

Reingestion of Feces in Rodents and Its Daily Rhythmicity

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Summary. The ingestion of feces is widespread among rodent species and is an extensively employed component of the repertoire of feeding behaviors in some species. Coprophagy is thus a significant consideration in the nutrition and dietary ecology of many rodents. As certain fecal pellets pass from the anus, they are taken up directly into the mouth, chewed, and swallowed. The nocturnally active herbivorous kangaroo rat *Dipodomys microps* ingests about $\frac{1}{4}$ of the feces it produces daily and the daily pattern of reingestion shows a consistent rhythm. For about 8 h of the daytime, during the non-foraging, resting phase of the day, *D. microps* reingests all fecal pellets produced; during the remainder of the day it leaves all feces produced. The reingested feces contain more nitrogen and water, and less inorganic ions than the non-reingested feces. The extent of reingestion varies among rodent species in relation to diet, and coprophagy is more important in the more herbivorous species. The granivorous kangaroo rat *D. merriami* ingests feces rarely. The herbivorous vole *Microtus californicus* ingests about $\frac{1}{4}$ of its feces, as does *D. microps*. However, in contrast to *D. microps*, *M. californicus* shows a series of rhythmic, short-term (one to several hour duration) alternations between reingestion and non-reingestion during the course of the day and night. This pattern correlates with the pattern of foraging in *M. californicus*, which extends over both night and day.

Introduction

Natural selection has operated on a broad suite of interrelated traits in the evolutionary development of patterns of foraging, feeding, digestion, and assimilation in rodents. By comparing members of this large and diverse group which differ in diet, it has been possible to identify some of the features of their nutritional biology which have undergone adaptive modification (Vorontsov, 1962; McNab, 1963; Baker, 1971; Carleton, 1973; Barry, 1976). Generally the quality, quantity, spatial distribution, and density of specific types of food have determined the kinds of dietary and nutritional adaptations – ecological, behavioral, physiological, and morphological – that have evolved in each species.

In the present paper we wish to focus on the general nature and adaptive variability of a special aspect of rodent nutrition: the recycling of materials through the digestive tract which occurs

when a rodent ingests its feces. What kinds of rodents employ coprophagy and how extensively is this strategy utilized? Many biologists who have studied rodents have been casually aware that some rodents reingest their feces. However, quantitative information on the frequency, amount, and timing of coprophagy in rodents has previously been lacking. We wish to report our findings on reingestion in rodents, which indicate the extent of coprophagy in this major mammalian group and suggest that coprophagy is normal adaptive behavior in rodents. We also show the existence of temporal coordination between the behavior pattern of coprophagy and the daily rhythmicity of digestive function.

We use “coprophagy” as the simplest available general term to describe *ingestion of feces*, without any implication of cause, circumstances, or the origin or nature of the fecal material consumed. “Reingestion” is an alternate general term for *consumption by an animal of its own feces*. Two other available terms imply special conditions which may not prevail exclusively and may require experimental confirmation: “Caecotrophy” was originally defined as the ingestion of feces which consist of material derived from the caecum (Harder, 1949). “Refecation” was originally defined (as a condition distinct from coprophagy in general) as the production of bulky, gas-occluded, whitish feces by rats on a vitamin-B-deficient diet of uncooked starch; under these conditions rats maintain healthy condition due to intestinal synthesis of deficient nutritional elements which are either directly absorbed in the lower intestinal tract or recycled to the small intestine by coprophagy (Fridericia et al., 1927; Guerrant, 1955, personal communication cited by Mickelsen, 1956).

Coprophagy is best known in the mammalian order Lagomorpha – rabbits, hares, and pikas. Since the discovery that domestic rabbits produce two kinds of feces, a soft type which is swallowed whole as it passes from the anus and a hard type which is not consumed (Morot, 1882; Madsen, 1939; Taylor, 1940a, b; Eden, 1940a, b; Southern, 1940, 1942), this pattern has been confirmed in a variety of other lagomorphs (Watson and Taylor, 1955; Hamilton, 1955; Kirkpatrick, 1956; Lechleitner, 1957; Haga, 1960). Reingestion has also been reported in other mammalian orders: in shrews, order Insectivora (Crowcroft, 1952; Booth, 1956; Loxton et al., 1975); in the family Phalangeridae, order Marsupialia (Tyndale-Biscoe, 1973: p. 149); and in the folivorous prosimian *Lepilemur leucopus*, order Primates (Charles-Dominique and Hladik, 1971).

Early studies with rats, guinea pigs, and hamsters suggested that rodents also reingest feces, at least occasionally (Swirski, 1899; Grützner, 1905; Osborne and Mendel, 1911; Krzywaneck, 1927). However coprophagy appeared to be less marked than in lagomorphs. The behavior pattern of reingestion in rodents

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was not described until Krzywanek (1927) reported that rats, guinea pigs, and hamsters remove feces directly from the anus and consume it. A subsequent report on the occurrence of coprophagy in several other rodents was made by Harder (1949). One reason for the early impression that reingestion was of limited significance in rodents is that whole fecal pellets were not found in the stomachs of rodents, as they occur in lagomorphs (Madsen, 1939).

Other than additional casual references to coprophagy in rodents (Howell and Gersh, 1935; Ingles, 1961; Hamilton, 1962; Wilks, 1962; Rood, 1970), attention to this phenomenon has focused only on the general nutritional consequences of reingestion, particularly in growing rats. Rats which are mechanically prevented from reingesting their own feces by restraint collars show reduced growth rates (Barnes et al., 1963). Presumably some nutritional elements (such as B vitamins and amino acids) which are unavailable in the natural diet can be produced by endofloral synthesis in the lower digestive tract and then reingested to be assimilated in the small intestine (Fridericia et al., 1927; Elvehjem, 1948; Harder, 1949; Frank et al., 1951; Mickelsen, 1956; Daft et al., 1963; Fitzgerald et al., 1964). These micronutrients have, unfortunately, not been specified with precision (Elvehjem, 1948; Mickelsen, 1956; Barnes et al., 1963). However, the nutritional benefits of coprophagy are probably qualitatively similar for both rodents and lagomorphs (cf. previous references to coprophagy in lagomorphs; Scheunert and Zimmermann, 1951; Thacker and Brandt, 1955).

Although reingestion by rodents is considered to be nutritionally beneficial, the extent to which it occurs and the accompanying mechanism of digestive function have not previously been directly examined for any rodent species. In fact, many reports have questioned the adaptive value of coprophagy in rodents, suggesting that it occurs randomly or under conditions of dietary restriction (Howell and Gersh, 1935) or unusual artificial diets (Fridericia et al., 1927), or that occasional reingestion might be significant only for inoculation of the gut (Hamilton, 1962; Kalugin, 1974). A special case of coprophagy is that in maternal rodents, which consume the feces and urine of their young in the nest; this behavior maintains nest sanitation and also promotes water conservation (Baverstock and Green, 1975).

Materials and Methods

Our technique for observing the amount and timing of reingestion is direct and employs hind sight. In order to observe the behavior patterns with precision, we placed animals in a cage with a bottom of wire screen ($1/4$ -inch mesh) or glass, below which a mirror was situated at a 45° angle. Animals were placed on the screen or glass in separate compartments (wooden dividers of about 10×15 cm; or inverted metal cans of about 15 cm diameter) and, for most species, one observer could obtain data from as many as four animals at a time. Glass-bottom cages (aquaria) were useful for photography, but due to accumulation of urine and feces these were not useful for extended observations. By rotating observational shifts between ourselves every hour or two, we made continuous records of the frequency of reingestion and of defecation, for as long as 33 h without interruption.

We made observations on 13 rodent species, all within several weeks of their capture. The animals were live-trapped in natural habitats typical of each species in California or Washington. Some species, as noted in Results, were observed within a few hours of their capture in the field. With one exception, all captive animals

were maintained on their respective experimental diets for a least 2 weeks before observations were made. The exceptions were animals fed an exclusive diet of Romaine lettuce and transferred to the lettuce diet only five days prior to the onset of observations. Laboratory photoperiod was always a daytime of 12 h light (0600–1800 h) followed by 12 h dark. However, three days before each extended observation period a dim light (shaded 25-watt incandescent bulb) was added at night to allow the animals to become accustomed to the light required by us for nighttime observations.

Water content of feces was determined by drying fresh feces to constant weight at 60° C. In an experiment on 39 *Dipodomys microps* on a diet of seeds and lettuce, groups of 7, 8, 8, 8, and 8 animals respectively were killed at five different times of day and a maximum of six formed fecal pellets was removed from the last 3 cm of the colon; water was also determined in these samples by drying at 60° C.

Several nutritional parameters were determined in a group of six freshly captured *D. microps* held on an exclusive diet of the leaves of the saltbush *Atriplex confertifolia*. The animals were held for a day following capture on their saltbush leaf diet and then placed in a clean stainless-steel solid-bottom cage at 2200 h with a supply of leaves and a cotton wad for nesting. At intervals during the next 14 h feces were collected from each cage for analysis. At noon the next day the animals were killed and the formed fecal pellets in the colon collected for analysis. Observations of eating and reingestion behavior were made at intervals during the 14 h period. Ash was determined on a subsample, previously dried at 60° C, by placing each sample in a muffle furnace for five hours at 500° C. Nitrogen content was determined after Kjeldahl digestion by measuring ammonium ion concentration with an Orion electrode on two replicates of five of the samples and only one of the sixth sample. Energy content was determined with a Phillipson Microbomb calorimeter on at least two replicates, without correction for acid formation. In some of the intestinal analyses, determinations of pH were made using pH paper briefly blotted onto the intestinal contents.

Results

Behavioral Patterns of Coprophagy

A common pattern of behavior characterizes reingestion of feces as we have observed it in 10 species of rodents representing four families (Fig. 1). The animal flexes its head, neck, and back deeply to bring the mouth adjacent to the anus. As a fecal pellet exits the anus, the animal grasps it directly with the incisors, sometimes assisting with the front limbs. Feces are always chewed thoroughly before swallowing. The animals apparently detect the oncoming passage of feces, and defecation seems to be under voluntary control. This is apparent because, although several pellets are usually passed in succession, an animal removes and chews them one at a time, waits in an intermediate posture while chewing and swallowing (Fig. 1, right), and then returns to the feces capturing position to release and obtain another pellet from the anus (Fig. 1, middle). Release of each pellet is accompanied by pulsing movement of the abdominal muscles. Because we have observed coprophagy in several species of rodents within several hours of capture in the field, we assume that coprophagy occurs under natural conditions.

The animals apparently distinguish, by some combination of smell, taste, and touch, the quality of feces appropriate for reingestion. This is suggested by observations during times of transition

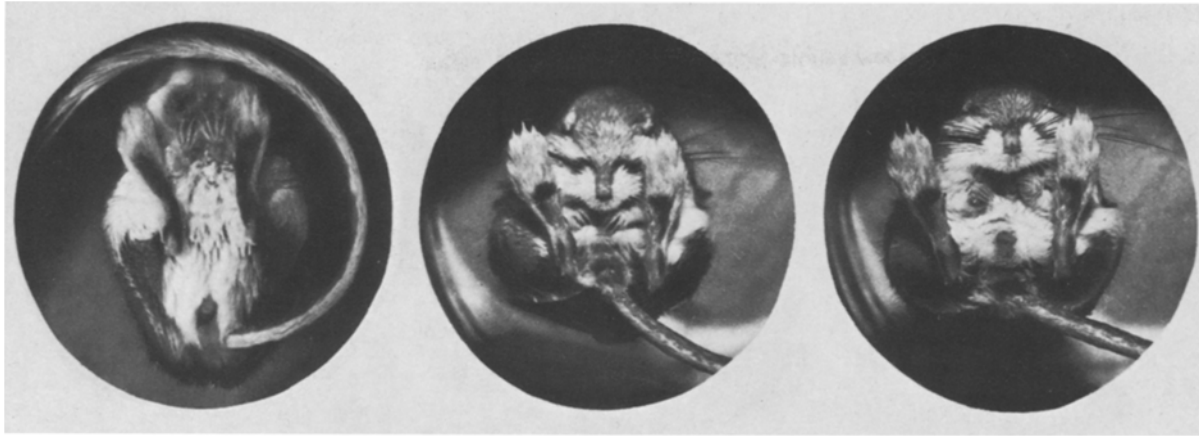


Fig. 1. Reingestion of a fecal pellet by a kangaroo rat, *Dipodomys microps*, viewed from beneath. *Left:* a normal resting or feeding posture with front feet near mouth. *Middle:* front feet extended onto ventrum near anus, and head flexed toward anal region as fecal pellet emerges. *Right:* animal chewing fecal pellet and waiting in partially flexed position for emergence of subsequent pellets. Photograph is about half natural size, taken by directing camera toward mirror mounted at 45° angle beneath glass-bottom cage

between phases of reingestion and non-reingestion. At these times the rodents took feces into their mouths in the usual fashion, but then manipulated the pellet within the mouth for several seconds, using the tongue or forepaws. During transition from reingestion to non-reingestion, the animals rejected pellets with increasing frequency. Finally the animals ceased to examine feces and defecated in the head-up position. During the return to reingestion phase, the animals reinitiated feces-sampling behavior and increased the frequency of reingestion until finally feces were chewed and swallowed without delay.

Occurrence of Coprophagy in Rodents

Coprophagy is extensive in some rodent species and uncommon in others. Its occurrence is more strongly related to diet than to taxonomic association. *Dipodomys microps* (Heteromyidae), a kangaroo rat which feeds largely on leaves of perennial shrubs (Kenagy, 1972, 1973), reingested a mean of 26% of total fecal pellets produced. In a 24 h period of continuous observation four animals produced an average of 129 fecal pellets each. A related but primarily granivorous species, *D. merriami*, reingested almost no feces. Four individuals observed for 24 h produced an average of 25 fecal pellets. Two reingested one fecal pellet each and the other two reingested none. The herbivorous vole *Microtus californicus* (Cricetidae, Microtinae) ingested an average of 29% of total feces produced. Four individuals observed for 24 h produced an average of 93 fecal pellets.

We observed coprophagy in the following additional species: *Perognathus formosus*, *P. longimembris* (Heteromyidae); *Peromyscus maniculatus*, *P. crinitus*, *Neotoma lepida* (Cricetidae, Cricetinae); *Thomomys bottae* (Geomysidae); and *Aplodontia rufa* (Aplodontidae). Reingestion did not appear to be as common in all these species as in *Dipodomys microps* and *Microtus californicus*. However, our observations of the additional species were not as extensive as those of *D. microps* and *M. californicus*. We observed coprophagy in the squirrel family, Sciuridae, on only one occasion, when a *Spermophilus saturatus* reingested a fecal pellet which had

fallen to the floor of its cage. However, in several hours of observation of two other *S. saturatus* and of several individuals each of the sciurid species *Ammospermophilus leucurus* and *Eutamias minimus* we saw no additional signs of coprophagy.

Temporal Patterns of Coprophagy

We investigated the timing of coprophagy in two species which reingest feces extensively. *Dipodomys microps* showed a marked daily rhythmic alternation between a phase of reingesting all feces produced and a phase of reingesting no feces (Fig. 2). Coprophagy occurred primarily during an interval of about 8 h of the daytime, between 0900 and 1700 h. Of all feces reingested 95% were taken during the 12 h of daytime.

The phases of reingestion and non-reingestion were not mutually exclusive in individuals (Fig. 2). The times of overlap between the two phases represent a transition during which animals exhibit the feces-testing behavior described above.

The daily rhythmic alternation between reingestion and non-reingestion in all four kangaroo rats is particularly remarkable in light of two additional facts. First, two animals (Nos. 1 and 2) were on an exclusive diet of lettuce and two others (Nos. 3 and 4) received only seeds and water. Thus the coprophagy rhythm was expressed despite sharply contrasting differences in dietary quality. Second, the animals consumed their food more or less continuously both day and night; this observation applies more strictly to the animals eating lettuce than to those eating seed. In any event the reingestion of feces shows a biphasic daily rhythm whereas food consumption continues both day and night.

Microtus californicus did not show the twice-daily alternation between reingestion and non-reingestion which was exhibited by *D. microps*. In contrast, *M. californicus* alternated frequently throughout the day and night between reingestion and non-reingestion (Fig. 3). As a result coprophagy occurred with nearly equal frequency in both day and night.

The general temporal pattern of reingestion and non-reingestion was not influenced by sharply contrasting differences in diet

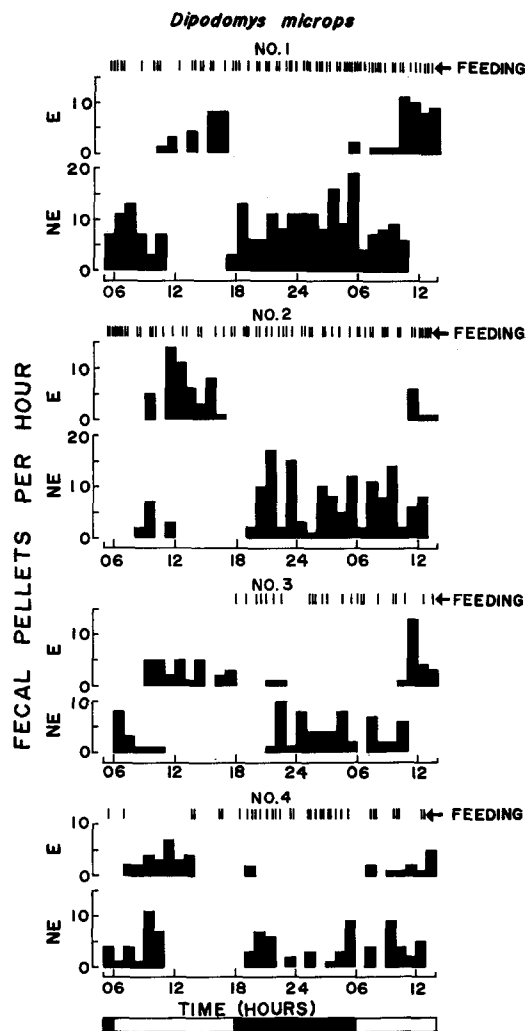


Fig. 2. Daily rhythm of coprophagy in the Great Basin kangaroo rat *Dipodomys microps*. Individual records are shown for four animals each over a period of 33 h of continuous observation. The vertical bars show numbers of fecal pellets eaten (*E*) and not eaten (*NE*) in each hour, and the single vertical lines labelled "Feeding" indicate quarter-hour periods in which each animal fed. Animals 1 and 2 were provided with lettuce only and animals 3 and 4 with seeds and water. The black and white horizontal bar at the bottom of the figure represents the daily light-dark cycle of LD 12:12

offered to the four *M. californicus* (Fig. 3). Like *D. microps*, *M. californicus* consumed food both day and night.

Temporal Patterns of Gut Activity

The feces-testing behavior of rodents suggests that reingested feces differ in quality from non-reingested feces. Because the rhythm of coprophagy was more marked in *D. microps* than in any other species we investigated, we studied *D. microps* in further detail in order to compare the characteristics of reingested and non-reingested feces.

Water content of feces showed a maximum at midday (Fig. 4), during the middle of the reingestion phase (Fig. 2). Quality of the solid matter in feces was examined in freshly captured animals maintained on their natural diet of saltbush (*Atriplex confertifolia*)

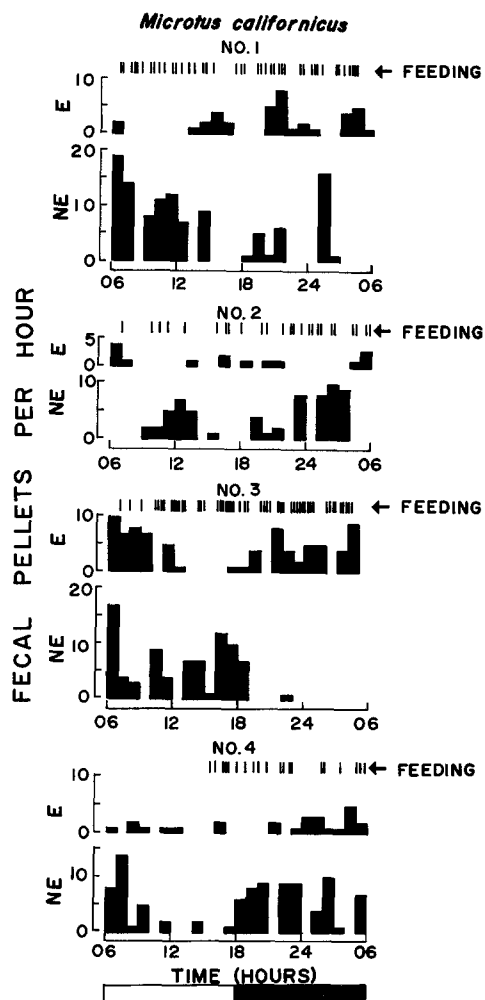


Fig. 3. Daily temporal pattern of coprophagy in the California vole *Microtus californicus*. Individual records of four animals are shown for a period of 24 h of continuous observation. Explanation as in Fig. 2. Animals 1 and 2 received lettuce only and animals 3 and 4 received lab chow and water

leaves (Fig. 5). Ash content was significantly lower in the reingested type of feces than in the non-reingested feces ($p < 0.01$, *t*-test of paired means). Nitrogen content was significantly greater in the type of feces that are reingested ($p < 0.05$) than in the non-reingested type of feces. The energy content, however, was essentially identical in eaten and not-eaten types of feces.

We measured mass and pH of four sections of the gut of *D. microps* in order to examine the mechanism of cyclic change in composition of the feces. In the experiment measuring the rhythm of fecal water content (Fig. 4), we found no significant temporal change in mass of the stomach, caecum, small intestine, or large intestine. Furthermore pH did not vary within any of these four compartments of the gut during the course of the day. Modal values were 7.2 in the lower small intestine and 6.4 in the caecum and upper large intestine.

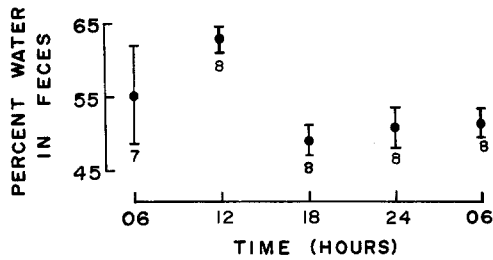


Fig. 4. Daily pattern of water content in feces of *D. microps* on a diet of seeds and lettuce. Fecal pellets were removed from the last 3 cm of the colon from animals killed at five different times of day. Vertical bars indicate 95% confidence interval around the mean, and number beneath each bar is sample size

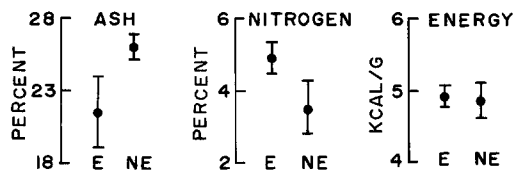


Fig. 5. Comparison of ash, nitrogen, and energy content of reingested ("eaten"=E) and non-reingested ("not eaten"=NE) types of feces. Both types of feces were collected from six freshly captured *D. microps* fed exclusively on their natural diet of *Atriplex confertifolia*. Non-eaten feces were collected from a clean cage during 14 h of the non-reingestion phase of the daily rhythm. The "eaten" type of feces were obtained by killing the animals at noon on the same day and removing fecal pellets from the terminal 3 cm of the colon. Mass of ash is expressed as percent of dry mass of feces; mass of nitrogen as percent of ash-free mass; and energy content as kilocalories per g ash-free dry mass. Vertical bars indicate 95% confidence interval around the mean

There are two possible explanations for the mechanism of daily cyclic change in the nitrogen and salt content of feces: (1) function of some compartment of the digestive tract changes cyclically during the day or (2) function of all compartments remains qualitatively the same, but there is a daily cyclic emptying of caecal contents during the reingestion phase. The constant mass of the four gut compartments throughout the day would seem to preclude explanation (2).

Discussion

Our observations show that coprophagy is a widespread, adaptive component of the nutritional biology of rodents. We found that coprophagy occurs in freshly caught animals and in a wide variety of species. The extent of its use by various species correlates with differences in diet. In relatively more herbivorous species, where coprophagy is more extensive, there is an organized rhythmic pattern of coprophagy which correlates with the activity pattern of the species. Feces which are reingested contain more nitrogen and water and less salts than non-reingested feces.

Daily rhythmic variation in the environment provides the selective pressure for temporal organization of adaptive behavioral processes (Kenagy, 1980; Daan, 1980). Previous attention has focused on temporal patterns of activities such as foraging, social interaction, and other overt activities. It is now apparent that rodent species for which coprophagy is of major importance ex-

hibit a high degree of temporal organization of this behavior as well. The timing of coprophagy involves interaction with external rhythmic events, and with foraging and ingestion of food. The timing of coprophagy also involves internal temporal coordination with physiological processes in the gut. Although daily rhythmicity of coprophagy has not previously been reported for rodents, consistent daily rhythmic patterns of coprophagy have been observed in lagomorphs, both in the field and in the laboratory (see previous citations on lagomorphs; Heisinger, 1962), and more recent experimental work has further clarified the nature and extent of this rhythmicity in rabbits (Jilge, 1976, 1979; Hörnicke and Batsch, 1977).

Two of the species which we investigated illustrate adaptive variation in natural rhythms of activity, foraging, feeding, and reingestion of feces. *Dipodomys microps* is only active on the surface and foraging at night (Kenagy, 1976). It shows only a single daily phase of reingestion amounting to about 8 h, during the daytime (Fig. 2). The activity of *Microtus californicus* contrasts strongly with that of *D. microps* in that it may be active on the surface, and thus foraging as well, both night and day (Pearson, 1960). In association with structural adaptations of the gut to a high-bulk diet (Vorontsov, 1962), such microtine rodents are furthermore known to exhibit short-term (2-3 h) cycles of activity and feeding (Lehmann, 1976; Daan and Slopsema, 1978). We suggest that the multiphasic alternation between reingestion and non-reingestion in *M. californicus* (Fig. 3) is correlated with adaptation for such short-term cycles of activity and feeding.

Strategies of digestion and assimilation are highly diverse within the order Mammalia. The strategy of pregastric fermentation (rumination) is characterized by immediate assimilation in the rumen and small intestine. Caecal fermentation, on the other hand, requires either (1) the development of specialized absorptive capabilities in the caecum or large intestine (Sperber, 1967) or (2) the reingestion of feces and subsequent assimilation of the derived nutrients upon their return to the upper digestive tract upon recycling. We have now observed that reingestion of feces is widespread in the order Rodentia. The rodents and members of the order Lagomorpha (rabbits, hares, and pikas) are the two major groups of small mammals which show caecal fermentation and reingestion of feces. Coprophagy is more strongly developed in the lagomorphs as a group than in the rodents. Presumably this is because lagomorphs are among the most highly herbivorous of small mammals. Coprophagy in rodents, which as a group are more omnivorous than lagomorphs (Landry, 1970), appears to be more common among the more herbivorous species. Coprophagy in shrews (order Insectivora) is a somewhat different phenomenon, because the diet of these animals is largely insectivorous and they possess no caecum.

Although lagomorphs and rodents both reingest feces, there are several differences in their patterns of reingestion. Reingested and non-reingested feces differ more sharply in composition in lagomorphs than in rodents. Additionally rodents chew their feces extensively before swallowing, whereas lagomorphs swallow the feces whole. These contrasts suggest that there must be further differences in the products of caecal fermentation and in the sites and extent of their absorption.

The nutritional benefits of coprophagy in rodents include several possibilities, the relative importance of which can only be determined by further investigation. Yields of energy, vitamins, essential amino acids and nutrients could all be increased by coprophagy, but their relative amounts and the site and mechanism of their resorption is not clear. Rhythmic organization of coprophagy behavior coupled with digestive rhythmicity is adaptively

significant, but the cyclic events in the gut responsible for the rhythm of composition of feces are unknown.

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