchilla: Fig. 5). In this case, it seems that the rhythm of the separation mechanism is regulated by feeding or other activity rhythms.

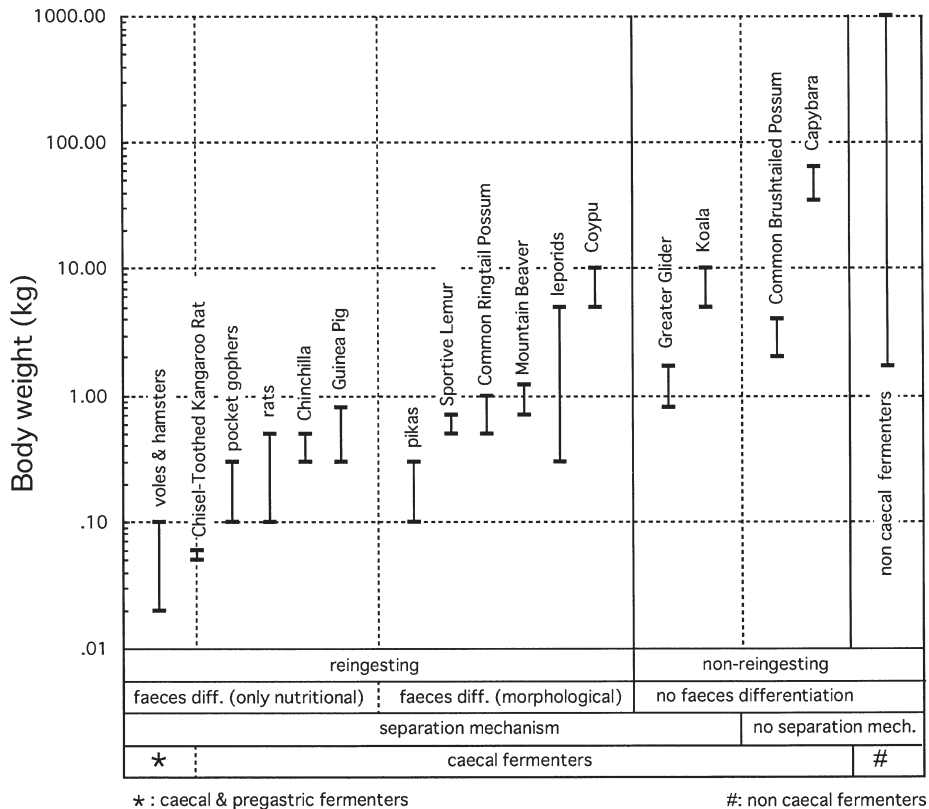
timing	timing to defecation	separate reingestion and defecation phases		reingesting a few from pellets excreted at a time	
	timing to feeding	no overlap with feeding	overlap with feeding	no overlap with feeding	overlap with feeding
faeces differentiation	nutritional and morphological	<div style="border: 1px solid black; border-radius: 50%; padding: 5px; display: inline-block;">                     Coypu leporids Ringtail Possum                 </div>		Mountain Beaver	
	nutritional but not morphological	Chinchilla <i>Meadow Vole</i>	<div style="border: 1px solid black; border-radius: 50%; padding: 5px; display: inline-block;"> <i>Chisel-Toothed Kangaroo-Rat</i> </div> <i>California Vole</i> Norway Lemming Guinea Pig		<i>pocket gophers</i>

**Fig. 5.** Tentative classification of diverse reingestion styles observed in small- to medium-sized mammalian herbivores. Those inside the circle have a distinctive reingestion period once a day (they are all nocturnal); those outside the circle practise reingestion multiple times a day. Italics indicate the species for which faeces-examination behaviour has been reported. Those on category lines cannot be classified into either of the categories due to the lack of information.

Nutritional studies of faeces all showed that ingested faeces were richer than discarded ones. Probably, all the species that regularly practise reingestion have a separation mechanism and differentiated faeces (Björnhag, 1989). However, recall that not all those that have the separation mechanism have differentiated faeces or practise reingestion, like the Greater Glider and the Koala (Fig. 6) (Foley & Cork, 1992). Their separation mechanism should operate continuously without a break.

Morphological differentiation in faeces requires a considerable development of the separation mechanism. It is reported from species weighing between 0.1 and 10 kg (Fig. 6). In contrast, nutritional-only differentiation is reported from species that weigh under 1.0 kg. Hence, morphological differentiation is probably related to body size.

The reingestion behaviour is so elusive that many small herbivore species that are highly dependent on the practice are probably still not recognized. However, as we have seen, reingestion activity is an essential element in the daily life of these small, strictly herbivorous mammals, so that the study of reingestion behaviour would be important to understanding their biology and ecology. Such studies are also needed to establish a comprehensive perspective on the development of the reingestion habit.



**Fig. 6.** Ranges of body weights of caecal and non-caecal fermenters arranged according to the reingestion behaviour and faeces differentiation. Although the forestomach fermentation chamber has not been reported for the Chisel-Toothed Kangaroo Rat, I put it on the border line because I suspect the possibility from its body weight. As for Sportive Lemur, the placement is tentative because details are not known. Body weights are from Walker (1964), MacDonald (1984) and Silva & Downing (1995).

- Tentatively, I divide the development of the reingestion habit into the following four stages.
1. In the most primitive stage, a digestive system specific for herbivory, such as the separation mechanism and the fermentation chamber, is not well developed and animals only make use of faeces in starvation. The food habit is not strictly herbivorous.
  2. In the second stage, herbivory is stronger, and the fermentation chamber and separation mechanism are developed but the faeces are not differentiated nor normally reingested. (Foley & Cork (1992) wrote, however, that the digestive system at this stage, observed in the Greater Glider and the Koala, might not be the precursor of the third stage.)
  3. In the third stage, the separation mechanism is developed to the degree that faeces are nutritionally, but not morphologically, differentiated. The reingestion of fermented faeces is nutritionally important and is vital on poor-quality diets. (e.g. the Chinchilla, the California Vole, the Guinea Pig)
  4. In the most developed stage, the separation mechanism is highly developed to produce morphologically differentiated faeces. The reingestion of fermented faeces is nutritionally imperative. Animals have distinctive reingestion periods, in which feeding activity is suppressed (e.g. leporids, the Coypu, the Common Ringtail Possum).

#### **Reingestion in digestive systems of herbivorous mammals**

Coarse plant material, like grasses and leaves, is generally poor in nutrients and contains a lot of barely digestible cellulose and hemicellulose. Herbivorous mammals digest these with a help of microbial fermentation in a specifically developed chamber. Ruminants like deer and cows, colobine monkeys, hippopotamuses and kangaroos have a fermentation chamber developed from the oesophagus (pregastric fermenter); horses, pigs and howler monkeys have it at the colon (colonic fermenter); and rodents and leporids at the caecum (caecal fermenter) (Van Soest, 1994).

Voles and hamsters, unlike other rodents, have a developed forestomach chamber for fermentation so that Van Soest (1994) classified them as 'pregastric fermenters'. However, hamsters have a more digestible inocula (bacterial flora) in the caecum than in the forestomach (Ehle & Warner, 1978), and voles have a separation mechanism at the proximal colon like other caecal fermenters (Björnhag, 1989, 1994). Hence, voles and hamsters should be regarded rather as variants of caecal fermenters, or specifically as 'caecal and pregastric fermenters'. Weighing less than 0.1 kg, they are not only far smaller than pregastric or colonic fermenters, but are also the smallest among reingesting herbivores (Fig. 6). Their extra fermentation in the forestomach may be an adaptation to that small size and the extra forestomach fermentation may be found in other small-sized herbivores like kangaroo rats (Fig. 6).

Reingestion behaviour is observed in small- to medium-sized herbivores, all of which are caecal fermenters, including voles and hamsters in the above sense. However, note that not all caecal fermenters have the separation mechanism nor practise reingestion. For example, the Capybara (*Hydrochoerus hydrochaeris*) (body weight: 35–64 kg) and the Common Brush-tailed Possum (*Trichosurus vulpecula*) (body weight: 2.0–4.0 kg) do not have the separation mechanism nor practise reingestion (Hörnigke & Björnhag, 1980; Foley & Hume, 1987; Sakaguchi & Hume, 1990); the Greater Glider and the Koala have the separation mechanism but do not practise reingestion (Fig. 6).

## **REINGESTION AND THE EVOLUTION OF LEPORIDS**

### **Scaling effect on reingestion-involved digestive system**

Why do small- to medium-sized herbivores practise reingestion? It is probably due to a scaling effect. The basal metabolic requirement per unit body weight is proportional to the 0.75

power of the body weight in kg, although the capacity of the digestive tract in herbivores varies almost linearly with the body weight (Demment & Van Soest, 1985). This means that smaller herbivores need to assimilate higher energy per unit capacity of the digestive tract than do larger mammals. They manage it by quickly excreting poorly digestible large particles and only retaining fine materials in the caecum for fermentation and subsequent reingestion (Foley & Cork, 1992; Cork, 1994). Then, why do not larger mammals adopt this 'efficient' digestive system? The answer is not known, but the fact indicates that there is another scaling constraint for the reingestion-involved digestive system to develop in larger herbivores.

The smallest of non-caecal fermenters are medium-sized, such as mouse deer (*Tragulus*) (body weight: 1.7–6.0 kg), colobine monkeys (*Procolobus*) (body weight: 2.9–10.0 kg) – both pregastric fermenters – and howler monkeys (*Alouatta*) (body weight: 4.3–9.5 kg) – a colonic fermenter (Van Soest, 1994). These animals selectively feed on highly nutritious and digestible parts of plants, and their ecological and geographical distributions are relatively limited. In contrast, leporids, medium-sized caecal fermenters that practise reingestion, can live on fibrous, low-quality grasses and leaves as well as woody parts of plants. They are widely distributed ecologically and geographically and, in fact, as a group they are the most common medium-sized mammalian herbivores in terrestrial ecosystems. Leporids have probably gained this niche by highly developing the reingestion-involved digestive system up to the limit of the unknown scaling constraint. The Coypu, another medium-sized caecal fermenter with almost the same reingestion-involved digestion system, is even larger than leporids and probably the largest among reingesting herbivores. However, the Coypu is semi-aquatic and its natural distribution is limited.

### **Reingestion and the evolution of leporids**

Leporids are known for their unique form: long ears, eyes covering wide angles to detect enemies, and long strong hind legs for fast running. They are also known for their 'absentee parental care (approaching and lactating newborns once a night for only several minutes)' (Eisenberg, 1981) and, for non-burrowing *Lepus*, 'backtracking (laying confusing trails before entering the form)' (Flux, 1981). All these morphological and behavioural traits of leporids are for antipredation. These traits must have developed since leporids became medium-sized, thereby exposed to a strong predation pressure. In this sense, we can see that the high development of their reingestion-involved digestive system has helped to make leporids what they are now.

Because animals make use of faeces when food is limited, even animals with nutritionally differentiated faeces are also likely to use low-nutrition (or hard) faeces as well as high-nutrition ones. Hence, the reingestion of low-nutrition faeces *per se* may not be unique to leporids. However, despite the high development of the separation mechanism and the clear differentiation of hard and soft faeces, leporids still regularly reingest hard faeces for efficient digestion. This certainly helps leporids live on low-quality food and thereby contributes much to their current success.

The reingestion system in leporids is certainly one of the most highly sophisticated among those in small- to medium-sized herbivores. However, note that a similar style of reingestion is observed in phylogenetically totally different species: the Coypu and the Common Ringtail Possum (Fig. 5). The Coypu probably does not practise the regular reingestion of hard faeces. One wonders whether the Common Ringtail Possum does.

The morphology of soft faeces is further differentiated into two types in leporids: the amorphous type and the capsule type. The capsule type is certainly more elaborate than the



amorphous type. However, the phylogenetic, physiological and ecological implications of this difference remain for future study.

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