

Coprophagy in the Japanese hare (*Lepus brachyurus*): reingestion of all the hard and soft faeces during the daytime stay in the form

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(Accepted 20 April 1993)

(With 3 figures in the text)

The daily rhythms of formation and reingestion of hard and soft faeces were studied in *Lepus brachyurus*. Although the Leporidae have long been known to reingest soft faeces, the Japanese hare also reingests a substantial amount of hard faeces. All the faeces excreted during the daytime stay in a form, comprising first hard faeces, then soft faeces and again hard faeces, were reingested. Hares repeatedly sit straight up from the squatting position to practise reingestion. A reingestion bout for hard faeces consists of repeated faeces-taking actions each followed by mastication, whereas that for soft faeces includes only one faeces-taking action without mastication. If deprived of food during foraging at night, the Japanese hare reingested most of the faeces that were normally discarded. Evidence in literature indicates that other Leporidae also practise reingestion of hard faeces.

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Introduction

Coprophagy in the Leporidae has long been known as the reingestion of soft faeces. For example, the early studies (Madsen, 1939; Taylor, 1940; Eden, 1940*b*) revealed that the domestic rabbit produces soft and hard faecal pellets in a daily rhythm; all the soft pellets are taken directly from the anus and swallowed without mastication, hence intact soft faecal pellets are found in the stomach of rabbits. The soft faeces are moist, round and mucus-coated, with a composition which is remarkably similar to the caecal contents.

Evidence of coprophagy has also been found in other Leporidae species (*Oryctolagus cuniculus*: Southern, 1940; *Sylvilagus palustris*: Hamilton, 1955; *Lepus europaeus*: Watson & Taylor, 1955; *S. floridanus*: Geis, 1957; Kirkpatrick, 1956; *L. californicus*: Lechleitner, 1957; *L. americanus*: Bookhout, 1959; *S. aquaticus*: Toll, Baskett & Conaway, 1960; *L. timidus*: Hewson, 1962). All these studies except for that of Kirkpatrick (1956), who recorded the reingestion behaviour of a free-ranging cottontail rabbit, looked for the presence of soft faeces in the stomach as the ultimate evidence of coprophagy. Furthermore, on the basis of the presence of soft faeces in the rectum and/or stomach of carcasses shot at various times of the day, the daily rhythm of reingestion was studied for several species (*O. cuniculus*: Southern, 1942; Watson, 1954 and Meyers, 1955; *L. europaeus*: Watson & Taylor, 1955; *L. californicus*: Lechleitner, 1957; *L. timidus*: Hewson, 1962 and Flux, 1970; *S. floridanus*: Heisinger, 1962 and Bothma, Steyn & Teer, 1982; *L. brachyurus*: Saitoh, 1978).

Physiological aspects of coprophagy have been studied almost exclusively in domestic rabbits. It is now known that soft faeces are rich in protein and vitamins, which have originated directly from the fermented caecal contents (Kulwich, Struglia & Pearson, 1953; Huang, Ulrich & McCay, 1954). A mechanism at the proximal colon has been shown to be involved in the alternate production of hard and soft faeces (Cheeke, 1987). The reingestion rhythm is regulated by photoperiod and feeding activities (Heisinger, 1965; Jilge, 1974; Hornicke *et al.*, 1984).

Although reingestion of hard faeces has been sporadically reported (Eden, 1940b; Southern, 1942; Hirakawa, 1983), it is not known how many, and on what occasions, hard faeces are reingested. This paper reports a study of the daily rhythms of feeding, defecating and reingesting activities of the Japanese hare (*L. brachyurus*). The methodology differed from previous studies in that intensive observations with video and computer devices were employed to monitor individuals kept in cages, rooms or enclosures.

Materials and methods

Feeding and defecating activities were observed by monitoring a 5-year-old female hare kept in a cage (80 × 80 × 80 cm) with a wire mesh floor. A portable computer connected to 2 electrical balances was used to monitor the decreasing weight of food stock in a feeder and the increasing weight of faeces under the cage. This system monitored these weights every 3 s, recorded the time and weight whenever there was a shift to new stable values, and stored the data in 24-h files.

Activities during the daytime stay in a form were observed by video-recording a hare in an enclosure. The 1-year-old male hare was released into the enclosure (26.6 m × 14.4 m) surrounding roofed pens (21.6 m × 10.8 m) 2 months before the observations began. The hare had by then become accustomed to staying in a form which was monitored from sunrise to sunset, and thus its behaviour during the daytime stay in the form was recorded. The observations were conducted from 12 August to 5 September 1992 for a total of 10 days.

Observations of night-time activities were conducted using a well-tamed 6-year-old female hare kept in a room (3.6 m × 3.6 m) with natural light conditions in the daytime but with dim red light during the night. The hare was released into the room 2 weeks before the observations began. An observer sat in a corner of the room and recorded all the feeding, defecating and reingesting activities. The continuous observations from 16:30 h to 07:00 h were conducted twice: once for normal night-time activities and once for activities when food was not provided.

Another supplemental observation was made using the same hare in the same room to confirm the types of faeces reingested during the daytime resting period. A plastic collar was attached to the hare from 06:00 h to 16:30 h to prevent it from reaching its anus, and the types of faeces and their excretion times were recorded by both direct observation and video-recording.

All the hares were fed with commercial food pellets during the observations. The hare in the enclosure also had some natural vegetation available, but this was limited owing to previous consumption.

Results

Daily feeding and defecating activities

Defecation started after the onset and ended after the cessation of feeding (Fig. 1a). Thus, the hare did not defecate (discard faeces) during the daytime resting period. When the food became depleted during the feeding hours at night, defecation ceased as well (Fig. 1b). If food was not

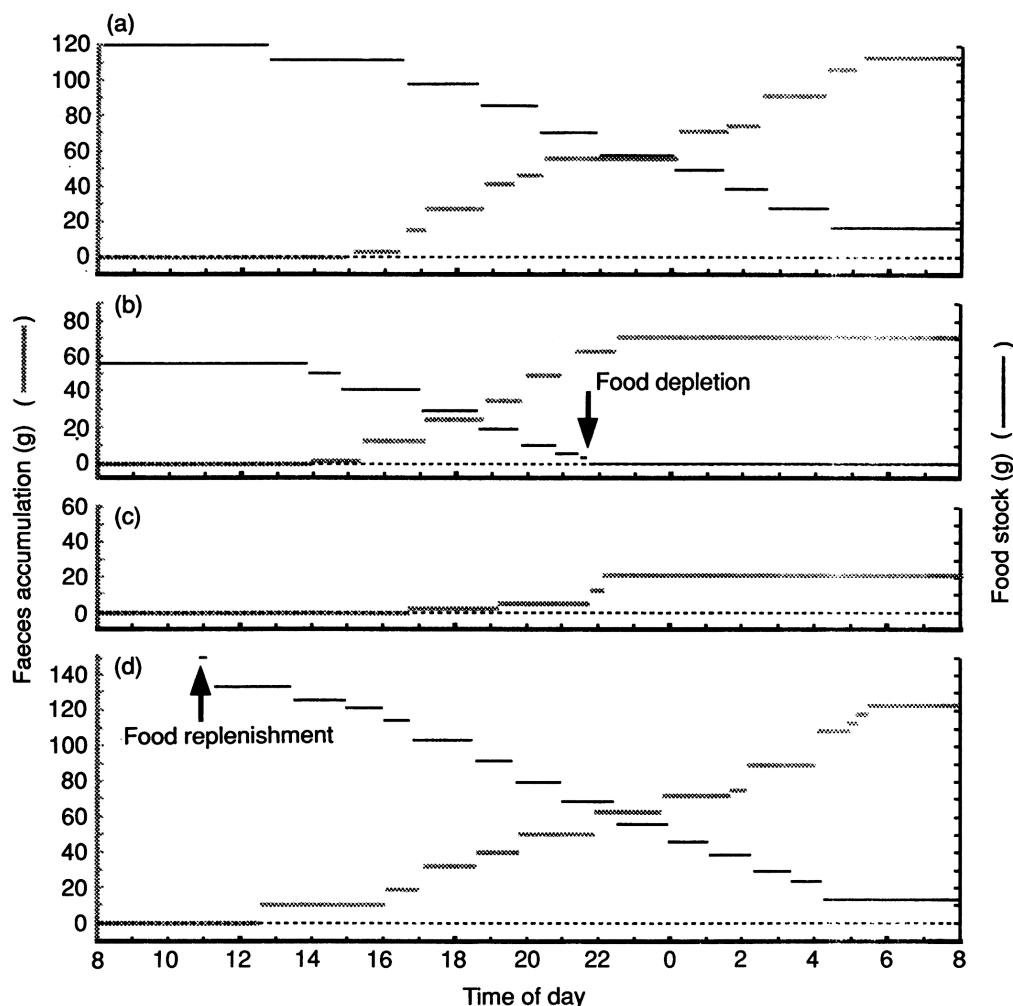


FIG. 1. Daily feeding and defecating activities of a hare for four consecutive days. The dark lines indicate the food stock: the light lines indicate the faeces weight. Sufficient food was available on the first day (a). On the second day (b), food became depleted in the midst of foraging hours in the night. On the third day (c), no food was available. On the fourth day (d), the starving hare started feeding immediately after food was provided in the morning.

replenished the next day, the hare, having no food, defecated only a little during the night (Fig. 1c). When food was provided the next morning, the hare immediately started feeding and defecating (Fig. 1d).

These results suggested that reingestion might occur when the animal was deprived of food during its normal feeding hours. Furthermore, reingestion could also occur in the daytime period when normally neither feeding nor defecation were observed. These observations suggested the need for an investigation of hares' daytime activity.

Activity during the daytime stay in a form

The hare entered the form early in the morning and finally left it late in the evening (Table I, Fig. 2). It remained in the form for most of this period. In the form the hare spent most of the time squatting. From time to time, however, the hare sat straight up; it then practised reingestion before resuming its squatting position (a sequence of behaviour referred to as a reingestion bout). All of the faeces produced during the daytime stay on the form were thus reingested.

Two distinct types of faeces-feeding (reingesting) behaviour were observed. Both began with the same faeces-taking action, but one was followed by quick jaw movements (3.8 times/s) for 10–70 s, indicating mastication, whereas the other lacked such activity, though brief mumbling jaw and lip movements were sometimes observed.

The faeces-taking action begins with the hare sitting still for several seconds. It then bends its head down, moving both forelimbs to one side (right or left), brings the anus forward and moves the mouth to the anus. It nods for several seconds keeping the mouth in contact with the anus (apparently taking faeces), and then raises its head.

The faeces-taking action followed by mastication is repeated several times without intervals in a multi-reingestion bout, which can last for more than 10 min. In contrast, the faeces-taking action unaccompanied by mastication mostly occurred only once at a single-reingestion bout, which usually lasted no more than a minute.

The multi-reingestion bout occurred once, or rarely twice, during the first hour after the hare entered the form (Fig. 2, Tables I & II). Later, the single-reingestion bouts started and occurred intermittently more than 10 times until the early afternoon. Finally, the multi-reingestion bouts recurred several times until the hare left the form.

A third type of faeces-feeding behaviour was occasionally observed. This was characterized by a much longer faeces-taking time of around 20 s (Table II). This was not usually followed by mastication, but was repeated in a reingestion bout consisting only of this type of behaviour, or

TABLE I
Time at which reingestion of hard and soft faeces took place during the daytime stay in a form. Data are based on observation for 10 days from 12 August to 5 September 1992

Incident	Mean	(Range)	n
Enter form	06:34 h	(06:23–06:50 h)	9
End hard faeces reingestion	07:38 h	(07:22–08:20 h)	8
Start soft faeces reingestion	07:49 h	(07:31–08:39 h)	8
End soft faeces reingestion	13:37 h	(11:45–15:09 h)	7
Start hard faeces reingestion	14:13 h	(12:19–15:49 h)	7
Leave form	17:23 h	(17:05–17:38 h)	6

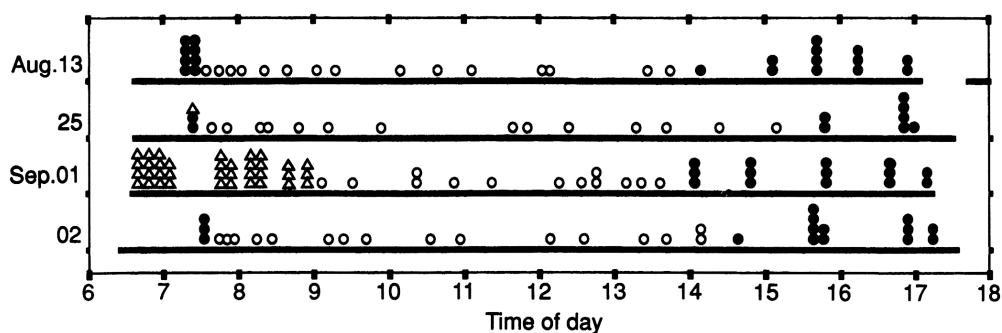


FIG. 2. Reingesting activities during the daytime stay on a form. Each circle represents a single faeces-taking action; ● = faeces-taking action followed by mastication; ○ = faeces-taking action with no mastication; △ = longer faeces-taking action with no mastication. The solid horizontal bars indicate the hare was in the form; absence of bars indicates the hare was out of the form.

TABLE II
Types of reingestion and their characteristics

Type of reingestion	Average duration of faeces-taking action (s)	Average duration of mastication (s)	Average number of faeces-taking actions per bout	Average number of reingestion bouts per day
Mastication (morning)	5.9	32.9	4.2	1.3
Non-mastication	9.0	—	1.1	13.3
Mastication (afternoon)	5.6	36.1	2.9	2.9
The third type ^a	19.5	0.4	—	—

^a This type of reingestion refers to the faeces-taking actions represented by open triangles in Fig. 2, for which corresponding faeces type is unknown.

occurred at the end of a multi-reingestion bout (Fig. 2). On one day, the early reingestion bouts consisted only of this type of behaviour, which occurred six times in the morning (Fig. 2).

Reingestion during foraging hours at night

During the night when food was available, the hare fed and defecated (discarded hard faeces) normally. However, the hare consumed once-discarded hard faeces from the floor on several occasions during the early morning (c. 03:00 h). After the hare became inactive, at around 04:40 h, it performed a multi-reingestion bout and three single-reingestion bouts before 07:00 h.

During the night when food was not available, the hare did not defecate until about 1 h after it became active. It then started to discard faeces, but after 23:05 h all the faeces were reingested. Even before 23:05 h, reingestion followed by mastication was observed once and feeding on once-discarded faeces from the floor was observed several times. After 23:05 h both mastication- and non-mastication-type reingestions were observed but no definite pattern was recognized. Feeding on once-discarded faeces from the floor was also observed during this period.

Types of faeces excreted during the daytime resting period

A collar to prevent reingestion was attached from 06:00 h to 16:15 h. From 07:05 h to 12:34 h, soft faeces were excreted 12 times (one faecal piece at a time). Hard faeces were first seen at 12:35 h, and these were excreted six times until the collar was removed. Several hard faeces were excreted at each episode, giving a total of 45 hard faeces.

The soft faeces were 23–42 mm long and 10–12 mm in diameter, amorphous, lacking any surface structure and with an unpleasant smell. Their dry weights were highly variable with a mean of 1.34 g (0.90–2.10, $n=3$). The hard faeces were dry, spherical, 7–9 mm in diameter and with a mean dry weight of 0.1 g ($n=45$).

The hare struggled to take both types of faeces every time they were excreted, but it showed a much stronger craving for soft faeces than hard faeces. The hare ate most of the discarded soft faeces by licking them from the floor in spite of the difficulty imposed by the collar, whereas some of the discarded hard faeces were left uneaten. Soft faeces taken from the floor and offered to the hare were devoured, whereas hard faeces were not eaten.

The temporal pattern of excretion of hard and soft faeces agreed with the pattern of mastication and non-mastication reingestion observed during the daytime stay in the form. The results thus indicate that reingestion is followed by mastication for hard faeces but reingestion of soft faeces does not result in mastication.

Amounts of hard and soft faeces reingested

After allowing for possible missed reingestions in the above experiments, it was estimated that a dry weight of around 16–22 g of soft faeces and 6–9 g (60–90 pellets) of hard faeces were reingested per day. The hare usually defecated around 30 g of hard faeces during a night. This indicates that around a third of the faeces produced per day are soft faeces and that around a quarter of the daily output of hard faeces is reingested. The above results also suggest that hares take several hard pellets in a faeces-taking action.

Discussion*How general is the habit of reingesting hard faeces?*

This study showed that the Japanese hare reingests all the soft and hard faeces excreted during the daytime stay in a form. The fact that hard faeces are reingested on such a regular basis has not been reported before, despite the interest in the phenomena of coprophagy which had existed since the report by Madsen in 1939. It is therefore pertinent to ask if this habit is unique to the Japanese hare or to hares provided with commercial food pellets.

Watson (1954) observed wild rabbits take faeces at intervals both of a few minutes and of 10–20 min. Lockley (1964) described jaw movements of wild rabbits taking place for up to 100 s after taking faeces. These authors probably described hard faeces reingestion without realizing what they had seen. K. Ebino (unpubl. note) observed domestic rabbits by video-recording and found that all of them practised hard faeces reingestion. He saw hard faeces fall from cages when faeces were being taken at intervals of a few minutes. Faeces-taking actions which occurred at intervals of 10–60 min were considered to be of soft faeces. These facts suggest that hard faeces reingestion may be a common practice among the Leporidae.

Most of the studies of coprophagy in the Leporidae in the past have focused on soft faeces reingestion. This makes it highly probable that they have overlooked hard faeces reingestion, but it is of interest to consider whether it is possible that such a significant aspect of coprophagy in the Leporidae could have been overlooked for such a long time.

One possible reason is that hard faecal pellets cannot be found in the stomach if they are fully masticated on reingestion, as was observed in this study. A second reason why hard faeces reingestion is difficult to detect may be because hard faeces as well as soft faeces are taken directly from the anus to the mouth. The third reason is that reingesting behaviour is so elusive that it is hard to observe, even with domestic rabbits (Taylor, 1939). Besides Kirkpatrick (1956), few studies involved observations of coprophagy (Southern, 1940; Watson, 1954; Lechleitner, 1957; Hewson, 1962) and none of these noticed variations in reingestion behaviour.

Daily rhythms of hard and soft faeces formation and reingestion

In terms of the daily rhythm of soft faeces formation and reingestion (Fig. 3), the present results agree with those of the previous studies for other Leporidae species (*O. cuniculus*: Southern, 1942; Watson, 1954; Meyers, 1955; *L. europaeus*: Watson & Taylor, 1955; *L. californicus*: Lechleitner, 1957; *S. aquaticus*: Toll *et al.*, 1960; *L. timidus*: Hewson, 1962; Flux, 1970; *S. floridanus*: Heisinger, 1962, 1965; Bothma, Steyn & Teer, 1982; *L. brachyurus*: Saitoh, 1978). In spite of the species difference, these studies revealed strikingly uniform temporal patterns of soft faeces formation. Although these studies do not explicitly address the fate of daytime hard faeces, it seems reasonable to assume that these are reingested as well.

In support of this, it is known that faeces are not generally found in forms or warrens. For example, Lockley (1964) notes that he never saw the wild rabbits discard faeces in the burrows in the course of a four-year observation period. Heisinger (1962, 1965) regarded the 4- or 5-h period after the reingestion of the last soft faeces until the evening, during which fresh food was not eaten and only hard pellets were in the rectum, as a fasting period. This interpretation is based on the assumption that hard faeces are not reingested and it may be unjustifiable.

Passage and recycling of food materials in alimentary tracts

Figure 3 shows the speculated pattern of the passage and recycling of food materials in the alimentary tract of the Japanese hare. The minimum passage time of food is very short in Leporidae, ranging from 4 to 12 h (e.g. Flux, 1970; Jilge, 1974). Hence, fresh food quickly fills the alimentary tract at the end of the foraging period (Fig. 3a). While the hare is foraging, the caeco-colonial selective excretion mechanism at the haustrated proximal colon (Cheeke, 1987) works to pass the large particles of food to the rectum to produce hard faeces while moving fine particles and fluids back into the caecum in a retrograde manner.

When animals enter a form, the mechanism ceases and caecal materials start flowing into the colon (Heisinger, 1962). Fresh forage taken later in the night is left in the stomach and ceases to move forward. For around an hour, the remainder of the hard faeces in the colon and rectum are voided and reingested (Fig. 3b). Afterwards, soft faeces derived from the caecum are voided and reingested for several hours (Fig. 3c, d).

The hard faeces voided and reingested in the early afternoon are probably derived from the fresh forage that was taken late in the previous night and retained for several hours in the stomach

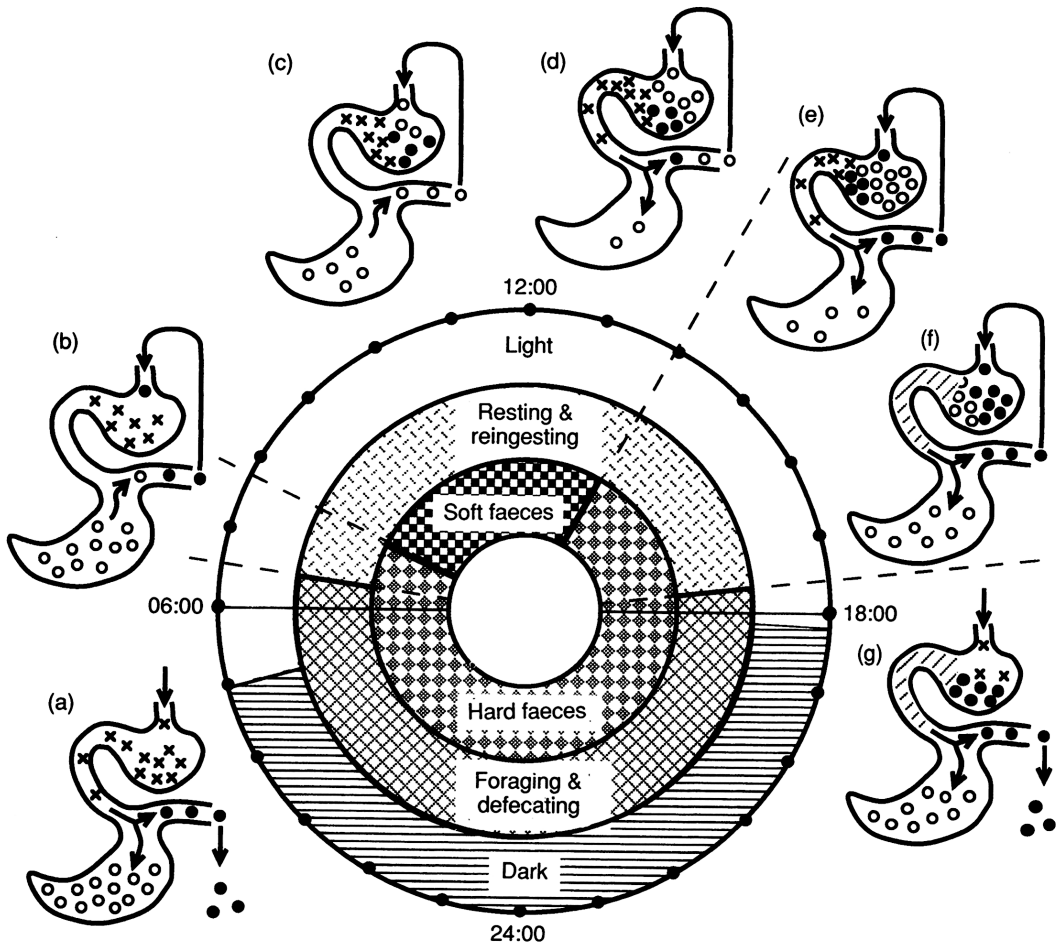


FIG. 3. Phase relationships relating photoperiod, feeding and resting, reingesting and defecating, and the production of hard and soft faeces. A schema (a-f) of the circulation of food materials is also presented. $\times$ = fresh food; $\circ$ = caecal materials and their resultant soft faeces; $\bullet$ = hard faeces produced at the proximal colon.

(Fig. 3e). Materials voided when the next foraging phase starts in the evening might either be the final portion of fresh forage or the second-passage materials reingested previously in the day (Fig. 3f). Later, all the hard faeces voided are discarded (Fig. 3g). The daily fluctuation patterns reported in the stomach contents of *O. cuniculus* (Watson, 1954) and of *L. timidus* (Flux, 1970) are in agreement with the above speculation.

As for the fate of the reingested material, most of the components of the reingested soft faeces are probably digested and absorbed in the small intestine. Those not absorbed would be filtered again by the separation mechanism at the proximal colon, to be stored in the caecum. As a result, small but hard-to-digest fragments can be recycled many times: for example, five weeks for copper (Eden, 1940a). In contrast, if large fragments in reingested hard faeces are not broken down by remastication and redigestion, they are highly likely to be discarded after the second passage.

Soft faeces

The soft faeces observed in this study were amorphous and without a tough membrane, and thus can hardly be called 'pellets'. They are different from the rabbit soft faeces, described as well-formed, spherical and mucus-coated pellets (Taylor, 1940; Watson, 1954). Other descriptions in literature reveal that both spherical and amorphous types of soft faeces are observed in all three genera of Leporidae. However, the spherical type seems normal in *Oryctolagus* (Watson, 1954; Meyers, 1955) and *Sylvilagus* (Hamilton, 1955; Geis, 1957; Dexter, 1959; Heisinger, 1962), as opposed to the amorphous type in *Lepus* (Watson & Taylor, 1955; Lechleitner, 1957; Hewson, 1962; Flux, 1970).

In *L. brachyurus*, Saitoh (1978) reported spherical soft faeces in the rectum but only noted the presence of amorphous material in the stomach. S. Horino (pers. comm.) did not find any pellets in the stomachs of 20 Japanese hares shot during the daytime. These facts suggest that soft faeces are amorphous in free-ranging Japanese hares as well as in those fed with commercial food pellets.

Intact soft faecal pellets in the stomach of rabbits produce lactic acid by the action of gut bacteria (Griffiths & Davies, 1963). The facts that soft faeces in *Oryctolagus* and *Sylvilagus* are coated by a tough membrane, reingested without mastication, and remain intact in the stomach for several hours have significance as regards their digestion. The absence of a membrane in most soft faeces in *Lepus* is in sharp contrast with this, suggesting physiological differences between the two groups of Leporidae in the functions of soft faeces.

Significance of hard faeces reingestion

The physiological aspects of the coprophagy of Leporidae have been recognized only in respect of soft faeces reingestion; and, indeed, the hare in the present study showed a much stronger craving for soft faeces than for hard faeces. However, we should not neglect the significance of the regular reingestion of a substantial number of hard faeces.

Using the selective excretion mechanism, the Leporidae can achieve high digestive efficiency by quickly excreting hard-to-digest materials and only fermenting high-quality food materials in the caecum. Why then do they eat hard faeces?

One possibility is that this allows them to make the most of their time in the form by remasticating and recycling poor-quality food material. This might be important for an escape strategist that does not spend daylight time foraging because of the predation risk. Another possibility is that this behaviour maintains the sanitation of the form.

More than 100 24-h records of feeding activity of hares kept in pens never showed grazing activity in the morning from 07:00 to 11:30 h, but sporadic feeding was often observed in the afternoon, particularly in summer (unpubl. data). Thus hares never graze while reingesting soft faeces but they occasionally do so at other daylight hours, which suggests that hard faeces reingestion is optional whereas soft faeces reingestion is imperative.

Another important aspect of hard faeces reingestion shown here is that it provides food when fresh forage is not available. This could have a great influence on survival of the hares under adverse climatic circumstances when they cannot forage.

I am grateful to Fumio Yamada for his helpful comments on the early draft of this manuscript. I am greatly indebted to an anonymous referee for suggesting a number of improvements on the early manuscript.

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