

Daily Rhythms of Food Intake and Feces Reingestion in the Degu, an Herbivorous Chilean Rodent: Optimizing Digestion through Coprophagy

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ABSTRACT

Animals must match their foraging and digestion to seasonal changes in availability and quality of food. When these parameters decline, the animal's performance limits for extracting energy and nutrients may be challenged. In the laboratory, we investigated daily patterns of food processing on a low-quality (high-fiber) diet of alfalfa in an herbivorous, day-active rodent, the degu (*Octodon degus*), which inhabits semiarid central Chile. We manipulated timing of food availability, from continuous availability down to as little as 5 h/d. Degus maintained weight while digesting only 53% of dry-matter consumption. With food continuously available in a metabolic cage, the animals ate more food and deposited about twice as much feces in the day as at night. Continuous 24-h behavioral observation revealed that degus were actually defecating at the same rate both night and day but then ingesting most of the feces they produced at night. Further experimental treatments challenged animals with limited periods of food availability that matched natural foraging patterns. With either 11 h of daytime food availability or only 5 h (in morning and afternoon periods of 2.5 h each), degus consumed as much food as those with 24-h food availability. Continuous 24-h behavioral observations revealed in the 11-h group that nearly all feces produced at night were reingested and nearly none were reingested in the day, whereas the 5-h group resorted to further coprophagy during the 6-h midday interval with no food. Despite these differences in timing of food intake and coprophagy in response

to the three experimental treatments, the degus were defecating at the same rate both night and day, which indicated a constant rate of output from the colon. This suggests a range of adjustments of digestive physiology to the timing of gut function by balancing coprophagy with ingestion of food. Overall, 38% of 24-h feces production was reingested, and 87% of this coprophagy occurred at night. The ingestion of feces during parts of the day when food is unavailable provides for continued intake into the digestive tract and appears to represent an increase in overall efficiency of gut use.

Introduction

On a daily basis, animals search for and ingest food in discrete blocks of time that vary minute by minute, hour by hour, and from day to night. The basic structural and functional design of an organism, its behavior, and its environment determine the limits on what food can be obtained and ingested and when. Although the input of food into the digestive tract is typically periodic, it is clear that some aspects of gut function, particularly in endotherms, are likely to be operating more or less continuously day and night. Optimal timing and efficiency of digestion are, therefore, dependent on a balance among behavioral strategies, ecology, and the physiology of the digestive tract.

Herbivorous rodents are interesting among small mammals because of their high rates of food intake and use of foods that are abundant but low in quality (Vorontsov 1962). As "hindgut fermenters," these rodents rely on microbial fermentation in the cecum and subsequent reingestion of feces (coprophagy) to enhance the extraction and absorption of nutrients in their diets (Kenagy and Hoyt 1980; Stevens and Hume 1995). Just as the ingestion of food is limited to discrete times of day and organized rhythmic bouts (Aschoff et al. 1983), coprophagy in rodents is rhythmic and complementary to feeding, apparently being employed mainly during the rest phase of the 24-h cycle (Kenagy and Hoyt 1980). Although few data are available that address the optimization of gut use in small herbivorous mammals that are hindgut fermenters (Sibly 1981; Stevens and Hume 1995), theoretical analyses have suggested that the use of coprophagy provides energetic and nutritional benefits for

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these animals under conditions of low food quality and high volume of ingestion (Alexander 1993).

We present an analysis of variables that must be balanced by an herbivorous rodent to maintain an adequate daily rate of energy and nutrient extraction when challenged with a low-quality diet. We studied the degu (*Octodon degus*, family Octodontidae), a common, herbivorous caviomorph rodent in semiarid regions of central Chile, and the only small mammal active in the daytime in this area (Bustos et al. 1977; Yañez and Jaksic 1978). Although degus in captivity preferentially ingest high-quality (low-fiber) food (Bozinovic 1997), they are able to digest low-quality (high-fiber) diets (Veloso and Bozinovic 1993; Bozinovic 1995), and they are faced with the use of low-quality food for much of the year in nature (Meserve et al. 1984; Zunino et al. 1992). In the present study, we provided degus with a diet of alfalfa pellets, which is relatively low in quality and high in fiber. We then further restricted the daily timing of food availability to reflect ecologically realistic situations, rather than the typical laboratory paradigm of continuous food availability. In preliminary field observations, we found that, in the dry period that follows the annual reproductive season, degus consume dry grasses and other fibrous plant materials and that the daily foraging time of the study population is limited to only about 5 h/d, consisting of morning and afternoon intervals of about 2.5 h each. We designed our laboratory studies to provide treatment groups with food availability restricted to 11 h/d and 5 h/d. We report here on the amounts of food consumed and feces deposited by animals in metabolic cages, and then we provide a further quantitative analysis of the amount and temporal distribution of feces production (defecation) and coprophagy during the day and night in animals that we observed directly and continuously in a specially constructed apparatus.

Material and Methods

Animals, Maintenance, and Experimental Plan

Degus were captured near Lampa Metropolitan Region of Santiago, Chile, in November 1996 (experiment 1) and April 1997 (experiment 2). They were maintained in an animal room at $22^{\circ} \pm 2^{\circ}\text{C}$. They were fed a diet solely of pure alfalfa pellets (no supplementary materials included), and water was provided continuously. Analysis of our alfalfa pellets by the Laboratory of Analytical Services at the Faculty of Agronomy, Catholic University of Chile, indicated neutral detergent fiber of 49.7%, acid detergent fiber of 38.1%, crude fiber of 32.8%, crude protein of 13.7%, and lipids of 1.7% on a dry-matter basis.

Animals used in experiment 1 were provided with pellets ad lib. and exposed to a photoperiod of 13L : 11D, with lights on 0700–2000 hours, a regime that prevailed in the facility prior to our initiation of a uniform experimental design. The 10

animals used in these studies maintained mass throughout the 5 wk of data collection.

Animals in experiment 2 received food ad lib. only during restricted hours of the daytime: one group for 11 h/d (0730–1830 hours) and another group for only 5 h, consisting of two bouts of 2.5 h each (0730–1000 hours and 1600–1830 hours). The photoperiod during experiment 2 was 12L : 12D, with lights on 0700–1900 hours. The 10 animals receiving food 11 h/d and the 11 animals on 5 h rations maintained mass throughout the studies. Upon capture and arrival in the laboratory, all of these animals were immediately restricted to receive pellets for 11 h/d; the decrease to 5 h was made 3 d before the beginning of the first measurements.

Animals were initially held in plastic box cages of $33 \times 33 \times 16$ cm, which were covered with a wire grill, and maintained in wood shavings. “Metabolic cages” were used to determine food consumption and feces deposition; they were of galvanized sheet metal, with wire grill floors and fronts (6-mm space between wires), a collection tray beneath the floor grill, and overall dimensions of $30 \times 30 \times 20$ cm.

Digestibility, Consumption of Food, and Production of Feces

Food consumption was monitored in the metabolic cages in conjunction with the regular addition and removal of food required to maintain the degus on the respective temporal patterns of food availability. A surplus of preweighed food was provided for each period, and the remaining food retrieved from the cage (both the grill floor and the collecting tray) at the end of the period; the difference in wet weight for each period was corrected for water content, which we determined to be 6.2%, and thus, all values of consumption are presented on a dry-mass basis.

We determined the apparent dry-matter digestibility of the alfalfa diet by animals in the two experiments and three groups over the same 48-h period for which food consumption and feces production were being determined for the animals in metabolic cages. For the 48-h period, we obtained total dry mass of food consumed, subtracted dry mass of feces produced, and divided by the total dry mass of food consumption; materials were always dried at 80°C in an oven to constant mass, over about 24 h.

We determined day versus night patterns of food ingestion for 48 h in the metabolic cages by collecting and weighing leftover food just after lights-on and just before lights-off in experiment 1 and over each feeding interval of 2.5 h or 11 h in experiment 2. Likewise, to determine day-night patterns of feces deposition, we collected, counted, dried, and weighed all feces just after lights-on and just before lights-off in all experimental groups for the same 48-h period in which food consumption was measured.

Table 1: Daytime versus nighttime consumption of alfalfa pellets and deposition of feces by degus living in metabolic cages on a regime of continuous food availability and photoperiod of 13L : 11D

	Day	Night	Total
Food consumption (dry mass, g)*	9.40 ± 1.46	5.68 ± .94	15.08 ± 2.08
Feces deposition (dry mass, g)*	4.96 ± .70	2.34 ± .37	7.30 ± .91
Feces deposition (<i>n</i> of pellets)*	119.8 ± 27.3	62.2 ± 9.5	182.0 ± 33.7

Note. Values are means ± SD. Feces deposition refers to pellets collected in the metabolic cage, that is, not accounting for feces that were reingested (*n* = 5).

* *P* < 0.01, paired *t*-test, indicating probability that day and night values differ.

Continuous Visual Observations of Feeding, Activity, Coprophagy, and Defecation

We observed four degus from each of the three treatments in experiments 1 and 2 in a special apparatus that allowed us to record timing of feeding, activity, defecation, and coprophagy for a full 24-h period. The animals were placed in the apparatus for an initial 3-h period, for which data were discarded, and then beginning with the evening lights-off, data were recorded for the entire night and the following day. These observations were made in a different room from the animal room, under bright overhead fluorescent light in the day, alternating with a pair of 25-W incandescent bulbs filtered through heavy brown paper at night, corresponding to the timing of the photoperiod on which each group was maintained. The observation apparatus was similar to that used in earlier research (Kenagy and Hoyt 1980), and in addition to its use for the reported 27-h periods, it was also used earlier for several shorter periods to obtain our first impressions of the existence and nature of feces reingestion behavior in degus. Our apparatus was a 60-cm-long aquarium mounted on a rack, beneath which was fixed a mirror of 58 × 43 cm at a 45° angle. With the mirror arranged at the eye level of the observer (two of us, who alternated, observing one at a time, during the three 27-h studies), it was possible to observe comfortably and as close as necessary to record all of the parameters simultaneously from four animals. Each of the four animals was placed in an aluminum cylinder of 15.5 cm diameter and 18 cm height and covered with a wire screen on top. In experiment 1, no water was provided; instead of water, occasional pieces of cucumber provided a water source. In the two sets of observations for experiment 2, we mounted a small water bottle on each cylinder, allowing the usual avenue of ad lib. water availability.

Results

Degus maintained or gained body mass over a period of 20 d under all the conditions reported here. During the 48-h measurements of food consumption and feces deposition in metabolic cages, each group remained within 1% of original mass.

For experiment 1 (continuous food availability), initial mean mass was 170.4 ± 22.2 g (*n* = 5, mean ± SD). For experiment 2 (periodic food availability), group A, with 5 h food, had an initial mean mass of 180.0 ± 29.3 g (*n* = 11), and group B, with 11 h food, had an initial mean mass of 179.6 ± 27.6 g (*n* = 10). Group A was treated like group B for the first 13 d of maintenance (11 h of food availability daily) and was shifted to 5 h only for the last 7 d. Digestibility of the alfalfa diet did not differ significantly among the three treatments, which differed in daily duration of food availability (arcsine transformation, *P* > 0.05), and the overall mean dry-matter digestibility was only 52.8% ± 1.7% (*n* = 26), which is comparable to that of the low-quality foods consumed in nature.

We found that reingestion of feces (coprophagy) amounted to a substantial component of total daily ingestion in the degus, which were all maintaining body mass and energy balance under the different imposed temporal regimes of food availability. We initially discovered the use of coprophagy through direct observations of the behavior viewed from beneath the animals with a mirror. Degus took individual fecal pellets, only one at a time, directly from the anus into the mouth by flexing the trunk and placing the mouth near the anus and without assistance from the hands. Each reingestion event was accomplished, beginning from a standing posture, within about 1 s. On occasion, a fecal pellet was grasped by the hands and examined and tested in the mouth, then either fed into the mouth or rejected. Each pellet was chewed for the better part of a minute before being swallowed. Jaw movements appeared exaggerated and included a great deal of side-to-side motion. Individuals ingesting feces during periods of sleep remained in a stance while sleeping, then appeared to waken briefly and remove and ingest each pellet one at a time as it emerged. Individuals that were not ingesting feces during a period of sleep stretched out flat on their bellies or sides and allowed feces to pass uneventfully and without inspection.

Experiment 1: Continuous Food Availability

Day versus Night Patterns of Feeding and Feces Deposition. Degus with food continuously available consumed at least 60% more

food and deposited more than twice the feces in the day as at night (Table 1). Note that we refer to “deposition” of feces based on our retrieval of fecal pellets from the metabolic cage; this measure of apparent defecation is limited because it ignores coprophagy and, thereby, information on the total number of pellets that actually exited from the anus (defecation); we refer, below, to feces “production” as the actual number of pellets observed to leave the anus.

Because the 13L : 11D photoperiod used in our first experiment contains a daytime that is 18% longer than the night, we can correct the data accordingly, which yields a reduction in the hourly rates during the daytime, as compared to the all-day rates. With these corrections, the consumption of food per hour was 40% greater in the day than at night (rather than 60%), the production of fecal mass was about 80% greater in the day (rather than being double), and the number of fecal pellets was about 60% greater in the daytime (rather than being double).

24-h Rhythms of Feeding, Defecation, and Coprophagy. To investigate the total daily quantitative significance of coprophagy in relation to food consumption and digestion, we directly watched and recorded the behavior of four individuals in our observation apparatus simultaneously and continuously for a full day and night. We recorded times of all food consumption, feces production (defecation), and reingestion; counted numbers of fecal pellets produced and consumed; and measured amounts of food consumed during the day and night. Reingestion occurred mainly during the night, but some feces were also consumed in the day (Fig. 1). Defecation appeared to occur at a comparable rate both day and night.

Over 24 h, the continuously observed degus showed a day-night feeding rhythm like that of the degus held in metabolic cages, in that mass of daytime consumption and total time spent consuming food in the day were significantly greater than at night (Table 2). Total mass of food consumed was somewhat lower in the animals observed continuously than in those living in metabolic cages (cf. Table 1), perhaps due to behavioral inhibition associated with the novelty of being observed continuously.

A strikingly different 24-h pattern appeared when we made continuous visual observations of the animals. The number of pellets produced from the anus was essentially the same day and night, but at night, more than half of those feces were eaten, and, thus, fewer feces were deposited in the cage (Table 2). About 3.5 times as many feces were consumed at night as in the day.

Experiment 2: Intermittent Food Availability

Day versus Night Patterns of Feeding and Feces Deposition: 11-h versus 5-h Food Availability. Total daily consumption of food did not differ significantly ($P > 0.05$, Mann-Whitney U -test) be-

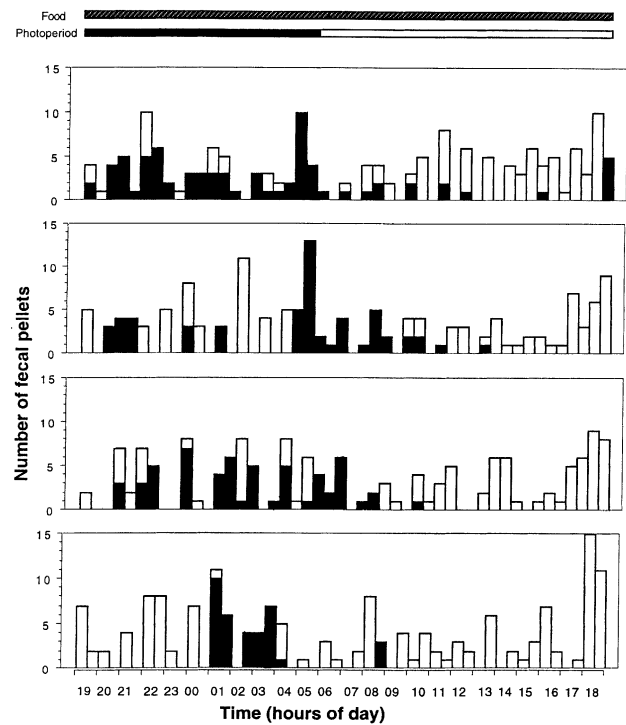


Figure 1. Daily rhythmic patterns of production (defecation) and consumption of feces in four degus observed continuously for 24 h on a regime of continuous food availability and a photoperiod of 13L : 11D. Each panel represents a single degu. The upper tracing in each panel represents total fecal pellets produced each half hour. The darkened records indicate the total of the former that were reingested. Horizontal bars at top represent hours of food availability (dark stippling) and hours of light and dark in the photoperiod.

tween the degus that had alfalfa pellets available for 11 h/d ($n = 10$) and 5 h/d ($n = 11$), with mean values of 14.6 ± 2.4 g (dry mass) for the former and 12.7 ± 3.4 for the latter. In the group with only 5 h/d food availability, animals consumed significantly more in the 2.5 h of afternoon availability (7.1 ± 1.9 g) than in the 2.5 h of morning availability (5.6 ± 1.6 g; $P < 0.001$, paired t -test).

Deposition of feces in metabolic cages was considerably greater in the day than at night in both food-availability treatments (Table 3). Degus with 11-h food availability deposited more feces in the day than the group with 5-h food availability, both in terms of mass and number of fecal pellets. The small overall quantity of feces deposited at night did not differ significantly between the 11-h and 5-h treatments (Table 3).

24-h Rhythms of Feeding, Defecation, and Coprophagy. We observed four each of the animals on the 11-h and 5-h food-availability treatments continuously for 24 h, as with the ani-

Table 2: Daytime versus nighttime food consumption and the production (defecation) and consumption of feces by degus with continuous food availability during a 24-h period of continuous observation (Fig. 1)

	Day	Night
Food consumption(dry mass, g)*	7.65 $\pm$ 1.45	4.88 $\pm$ 1.47
Time ingesting food (min)*	115.0 $\pm$ 15.8	58.5 $\pm$ 14.3
Feces production (<i>n</i> of pellets)**	77.5 $\pm$ 8.4	77.5 $\pm$ 1.7
Feces consumption (<i>n</i> of pellets)*	12.3 $\pm$ 6.8	43.5 $\pm$ 12.2

Note. Values are means $\pm$ SD. Feces production refers to all pellets that passed from the anus (defecation), and feces consumption is the number of that total that was eaten ($n = 4$).

* $P < 0.05$; Friedman test, indicating probability that day and night values differ.

** $P > 0.05$; Friedman test, indicating probability that day and night values differ.

imals in experiment 1. The degus with 11-h daytime food availability showed discrete and consistent unimodal patterns of coprophagy, concentrated in the night, when food was not available (Fig. 2). Feces production appeared to occur at a uniform rate over both day and night. The degus with two 2.5-h bouts of food availability, totaling only 5 h/d, likewise showed uniform continuous feces production day and night, and they also showed their most extensive coprophagy during the night; however, three of these four individuals resumed coprophagy during the six daytime hours from 1000 hours to 1600 hours when food was again not available (Fig. 3).

Total daily food consumption of the animals in our observation apparatus did not differ significantly among the three treatments (Kruskal-Wallis test, $P = 0.84$). Respective values (mean dry grams $\pm$ SD) were 12.5 ± 2.7 for the 24-h food availability regime (experiment 1), 14.3 ± 3.4 for 11-h food availability and 12.1 ± 2.1 for 5-h food availability (experiment 2).

While consuming the same daily amount of food under different temporal regimes of food availability, individuals in each

treatment made adjustments in duration of feeding bouts or "meal patterns," with longer meal durations in the animals that had shorter hours of food availability. Grand-mean feeding bout duration for the four individuals observed in each treatment was 5.8 ± 0.9 min/meal for continuous food availability, 15.0 ± 5.1 min/meal for 11-h food availability, and 19.8 ± 5.0 min/meal for 5-h food availability. Applying a Kruskal-Wallis test to these three groups of only four samples each, we obtained a significant difference ($P = 0.018$) with only the 5-h group differing significantly from the 24-h group in the a posteriori test. When we applied the same nonparametric analysis to values of food consumption rate, expressed in milligrams per minute, we found that this measure of the apparent instantaneous intensity of food consumption did not differ significantly among the three treatments ($P = 0.28$).

Direct counts of feces actually produced by the four animals observed in each of the three treatments revealed no significant differences among the three groups in numbers of pellets produced at night, numbers produced in the day, numbers consumed at night, or numbers consumed in the day (Table 4).

Table 3: Daytime versus nighttime feces deposition by degus on a photoperiod of 12L : 12D and living in metabolic cages on two different regimes of daytime food availability

	Day	Night	Total
Feces deposition (dry mass, g):			
11 h*	5.93 $\pm$ 0.97	1.16 $\pm$ 0.67	7.09 $\pm$ 1.32
5 h*	4.39 $\pm$ 1.21	1.50 $\pm$ 0.62	5.89 $\pm$ 1.72
Test ^a	$P < .01$	$P > .1$	...
Feces deposition (number of pellets):			
11 h*	141.2 $\pm$ 24.7	25.0 $\pm$ 13.5	166.2 $\pm$ 28.9
5 h*	101.0 $\pm$ 15.9	36.4 $\pm$ 10.4	137.4 $\pm$ 19.1
Test ^a	$P < .001$	$P > .01$	...

Note. Values are means $\pm$ SD. Feces deposition refers to pellets collected in the metabolic cage, that is, not accounting for feces that were reingested. The two regimes are: 11 h/d ($n = 10$) and 5 h/d, consisting of a morning and afternoon session of 2.5 h each ($n = 11$).

^a t -test indicating probability that 5-h and 11-h values differ.

* $P < 0.001$; paired t -test indicating probability that day and night values differ.

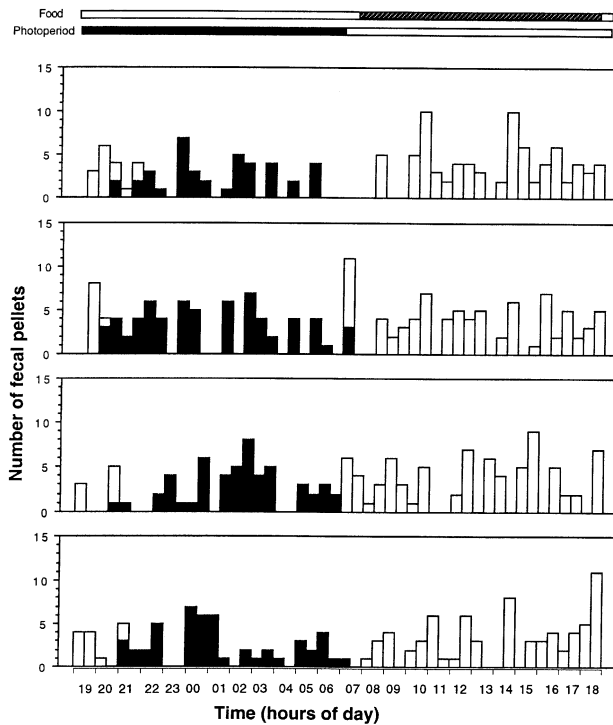


Figure 2. Daily rhythmic patterns of production (defecation) and consumption of feces in four degus observed continuously for 24 h, on a regime of 11-h food availability during the daytime and a photoperiod of 12L : 12D. Symbols as in Figure 1.

However, in each of the three treatments, the number of pellets consumed at night was significantly greater than the number consumed in the day, whereas the production of feces usually did not differ between night and day (Table 4).

Discussion

Our results indicate a role for coprophagy, together with adjustment in timing of food consumption and processing, in the extraction of the energy and nutrients required to maintain body mass. Challenged with a low-quality diet similar to what they encounter in nature, degus used coprophagy extensively, reingesting on average 38% of their 24-h feces production, with the majority of all coprophagy (87%) occurring at night (Table 4). Although alfalfa consumption was predominantly or exclusively in the day, depending on experimental treatment, the rate of fecal output was uniform both day and night, amounting to about 6 pellets/h (Table 4, daily total divided by 24). The animals whose temporal food availability was restricted to approximate natural conditions switched to eating feces when food was not available. The animals with 11-h food availability in the day averaged only one fecal pellet consumed in the day, and the animals restricted to only 5-h food availability consumed about nine pellets in the day, mainly during the midday

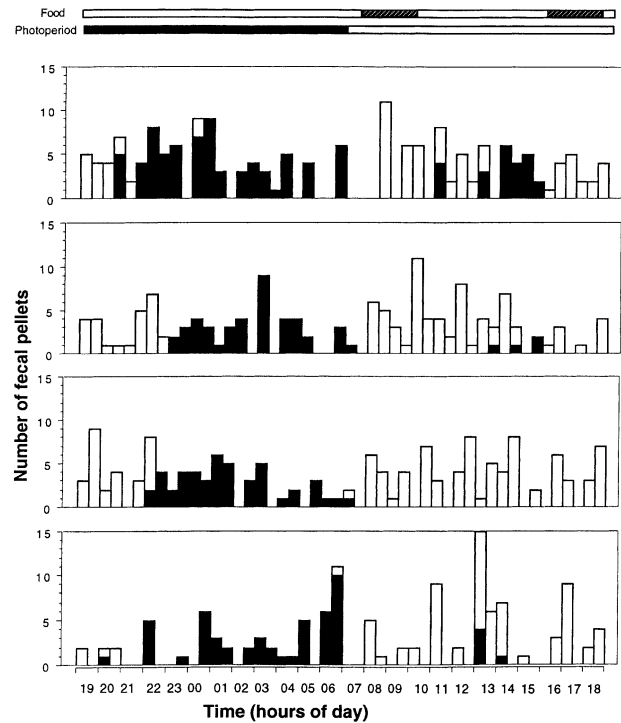


Figure 3. Daily rhythmic patterns of production (defecation) and consumption of feces in four degus observed continuously for 24 h on a regime of 5-h food availability during the daytime (consisting of two sessions of 2.5 h each) and a photoperiod of 12L : 12D. Symbols as in Figure 1.

period of no food availability, whereas both groups consumed more than 50 fecal pellets at night, when no food was available (Table 4; Figs. 2 and 3). The 52.8% digestibility of our experimental diet is at the bottom of the range of about 50%–88% digestibility reported for degus on a variety of artificial laboratory diets of varying quality (Veloso and Bozinovic 1993; Bozinovic 1995; Bozinovic et al. 1997). The diet we used is ecologically relevant as a seasonal minimum in quality, in that degus shift seasonally with availability, from fresh green herbs and grasses, later to fruits and seeds, and finally, in the driest part of the year following the breeding season, to dried vegetative plant parts including grasses (Meserve et al. 1984; Zunino et al. 1992).

Reingestion of feces (coprophagy) by small, herbivorous mammals has been inferred by investigators more often than it has been observed directly. Coprophagy has been documented in a variety of rodents and also in lagomorphs: the hares, rabbits, and pikas (Kenagy and Hoyt 1980; Stevens and Hume 1995). The pattern of fecal pellet production and consumption by lagomorphs differs from that of rodents, and perhaps cecal function and the derivation of energy and nutrients differ between these two orders of mammals. In lagomorphs, consp-

Table 4: Daytime versus nighttime production (defecation) and consumption of feces by degus during 24-h periods of continuous observation according to three different regimes of food availability

Food Availability	Day	Night	Total	Test ^a
Production of feces (<i>n</i>):				
24 h	77.5 ± 8.4	77.5 ± 1.7	155.0 ± 9.1	<i>P</i> > .05
11 h	77.5 ± 4.7	60.5 ± 7.5	138.0 ± 10.4	<i>P</i> < .05
5 h	75.0 ± 5.0	71.5 ± 15.8	146.5 ± 20.7	<i>P</i> > .05
Mean (<i>n</i> = 12)	76.7 ± 5.8	69.8 ± 11.8	146.5 ± 14.9	...
Test ^b	<i>P</i> > .05	<i>P</i> > .05	<i>P</i> > .05	...
Consumption of feces (<i>n</i>):				
24 h	12.3 ± 6.8	43.5 ± 12.2	55.8 ± 16.4	<i>P</i> < .05
11 h	1.0 ± 1.4	50.5 ± 9.1	51.5 ± 10.3	<i>P</i> < .05
5 h	8.8 ± 10.3	52.3 ± 10.3	61.1 ± 24.2	<i>P</i> < .05
Mean (<i>n</i> = 12)	7.4 ± 8.2	48.8 ± 11.5	56.2 ± 16.7	<i>P</i> < .05
Test ^b	<i>P</i> > .05	<i>P</i> > .05	<i>P</i> > .05	...

Note. Values are means ± SD. Feces production refers to all pellets that passed from the anus (defecation), and feces consumption is the number of that total that was eaten. The three regimes of food availability are 24 h (Fig. 1, *n* = 4), 11 h (Fig. 2, *n* = 4), and 5 h (Fig. 3, *n* = 4).

^a Friedman test, indicating significance of day versus night comparison. Production of feces is generally similar day and night; consumption of feces is much greater at night than in the day.

^b Kruskal-Wallis test, indicating no significant difference among three treatments (i.e., 24 h, 11 h, and 5 h).

uously soft feces derived from material that has resided in the cecum are apparently discharged during a brief period in the morning and evening, and all of these soft pellets are swallowed directly without chewing (e.g., Hirakawa 1994). As described in rodents here (see also Kenagy and Hoyt 1980), ingested feces do not differ conspicuously in texture and form from noningested pellets, and the former are simply ingested and then chewed, one at a time, at various times of the day. For small herbivorous mammals that are hindgut fermenters, it is not clear how coprophagy influences the overall balance of gut function and what role the cecum plays. Feces presumptively to be reingested by one rodent species contained higher levels of protein and water than the noningested feces, but the concentration of energy was indistinguishable in the two types of feces (Kenagy and Hoyt 1980).

It would be useful to understand how the three different daily regimes of food availability (24 h, 11 h, and 5 h) and the resulting differences in timing of ingestion led to energy and mass balance, while at the same time animals in each treatment showed similar rates of continuous day and night defecation (Figs. 1–3; Table 4). The design and function of animal digestive tracts have been examined from a variety of theoretical perspectives. The movement and processing of fluids and solids within and between the various “chambers” through the length of the tract has been modeled analogously to a series of treatments in linearly connected chemical reactors (Penry and Jumar 1987; Alexander 1991; Stevens and Hume 1995). The challenge for small herbivorous mammals, which as endo-

therms have particularly high mass-specific metabolic rates compared with large ruminant herbivores, has been to exercise further processes that can offset the metabolic disadvantage of small body size (Foley and Cork 1992; Cork 1994); coprophagy appears to be such an adaptation.

The basic functional significance of coprophagy in small mammals that are hindgut fermenters (Stevens and Hume 1995), that is, use the cecum or colon for microbial fermentation of digesta, is that, following digestion in the hindgut, the materials are returned to the foregut by coprophagy. Upon being recycled through the digestive tract, materials pass through areas where they can be absorbed and also subject to further processing and digestion; this provides the potential of a higher overall digestibility of a particular original bolus of food, but it occurs at the cost of a second passage. The paradox of measurements of digestibility is that standard techniques always incorporate coprophagy and double passage of gut contents without being able to identify the separate digestibilities of the first and second passages. Regarding the possibility of further processing, it is significant that degus (as well as other rodents; Kenagy and Hoyt 1980) chew the reingested fecal pellets, which suggests the possibility of further liberation of nutrients beginning with the second mastication. An important aspect of the potential role of the cecum in providing fermentation to liberate and even to synthesize nutrients is the demonstration that fluid and smaller particles can be retained preferentially there (Stevens and Hume 1995). An experimental study has shown that degus are capable of fluid retention in

the cecum (Sakaguchi and Ohmura 1992). Nutritional and energetic benefits of coprophagy in rodents have been demonstrated in studies that included experimental prevention of coprophagy by mechanical means (Daft et al. 1963; Fitzgerald et al. 1964; Cranford and Johnson 1989).

What are the ecological applications of the kind of flexibility in gut function and coprophagy that we have observed in degus? We have observed (G. J. Kenagy, C. Veloso, and F. Bozinovic, unpublished data) that the timing of daily foraging varies from the bimodal regime of 5 h/d (in two bouts of 2.5 h each) in summer, as simulated in our experiment 2, to essentially unimodal activity in midwinter, and finally to various bimodal activity situations in spring and autumn. Just as these environmentally defined windows for activity shift seasonally, the quality and availability of food also shift (Bozinovic 1995; Veloso 1997). Under natural conditions, coprophagy could be increased, for example, in response to either a decrease in diet quality or an increase in energy demand, such as during reproduction. These kinds of interactions need to be taken into account when typifying foraging and food processing for a species or when working with seasonal models of behavior, activity, and energetics. Seasonal dynamics have not typically been included in general and theoretical treatments of foraging (Stephens and Krebs 1986; Krebs and Kacelnik 1991).

Attempts to understand the limits to energy-processing rates in animals (Karasov and Diamond 1988; Kenagy et al. 1990; Hammond and Diamond 1992) must be developed in light of not only seasonal changes in the demands for energy (according to thermal conditions, reproductive performances, behavioral changes, etc.) but also in light of changes in food quality and quantity and further seasonal changes in the daily timing of inputs into the gut. We believe that recognition of the intensity and significance of coprophagy from our results should serve to encourage more attention to this phenomenon in physiological and behavioral investigations in rodents. Clearly, coprophagy occurs on a regular daily rhythmic basis, and our experimentation with temporally restricted food regimes demonstrates that when food is not available, rodents can switch to the consumption of feces. Under these conditions, feces are not placed in strict competition with food for space and time in the digestive tract. It is possible that coprophagy contributes more than previously thought to the survival and success of populations of small, herbivorous mammals.

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