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Behavioral Energetics of Lactation in a Herbivorous Carnivore, the Red Panda (*Ailurus fulgens*)

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With 5 figures

Abstract

In most mammals, the energetic costs of lactation significantly increase a female's daily energy requirements. Previous research indicates that such energetic costs may be met through changes in increased food consumption ranging from around 35 % to 150 %. In this paper, changes in food intake during lactation are measured in the red panda (*Ailurus fulgens*), a species of the order Carnivora which possesses a digestive system suited for a carnivorous diet but yet exclusively feeds on bamboo.

Four feeding characteristics were studied: duration of feeding bouts, number of bamboo leaves consumed per mouthful, number of bamboo leaves consumed per minute, and interval between mouthfuls of bamboo. In three lactating females, three of four feeding behaviors significantly increased up to 200 % above the rate observed during non-lactation. Males showed no change in feeding behavior during the same reproductive months with identical available foods. Red pandas appear to suffer a more severe energetic cost during lactation (at least with respect to food consumption) than other mammals previously studied. This may relate to their inefficient digestive capacity to process a herbivorous diet of bamboo. The data presented here suggest that general discussions of the relative costs of reproduction and in turn parental investment should include a female's relative digestive efficiency during stressful reproductive periods.

Introduction

The energetic costs of lactation are responsible for a major increase in the metabolic needs of a female mammal. Such costs may be paid out through increased ingestion of food, decreased respiration or changes in metabolic rate,

and/or utilization of stored energy (MILLAR 1977, 1978; RANDOLPH et al. 1977; CLUTTON-BROCK et al. 1982b; COSTA et al. 1986; for review, see GITTLEMAN & THOMPSON 1988). The reproductive energetics of only a few mammals have been studied in any detail (GITTLEMAN & THOMPSON 1988). These studies (primarily on rodents) indicate that, although changes in metabolism or use of fat deposits may occur, the consistent trend for all species examined to date shows dramatic changes in feeding behavior of lactating females. For example, CLUTTON-BROCK et al. (1982a) observed in red deer (*Cervus elaphus*) that hinds supporting calves grazed for approximately 2 h longer and on higher quality grasses than non-lactating hinds. Similarly, experimental studies on seven mammalian species (for complete listing of taxa and references, see 'Comparative Trends' below) all show dramatic increases in ingestion rates, ranging from 35 % in black-tailed deer (*Odocoileus hemionus*) to 149 % in the fox squirrel (*Sciurus niger*). Thus, the behavioral energetics of lactation may be important for measuring the actual cost of lactation and, in turn, parental investment (CLUTTON-BROCK et al. 1982a; ORTIZ et al. 1984).

Clearly, changes in feeding behavior during lactation depend to a certain extent on a female's condition (i.e. age, size, time of previous reproduction: see RANDOLPH et al. 1977; CLUTTON-BROCK et al. 1982a) as well as environmental conditions such as temperature, food availability and predation (see SADLEIR 1969). Many of these variables have been well-studied experimentally; however, because species other than domestic animals or rodents are rarely available for study, changes in feeding behavior during lactation are unknown for any species with an unusual dietetic niche, even though diet must be closely linked to lactation performance and energy allocation during lactation (see MCNAB 1986). The present work documents changes in feeding behavior with the onset of lactation in a herbivorous species of the order Carnivora, the red panda (*Ailurus fulgens*). These observations are then contrasted with comparative data on ingestion rates in other mammals to suggest that digestive efficiency influences the cost and behavioral energetics of lactation.

Except for anecdotal reports and short-term field observations on diet, home range movements and geographical distribution (see SCHALLER et al. 1985), all information on the red panda (*Ailurus fulgens*) is from captive studies (for review, see ROBERTS & GITTLEMAN 1984). The red panda is a solitary, herbivorous species of the order Carnivora, which inhabits mid to low elevations in temperate forests of the Himalayas and high mountains of northern Burma and western Sichuan and Yunnan provinces of China. Analyses of scat samples indicate that 95—99 % of their natural diet is comprised of bamboo leaves and shoots (ROBERTS & GITTLEMAN 1984; SCHALLER et al. 1985; K. JOHNSON, pers. comm.). In captivity, red pandas are strictly seasonal breeders (usually early Jan. to mid-Mar.), followed by a gestation period of 134.2 days (range 112—158 days), a litter size of one to four (mode 2), and exclusively maternal care. Compared to other carnivores, the red panda's growth pattern is slower than any other species' (GITTLEMAN & OFTEDAL 1987; OFTEDAL & GITTLEMAN 1988) and its behavioral development is also protracted: neonates weigh 110 to 130 g, grow at a rate of 7 to 20 g/d, eyes open at about 18 to 21 d, remain inside a natal nest for 2 to 3 months, and are

weaned around 4 to 5 months. As with the giant panda (*Ailuropoda melanoleuca*), it is hypothesized that these unusual reproductive characteristics are related to the bamboo diet, peculiar for a species of the order Carnivora (see GITTLEMAN & OFTEDAL 1987).

Methods

Data were gathered from May, 1983 to March, 1985 at the National Zoological Park (Smithsonian Institution), Washington, D.C. The observations presented herein are part of an ongoing study to examine behavioral development, maternal care, reproduction, and nutrition of red pandas. A total of six animals were studied, all housed outside in large (enclosure A = 330 m²; enclosure B = 115 m²) permanent enclosures with a natural grass substrate and access to trees, where they spend most of the daylight hours sleeping. In enclosure A, an adult female (with young) and adult male were observed through two reproductive seasons (for statistical analyses and figures these animals are represented by F1 and M1, respectively); in enclosure B, one reproductive pair was studied in 1983 (F2 and M2) and a different pair in 1984 (F3 and M3). A total of 952 obs. h were sampled.

The animals have access to three main sources of food: an oatmeal-like gruel (mixed with fruit); natural grasses, leaves or occasionally berries when in season; and bamboo leaves (usually one species of arrow bamboo, given to the animals twice a day). Although all animals readily eat the gruel or natural grasses, these foods are primarily supplemental, with no detectable change in the intake of these foods during lactation and bamboo comprising 90—95 % of the total duration of feeding. Undoubtedly, though, the caloric composition of gruel/fruit is high and would make up a greater proportion of total caloric intake.

When red pandas are eating bamboo, they have a distinct posture and method of feeding (see Fig. 1), similar to the giant panda (KLEIMAN 1983; SCHALLER et al. 1985). One bamboo leaf, or cluster of leaves, is grasped in a single forepaw and brought to the mouth while an individual is sitting, standing, or occasionally lying on its back. Leaves are inserted into the side of the mouth where they are sheared at the stalk, then chewed extensively before being swallowed (these observations have recently been verified in the field, K. JOHNSON, pers. comm.). This feeding behavior can be quantified and defined by four characteristics: (1) Feeding duration — when an animal is at a bamboo stalk and continuously pulling leaves to its mouth. In most cases (70 %), the beginning and end of a feeding bout, from which feeding duration was determined, is distinct because an animal approaches and then

Fig. 1: Posture and method of feeding in the red panda

leaves the bamboo with little time spent not feeding. In cases where animals paused between continuous feeding bouts, a given bout was distinguished from another when separated by 1 min; (2) Number of leaves per mouthful — number of leaves brought to the mouth in each paw movement during a feeding bout; (3) Number of leaves consumed per min — total number of leaves drawn into the mouth per min. When an individual was chewing a mouthful at the end of a 1-min sample but had not swallowed it, the mouthful was included in that sample; (4) Interval between mouthfuls — length of time (s) between taking leaves into the mouth.

It was difficult to gather data on the latter three feeding characteristics because the animal had to be seen in an unobstructed, head-on view for accurate observation. Red pandas are extremely sensitive to the presence of humans and, therefore, all observations were made from behind a natural blind. Consequently, the samples for these behaviors are smaller during certain observational periods (see Results) and correlations among the four feeding characteristics during a given feeding bout could not be calculated. Therefore, the results of changes in each feeding characteristic with respect to lactation must be considered separately.

Because a number of confounding variables may correlate with changes in feeding behavior, the following factors were considered in addition to lactation: litter size, growth rate of young, activity levels, temperature, and humidity.

Results

To account for variation among individuals, comparisons were made of feeding behavior during periods coinciding with before, during, and after lactation in each adult male and associated female. For females, significant differences were found among these periods with respect to duration of feeding, number of leaves taken per mouthful, and number of leaves (Table 1), with longer feeding bouts during lactation (Fig. 2) and greater number of leaves eaten per mouthful (Fig. 3) and per min (Fig. 4). For males, although sample sizes were reduced, no

Table 1: Analyses of feeding behavior across reproductive periods: females

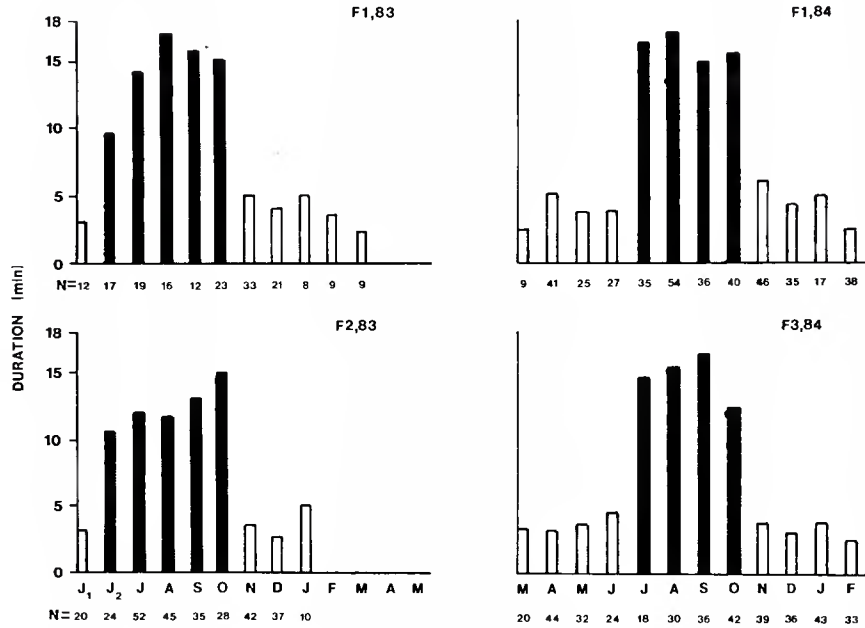| Animal	Variable	F value	P value
F 1, 83	Duration	54.30	.001
	Leaves/mouthful	6.30	.005
	Interval	1.02	n.s.
	Leaves/min	3.84	.025
F 2, 83	Duration	35.96	.001
	Leaves/mouthful	3.70	.025
	Interval	2.94	.10
	Leaves/min	4.25	.025
F 1, 84	Duration	216.01	.001
	Leaves/mouthful	4.37	.01
	Interval	2.37	.10
	Leaves/min	20.28	.001
F 3, 84	Duration	193.87	.001
	Leaves/mouthful	7.14	.001
	Interval	0.89	n.s.
	Leaves/min	3.25	.05

Fig. 2: Duration of feeding bouts across months in female red pandas. Black bars: months during which lactation occurred; abscissa: months and sample sizes. Individual animals are identified in upper right corner and further described in the text
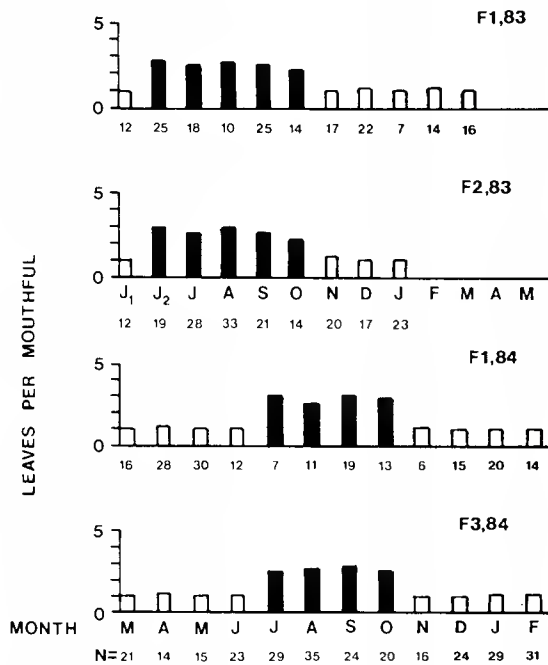

Fig. 3: Number of bamboo leaves eaten per mouthful during and outside of the lactation period in female red pandas. See Fig. 2 for details
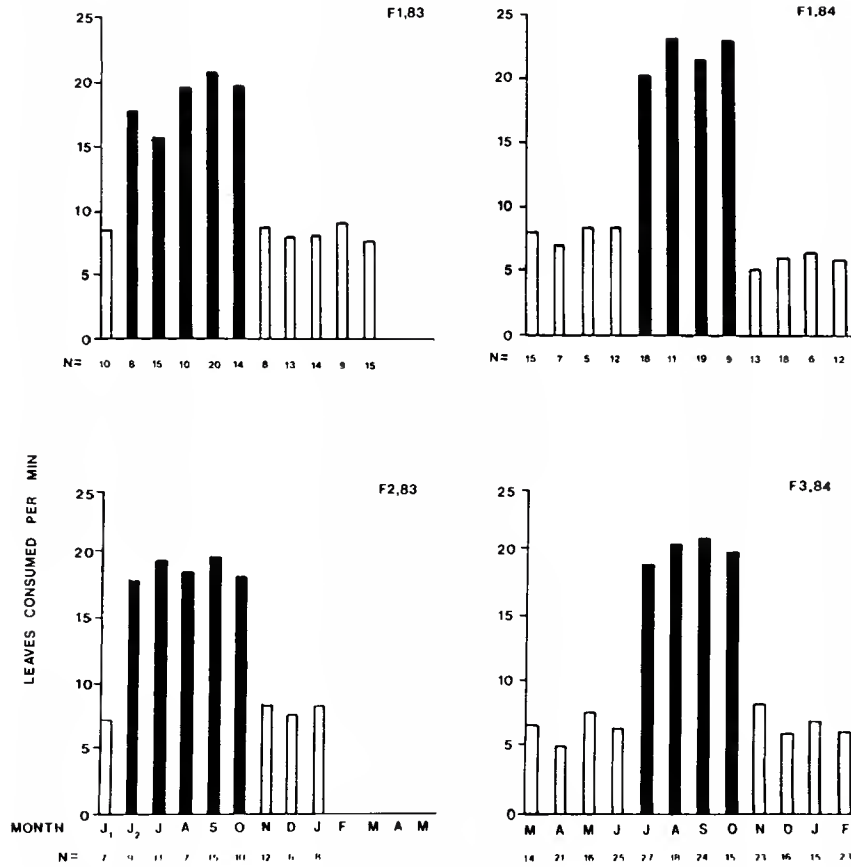
Fig. 4: Total number of bamboo leaves consumed per mouthful during and outside of the lactation period in female red pandas. See Fig. 2 for details

significant differences were observed with any feeding characteristic (Table 2) during the monthly periods during which lactation occurred (see, for example, Fig. 5).

Litter size was the same (N = 2 per litter) for each female across years, therefore this could not account for changes in feeding behaviors. The following factors were also found not to correlate with the observed significant changes in feeding (correlation coefficients, r, were calculated for each feeding characteristic after pooling samples for all adult females; statistics represent duration, leaves per mouthful, interval, leaves per min): growth rate — defined as incremental weight gain (g) per month of both young within each litter — (.01, .03, .06, .01); activity level — defined as total time period of walking or eating for each observation sample averaged across months — (.05, .03, .09, .03); temperature — defined as average temperature per day across months — (.02, .04, .05, .01); humidity (.02, .05, .06, .01).
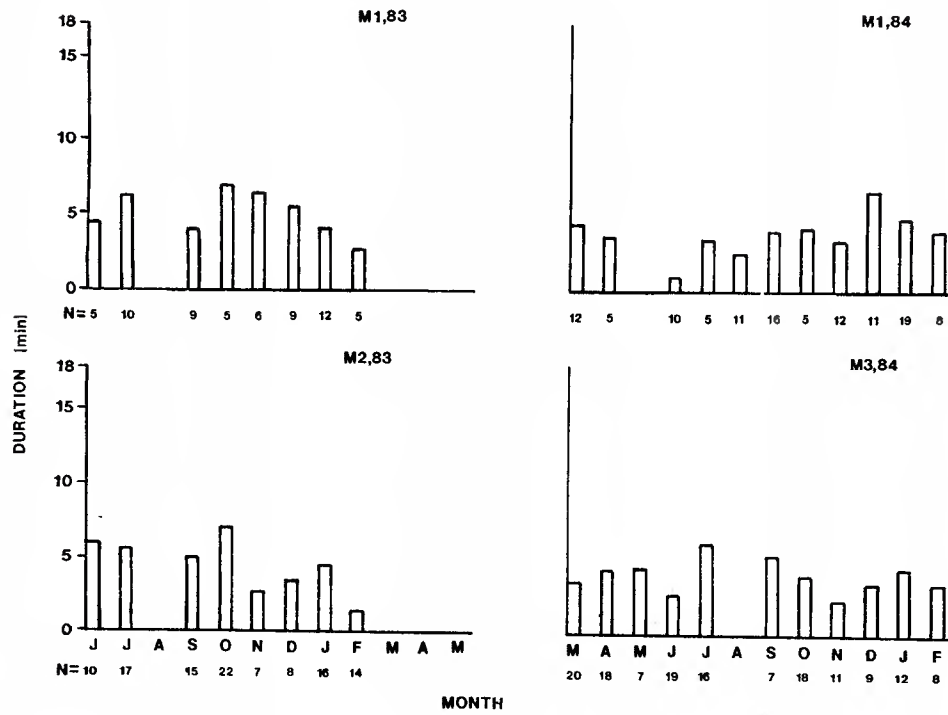
Fig. 5: Duration of feeding bouts for males during the same periods in which females were lactating. See Fig. 2 for details and see text for identification of individual males

Table 2: Analyses of feeding behavior across reproductive periods: males

Animal	Variable	F value	P value
M 1, 83	Duration	0.60	n.s.
	Leaves/mouthful	0.98	n.s.
	Interval	1.11	n.s.
	Leaves/min	0.56	n.s.
M 2, 83	Duration	1.01	n.s.
	Leaves/mouthful	0.66	n.s.
	Interval	1.42	n.s.
	Leaves/min	0.85	n.s.
M 1, 84	Duration	1.43	n.s.
	Leaves/mouthful	0.47	n.s.
	Interval	1.02	n.s.
	Leaves/min	0.91	n.s.
M 3, 84	Duration	1.05	n.s.
	Leaves/mouthful	0.74	n.s.
	Interval	0.43	n.s.
	Leaves/min	1.35	n.s.

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Table 3: Average increase in food intake during lactation

Species	%	Source
Common vole	133	MIGULA 1969
Bank vole	92	KACZMARSKI 1966
White-footed mouse	130	MILLAR 1975, 1978
Deer mouse	134	MILLAR 1979
Pine vole	48	LOCHMILLER et al. 1982
Cotton rat		
Tennessee	66	MATTINGLEY & McCLURE 1982
Kansas	111	MATTINGLEY & McCLURE 1982
Coypus	63	GOSLING et al. 1984
Black-tailed deer	35	SADLEIR 1982
Fox squirrel	149	HAVERA 1979

Discussion

The general results show that for three indicators of feeding behavior in the red panda (duration of feeding, number of leaves eaten per mouthful, total number of leaves eaten per min), significant increases occur during the lactation period. Increases in food intake have also been observed in lactating females of other eutherian mammals. However, the behavioral changes which are involved in the red panda's dietary shift as well as the extent (see Comparative Trends below) to which such changes occur, set this species apart from others.

In terms of actual behavioral changes, the most dramatic feeding index is the number of leaves eaten per mouthful. Males and nonlactating females methodically select one bamboo leaf (see Fig. 3) and extensively chew each leaf 4—10 times before swallowing and selecting another, but lactating females almost gorge themselves by eating 2—5 leaves per mouthful. Other studies have shown similar increases in food intake or a shift in preferred foods during lactation (BLAXTER et al. 1974; CLUTTON-BROCK et al. 1982b), but the red panda is unusual in that the feeding pattern actually changes with the onset of lactation.

The overall trend of significant increases in food intake during lactation could be explained by three other factors independent from the production of milk, and it is important not to assume that such factors are related to the lactation process per se (see GITTLEMAN & THOMPSON 1988). First, in some rodents, changes in food consumption during lactation have been shown to directly correlate with a rise in basal metabolic rate (BMR) (GLAZIER 1985a, b; see also McNAB 1980). Although red pandas have a relatively low BMR compared to other carnivores and adjustments in BMR are known to occur during physiological measurement in this species (McNAB 1988; pers. comm.), it is doubtful whether changes in BMR would explain much of the variation in feeding.

Second, in a variety of mammalian taxa increases in food consumption are related to life history characteristics such as larger litter sizes and rapid neonatal growth rates (RANDOLPH et al. 1977; MILLAR 1979; McCLURE & RANDOLPH 1980; MATTINGLEY & McCLURE 1982; GITTLEMAN & OFTEDAL 1987). As litter size was

consistent across females, this factor is not salient here. Nevertheless, growth rate may relate to food intake because neonatal development until weaning is exclusively controlled by milk reserves and, given greater nutritional demands during ontogeny, it is expected that maternal feeding behavior will reflect these demands. Even though growth rate did not correlate with change in any feeding index, it is probable that growth was an important factor but the resolution of monitoring food intake was simply not fine enough and, in measuring growth rate, no controls were taken for rate of energy loss in feces and urine.

Third, as female activity increases during lactation, in both attending young and feeding (CLUTTON-BROCK et al. 1982b; KÖNIG 1985), it is surprising that food intake did not correlate with activity levels during lactation. In breaking down the lactation period by day within months, it appears that activity does correlate with changes in feeding behavior in the first month of lactation (data are pooled for all females; duration: $N = 102$, $r^2 = 0.35$, $p < .01$; leaves consumed per min: $N = 79$, $r^2 = 0.30$, $p < .01$; leaves per mouthful: $N = 84$, $r^2 = 0.25$, $p < .05$), but not in subsequent months. To account for possible spurious results from pooling data (see MACHLIS et al. 1985), variances from individual animals were compared with pooled variance. Analyses reveal that variances with duration are significantly different ($F_{5,97} = 5.10$, $p < 0.05$), such that the previous analysis from pooling should be accepted with caution, but the remaining differences in variance were not significant (leaves consumed per min: $F_{5,73} = 2.34$, n.s.; leaves per mouthful: $F_{5,78} = 2.96$, n.s.). Because observations did not include many 24-h samples and nursing visits from the mother became more brief and nocturnal as lactation proceeded, it is difficult to determine the influence that activity levels exert on changes in feeding behavior of lactating red pandas.

Given that increases in bamboo consumption during lactation reflect (to a certain extent) the costs of lactation, it is interesting to note that changes in feeding behavior were not observed during other reproductive phases, especially gestation. Studies of the energetic costs of gestation have focused on caloric intake (GITTLEMAN & THOMPSON 1988), with increases in mean daily caloric intake over non-reproductive rates ranging from 0 % (REID 1961) to 46 % (National Research Council 1972). In general, though, for a given species caloric intake is (1) lower during gestation than lactation (MILLAR 1979; MCCLURE & RANDOLPH 1980) and (2) lower for larger mammals (many ungulates, carnivores and primates) that can utilize storage to offset the costs of gestation (FLEMING et al. 1981; FRISCH 1984; GITTLEMAN & THOMPSON 1988). Because adipose tissue is positively correlated with body mass (POND & MATTACKS 1985), it is possible that species the size of the red panda and larger (> 4 kg) will not significantly increase food intake during gestation, which may explain the lack of changes in feeding behavior during gestation.

Comparative Trends

Across mammals mean caloric intake during lactation increases from 35 % in black-tailed deer to 149 % in the fox squirrel (see Table 3 for comparative data and references). Although data presented here are not directly comparable to

other studies because of differences in measuring ingestion rates, these observations suggest that red pandas may increase food intake during lactation more than previously reported. From non-lactation to lactational periods, feeding duration changed from on average 5 to 15 min, an increase of 200 %; the number of leaves eaten per mouthful changed from 1 to 3, again an increase of around 200 %; and, the number of leaves eaten per min changed from 7 to 20, an increase of 186 %. In other species, as mentioned above, such changes have been explained in terms of variation in birth weight, litter size, maternal metabolic capacity or combinations of these factors (e.g. SMITH & MCMANUS 1975; MILLAR 1978; MATTINGLEY & MCCLURE 1982; SADLEIR 1982). A further factor which may explain the degree of food increase during lactation across species is digestive efficiency.

The digestive tract of the red panda is typical for a mammalian carnivore. Carnivores have a short intestine relative to their overall body length (DAVIS 1964; EWER 1973). The intestine of the red panda is approximately 260 cm in length in relation to a body length (excluding tail) of 56—62 cm (FLOWER 1870; ROBERTS & GITTLEMAN 1984). This body length to gut length ratio is more similar to that of carnivores than herbivores (BLEIJENBERG 1984). Further, the stomach of the red panda is a simple sac-like structure, with a relatively short colon and no caecum. Thus the red panda contains no modifications of the digestive tract to lengthen the retention time of digesta or to harbor microbial populations to enable the utilization of plant material as food. Systematic analyses have not been performed on the digestive capacity of the red panda although studies are now in progress (GITTLEMAN & OFTEDAL, in prep.). However, in the giant panda (*Ailuropoda melanoleuca*), a species with similar anatomical and physiological constraints, passage of digesta reveals that: (1) between 6—17 % of body weight in dry matter is consumed per day in comparison to at least 60 % in most ungulate species eating grasses; (2) given digestive coefficients of 27 % for hemicellulose and 8 % for cellulose, microbial digestion is minimal; (3) passage of digesta through the gastrointestinal tract is extremely rapid, with complete clearance of liquid and particulate markers in less than 12 h; and, (4) food intake of adults in the wild is estimated at 10—18 (average 12.5) kg per day of bamboo (DIERENFELD et al. 1982; VAN SOEST 1982; SCHALLER et al. 1985; SCHALLER et al. 1988). All of these digestive indices reflect a species which processes its primary diet (bamboo) poorly. To offset this digestive inefficiency, the red panda and giant panda may have to increase food intake during stressful periods (i.e. lactation) more than would be expected in other mammals. In sum, further studies of the energetics of lactation should consider the comparative digestive efficiency of individual species in order to explain the degree to which food intake, metabolism, or storage compensate for reproductive costs.

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