Effects of prey size, meal size, meal composition, and daily frequency of feeding on the recovery of rodent remains from carnivore scats

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Abstract: Recovery of rodent bone and teeth from coyote (*Canis latrans*) scats (feces) varied with prey size, meal size, energy content of the meal, and the frequency with which prey were consumed. Mean percentages of mouse and rat teeth recovered ranged from 1% (SE = 0.5%, n = 5) to 24.4% (SE = 3.6%, n = 4) and from 13.8% (SE = 3.8%, n = 5) to 52.5% (SE = 16.6%, n = 5), respectively. A significant portion of this variation resulted from physiological mechanisms affecting how long prey were retained in the digestive acids of the stomach. Recovery of hair did not vary and thus it was considered to be nondigestible. Owing to the variation in the recovery of bone and teeth and the lack of variation in the recovery of hair, we recommend the use of teeth or bone to identify the small rodents present in carnivore scats, and then the use of a visual estimate of hair, or sample of hair, to apportion the scat to the prey items present. We caution against using the numbers of teeth or diagnostic bones to determine the number or amount of a prey item represented by a scat without addressing the variability in their recovery. The effects of gastrointestinal physiology should be considered when planning feeding trials to derive correction factors for scat analysis.

Résumé : La récupération des os et des dents de rongeurs dans les fèces de Coyotes (*Canis latrans*) varient en fonction de la taille des proies, de l'importance du repas, de son contenu énergétique et de la fréquence de consommation de ces proies. Les pourcentages moyens de dents de souris et de rats retrouvées allaient de 1% (erreur type = 0,5%; n = 5) à 24,4% (erreur type = 3,6%; n = 4) et de 13,8% (erreur type = 3,8%; n = 5) à 52,5% (erreur type = 16,6%, n = 5), respectivement. Une partie significative de cette variation est attribuable aux mécanismes physiologiques qui déterminent la durée de séjour des proies dans les acides digestifs de l'estomac. La récupération des poils dans les fèces ne varie pas et les poils sont considérés comme non digestibles. Étant donné la variabilité dans la récupération des os et des dents et l'absence de variabilité dans la récupération des poils, nous recommandons d'utiliser les dents et les os pour identifier les petits rongeurs présents dans les fèces de carnivores, et d'utiliser par la suite une estimation visuelle des poils, ou un échantillon de poils, pour répartir les fèces selon la proie qu'il contiennent. Nous émettons une mise en garde contre l'utilisation du nombre de dents et d'os diagnostiques pour déterminer le nombre ou la quantité des proies représentées dans les fèces sans tenir compte de la variabilité dans leur récupération. Il faut tenir compte des effets de la physiologie gastrointestinale lors de la planification d'expériences sur l'alimentation afin d'apporter les corrections nécessaires dans l'analyse des fèces.
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Introduction

Prey remains recovered from scats (feces) are often used to describe the food habits of carnivores (e.g., Criddle and Criddle 1923; Johnson and Franklin 1994). Identifying and quantifying mouse- and rat-size rodent remains in coyote (*Canis latrans*) scats requires the recovery of a diagnostic component distinctive enough to be used to identify the size, species, or genera of prey present (Todd and Keith 1976; Litvaitis and Shaw 1980; Toweill and Anthony 1988).

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Implicit in the use of mammalian prey components (i.e., hair, bone, teeth) to identify and quantify prey consumed is the assumption that recovery of such components remains constant. Weaver and Hoffman (1979) showed this assumption to be untenable, as they found larger prey to be more readily recovered than smaller prey. Weaver and Hoffman (1979, p. 786) considered their work an "initial probe" and did not speculate on the mechanism(s) responsible for their results. Research on prey digestibility indicates that mammalian prey components can be digested by carnivores (Murie 1946; Meriwether and Johnson 1980; Johnson and Alred 1982; Gamberg and Atkinson 1988) and that large prey are digested less than small prey (Meriwether and Johnson 1980; Johnson and Alred 1982).

In domestic dogs (*Canis lupus*), high-calorie meals are retained in the stomach longer than low-calorie meals (Edelman 1906, cited in Thomas and Cridder 1939; Quigley and Hallaran 1932; Thomas and Cridder 1939; Hinder and Kelly 1977), and large meals empty from the stomach faster than small meals (Van Liere and Sleeth 1938). To our knowl-

Table 1. Masses of hair, bone, and teeth and numbers and percentages of teeth recovered in scats from coyote feeding trials.

No. fed[a]	n[b]	How fed[c]	Trial	Hair[d] (g)	Bone[d] (g)	Teeth[d] (g)	No. of teeth[d]	Percentage of teeth[d]
				Mouse prey				
10	5	With sheep meat (78)	T1	7.4 (1.6)	0.031 (0.011)	0.005 (0.002)	1.6 (0.9)	1.0 (0.5)
10	5	With rat	T1				6.8 (2.0)	4.3 (1.3)
10	5	No filler	T2	4.3 (0.8)	0.036 (0.019)	0.022 (0.011)	10.6 (4.3)	6.7 (2.7)
10	4	Over time	T2	5.6 (0.9)	0.258 (0.112)	0.030 (0.008)	20.3 (4.5)	13.3 (2.8)
20	5	With sheep meat (58)	T1	13.4 (2.2)	0.120 (0.068)	0.055 (0.032)	11.4 (5.5)	3.6 (1.7)
20	5	With rat	T1				19.8 (3.5)	6.2 (1.1)
40	5	With sheep meat (23)	T1	20.6 (0.7)	0.123 (0.046)	0.038 (0.010)	13.8 (4.8)	2.2 (0.7)
40	5	With rat	T1				63.0 (10.8)	9.8 (1.7)
40	5	No filler	T2	22.6 (1.1)	0.907 (0.251)	0.167 (0.045)	93.8 (22.5)	14.8 (3.6)
40	4	Over time	T2	22.9 (1.8)	1.065 (0.333)	0.298 (0.058)	153.5 (20.5)	24.4 (3.6)
50	5	No filler	T1	28.7 (1.7)	0.611 (0.102)	0.140 (0.024)	58.4 (7.8)	7.3 (1.0)
				Rat prey				
2	5	With sheep meat (63)	T1	9.8 (1.2)	0.517 (0.178)	0.046 (0.016)	4.4 (1.2)	13.8 (3.8)
2	5	With mice	T1				8.2 (2.5)	24.4 (8.4)
2	5	No filler	T2	9.2 (0.5)	0.940 (0.460)	0.366 (0.143)	16.8 (5.3)	52.5 (16.6)
2	5	Over time	T2	10.8 (0.4)	0.982 (0.296)	0.245 (0.066)	12.4 (3.3)	38.8 (10.2)
4	5	With sheep meat (19)	T1	19.6 (1.3)	0.755 (0.374)	0.093 (0.025)	9.0 (3.9)	14.1 (6.1)
4	5	With mice	T1				21.6 (4.8)	38.8 (7.5)
4	5	No filler	T2	18.5 (1.2)	2.558 (0.775)	0.701 (0.155)	30.4 (5.2)	47.5 (8.2)
4	4	Over time	T2	19.2 (1.9)	4.755 (1.460)	0.760 (0.225)	24.2 (9.2)	43.0 (12.8)
6	5	No filler	T1	25.9 (2.1)	2.126 (0.490)	0.331 (0.088)	28.0 (5.2)	29.2 (6.1)

[a]Total number of prey fed during each trial. To obtain the number of prey fed per meal, divide the trials not carried out over time by 2.
[b]Number of replicates of each trial.
[c]Numbers in parentheses show the mean percentage of the meal that consisted of sheep-meat filler.
[d]Values are given as the mean, with the standard error in parentheses.

edge, no studies have addressed the influence of meal composition or meal size on the digestibility of prey taken by a wild canid. Increasing the time that prey are exposed to the digestive acids of the stomach may result in more prey components being digested.

Our objective was to evaluate, via feeding trials with captive coyotes, how prey size, prey number, meal size, and meal composition influence the digestibility of mouse- and rat-size mammalian prey. We take three approaches to this question: (*i*) varying the number of prey fed but maintaining constant meal size by adding fillers providing different levels of energy, (*ii*) varying the number of prey fed while allowing meal size to vary, and (*iii*) varying the frequency of feeding per day but maintaining a constant daily intake.

Methods

Two sets of feeding trials were performed at the Logan, Utah, field station of the United States Department of Agriculture Denver Wildlife Research Center. The first set of trials (T1) was conducted during June–September 1986 and the second set (T2) during April–May 1988. A feeding trial consisted of feeding a known number and mass of dead prey to a captive coyote. We fed two size categories of prey, mouse (*Mus musculus*) ($\bar{x}$ = 23.1 g, SE = 0.117 g, n = 1400) and rat (*Rattus norvegicus* and *Neotoma micropus*) ($\bar{x}$ = 209.5 g, SE = 5.663 g, n = 122, and $\bar{x}$ = 253.4 g, SE = 7.640 g, n = 24, respectively). During T1, 20 coyotes (11 ♀♀, 9 ♂♂) ranging in age from 1.3 to 9.4 years ($\bar{x}$ = 4.1 years, SE = 0.60 years) represented the population from which a coyote was randomly chosen and assigned a meal. During T2, 22 different coyotes (8 ♀♀, 14 ♂♂) ranging in age from 1 to 9 years ($\bar{x}$ = 3.5 years, SE = 0.51 years) represented the study population. All coyotes were caged in outdoor covered kennels (3.6 × 1.2 × 1.8 m) during the trials and were cared for in accordance with the principles and guidelines of the Canadian Council on Animal Care.

Two types of feeding trials were performed: (1) meals were offered in their entirety once a day, and (2) meals were fed over time (every 2–4 h). The first type of feeding trial lasted 4 days. On days 1 and 4, we fed commercially available furbreeders' food mixed with ferric oxide (an undigestible red dye) to mark the beginning and end of the trial and to insure that all scats resulting from trial meals were collected. On days 2 and 3, half the total number of prey for a trial were fed. The second type of feeding trial lasted at least 3 days. Dyed furbreeders' food was fed 24 h before the first prey item fed and 24 h after the last prey item fed. One rat was fed every 4 h and 5 mice were fed every 2 h.

During T1, each trial meal (half the number of prey fed) was maintained at 600 g (Gier 1975). Meals that contained less than 600 g of prey were supplemented with the mass of ground sheep meat (with no fur, skin or bone) or alternative prey (rat if a mouse meal and vice versa) required to achieve a 600-g meal. Trials of 10, 20, 40, and 50 mice and 2, 4, and 6 rats were fed during T1 (Table 1).

During T2, the 10- and 40-mouse and 2- and 4-rat trials fed during T1 were repeated but were not supplemented to maintain a constant meal size. For comparison with the 10- and 40-mouse and 2- and 4-rat trials fed with and without sheep-meat filler, these levels of prey were fed over time during T2.

Scats were collected at 2-h intervals until red scats were produced. Each scat was placed in a paper bag and labeled with the

date, time of collection, and coyote number and stored frozen. Scats were oven-dried at 60°C for 24 h to obtain a constant dry mass and to kill eggs of the zoonotic parasite *Echinococcus* spp. (Colli and Williams 1972). After drying, scats were secured in a ripstop nylon bag (18 × 18 cm), soaked, washed in a clothes washer, and dried in a clothes dryer (Johnson and Hansen 1979).

To separate hair, bone, and teeth, each scat was emptied from the bag in which it had been washed into a 2.5-mm sieve situated above a 20 × 20 × 5 cm metal tray. Material that passed through and remained in the sieve was hand-separated into holding containers. After this sieving process was repeated on each holding container, the number of each tooth type recovered, by species, was recorded and the hair, bone, and teeth recovered were weighed using an electronic balance.

Counts of teeth were transformed by taking the square root of the count plus 0.5 (Zar 1984, p. 241). The mass of prey components was transformed by taking the natural logarithm of the mass plus 1 (Zar 1984, p. 238). Ratios and percentages were arcsine-transformed (Zar 1984, p. 286) whenever they were used as a dependent variable.

We used two-factor analyses of variance (ANOVA) to test for differences in the numbers and percentages of teeth recovered according to how prey were fed (all prey fed as a meal with no filler, sheep meat as filler, or different prey as filler, or prey fed over time) and the number of prey fed (10 vs. 40 mice, 2 vs. 4 rats). We used single-factor ANOVAs to test for an effect of how prey are fed (all prey fed as a meal with sheep-meat filler or no filler, or prey fed over time) on recovery of hair and bone, to test the effect of adding sheep-meat filler to meals on the mass of each prey component (hair, bone, teeth) recovered, and to compare ratios of bone mass to hair mass recovered (*B*:*H*) from trial scats and field-collected scats. Post-hoc comparisons were made using Fisher's least significant difference test. We used least-squares regression techniques to test the relationship between *B*:*H* and (*i*) percentage of sheep-meat filler, (*ii*) meal size, and (*iii*) percentage of teeth recovered. A significance level of $P < 0.05$ was set for all analyses.

Results

For mouse and rat prey, the number of teeth recovered varied with how prey were fed (mouse: $P = 0.0001$, $F_{[3,29]} = 20.06$; rat: $P = 0.0042$, $F_{[3,31]} = 5.39$). More mouse teeth were recovered when meals were fed over time than when meals contained rat as filler, had no filler, or contained sheep-meat filler. The fewest mouse teeth were recovered when meals contained sheep-meat filler. No difference was detected between mice fed with rat as filler and mice fed with no filler. As with mice, the fewest rat teeth were recovered when meals contained sheep-meat filler. We detected no difference in recovery of rat teeth between meals of rat with mouse filler or no filler or fed over time.

The percentages of teeth recovered also varied according to how prey were fed (mouse: $P = 0.0001$, $F_{[3,29]} = 20.89$; rat: $P = 0.0052$, $F_{[3,31]} = 5.16$). With one exception, the patterns of tooth recovery were identical in terms of the percentage and number of teeth recovered. We did not detect a difference in the percentages of rat teeth recovered from meals containing sheep meat as filler and those containing mice as filler. The mean percentages of mouse and rat teeth recovered ranged from 1% (SE = 0.5%, $n = 5$) to 24.4% (SE = 3.6%, $n = 4$) and from 13.8% (SE = 3.8%, $n = 5$) to 52.5% (SE = 16.6%, $n = 5$), respectively (Table 1).

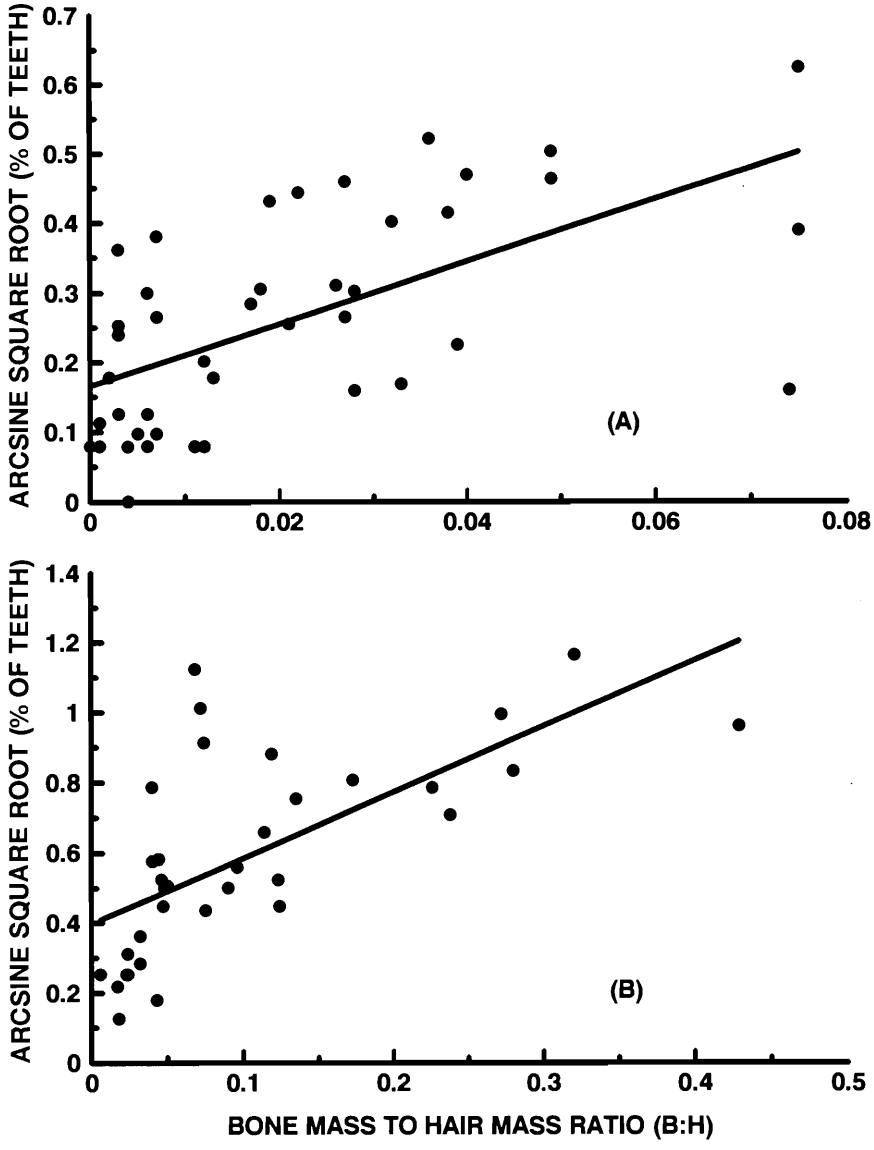
Recovery of mouse bone varied according to how mice were fed ($P = 0.0446$, $F_{[2,24]} = 3.55$), with more bone recovered from mouse meals fed over time than from mouse meals with sheep-meat filler. Bone recovery did not differ between mice fed with no filler and mice fed over time, nor between mice fed with no filler and mice fed with sheep-meat filler. The same pattern of bone recovery was evident for rat prey ($P = 0.0684$, $F_{[2,26]} = 2.98$). In contrast to bone, we were unable to detect a difference in the recovery of mouse and rat hair according to how prey were fed (mouse: $P = 0.9940$, $F_{[2,24]} = 0.01$; rat: $P = 0.9534$, $F_{[2,26]} = 0.05$) (Table 1).

When meal size was held constant at 600 g by adding sheep-meat filler when needed, the mass of hair, bone, and teeth recovered varied with the number of prey fed for both mouse (hair: $P = 0.0001$, $F_{[3,16]} = 18.52$; bone: $P = 0.0001$, $F_{[3,16]} = 17.03$; teeth: $P = 0.0017$, $F_{[3,16]} = 8.07$) and rat (hair: $P = 0.0001$, $F_{[2,12]} = 30.80$; bone: $P = 0.0121$, $F_{[2,12]} = 6.52$; teeth: $P = 0.0030$, $F_{[2,12]} = 9.76$) prey. The results of post-hoc tests support the previous finding that sheep-meat filler increased digestion of bone and teeth but not hair. For mouse prey, no difference was detected in the mass of bone or teeth recovered between the 10-, 20-, and 40-mouse trials, even though prey mass increased 4-fold. However, significantly more bone and tooth mass was recovered during the 50-mouse trials (0% sheep-meat filler per meal) than during the 10-, 20-, or 40-mouse trials (78, 58, and 23% sheep-meat filler per meal, respectively). Conversely, for hair, differences were detected between the 10-, 20-, and 40-mouse trials but not between the 40- and 50-mouse trials. This pattern of bone, tooth, and hair recovery was observed for rat prey also. No difference was detected in the mass of bone or teeth recovered between the 2-and 4-rat trials, even though prey mass doubled. However, significantly more bone and tooth mass was recovered from the 6-rat meals (0% sheep-meat filler per meal) than from the 2- or 4-rat meals (63 and 29% sheep-meat filler per meal, respectively). Less hair was recovered during the 2-rat trials than during either the 4- or 6-rat trials; no difference was detected between the 4- and 6-rat trials. For mouse prey, *B*:*H* decreased as the percentage of sheep-meat filler fed increased ($P = 0.0081$, $F_{[1,18]} = 8.872$, $r = 0.57$). However, this relationship was not significant for trials with rat prey ($P = 0.3718$, $F_{[1,14]} = 0.856$, $r = 0.25$).

These results indicate that bone is digestible and hair is not. Therefore, *B*:*H* should serve as a relative index to digestion. The higher the *B*:*H* value, the less prey are digested. The *B*:*H* value of mouse prey increased with meal mass ($P = 0.0297$, $F_{[1,12]} = 6.083$, $r = 0.53$), indicating that large meals are digested less than small meals. No such relationship was found for trials with rat prey ($P=0.7071$, $F_{[1,8]} = 0.152$, $r = 0.14$). For both mouse and rat prey, the percentage of teeth recovered increased with the *B*:*H* value obtained from a trial (Fig. 1, Table 2).

The *B*:*H* value of scats collected from free-ranging coyotes in Curlew Valley, Utah, in 1986, which contained only mouse-size prey, indicate that the *B*:*H* values of our trial scats are not representative of values occurring in the wild. The *B*:*H* values of the Curlew Valley scats ($\bar{x} = 0.185$, SE = 0.042, $n = 25$) are greater than those from either the 50-mouse trials, where 25 mice were fed together as a meal for 2 days ($\bar{x} = 0.023$, SE = 0.008, $n = 43$), or the trials in which mice were fed over time ($\bar{x} = 0.054$, SE = 0.006, $n = 31$) ($P = 0.001$, $F_{[2,96]} = 17.23$). We detected no

Fig. 1. Percentages of all teeth of mouse (A) and rat (B) prey ingested per trial recovered during scat analysis. Statistics for each regression are given in Table 2.



difference in the *B*:*H* values from the trials in which 25 mice were fed all at once (50-mouse trials) and those in which 40 mice were fed over time to mimic natural prey-consumption rates. However, 96% of the scats in the 40-mouse trials contained bone, very similar to the naturally occurring scats, which all contained bone. In contrast, only 65% of the scats from the meals consisting of 25 mice fed all at once (50-mouse trials) contained bone.

Discussion

The amount of bone and teeth digested by coyotes varies with prey size, meal size, meal composition, and the frequency with which prey are ingested. The amount of hair digested does not appear to be affected by these factors.

Using published values for mouse and rat body composition (Douglas et al. 1994), the caloric density of mouse and rat prey was determined to be 5.0 and 5.4 kcal/g dry matter, respectively (Lewis et al. 1987). The caloric density of lamb obtained from the literature was 7.3 kcal/g (Geigy Scientific Tables 1981). Adding ground sheep meat to meals appears to have increased the gastric retention time of prey in the same way as increasing a meal's caloric content increased gastric retention time of plastic spheres in domestic dogs (Hinder and Kelly 1977). Hinder and Kelly found that undigestible plastic spheres were retained in the stomach's acid environment until the initiation of the interdigestive myoelectric complex (IMC) (Code and Marlett 1975), which is a series of powerful stomach contractions that, after digestion ceases, serve to expel material too large to pass from the stomach during digestion. Although the mechanism is poorly understood, the IMC is initiated by (*i*) the distension of the stomach and (*ii*) the presence of the products of digestion in the upper small intestine (Code and Marlett 1975). The physiological processes surrounding the initiation and cessation of the IMC appear to explain the variability in the digestion of prey observed during this study. Recovery of teeth and bone increased (retention time decreased) when prey

Table 2. Regression models of arcsine square root of the percentage of teeth detected (Y) to the ratio of bone to hair mass recovered, $B{:}H$ (X), during a trial.

Prey	Teeth	Model	P	F	df	r^2
Mouse[a]	All teeth	$Y = 0.1535 + 4.7355X$	0.0010	24.98	1,40	0.38
	Upper incisor	$Y = 0.1056 + 4.2730X$	0.0070	13.57	1,40	0.25
	Lower incisor	$Y = 0.1898 + 3.9407X$	0.0048	8.93	1,40	0.18
	Molar	$Y = 0.1347 + 5.2499X$	0.0010	26.61	1,40	0.40
Rat[b]	All teeth	$Y = 0.3974 + 1.8797X$	0.0010	25.51	1,32	0.44
	Upper incisor	$Y = 0.4390 + 2.3553X$	0.0010	25.83	1,32	0.45
	Lower incisor	$Y = 0.2353 + 2.4911X$	0.0004	15.61	1,32	0.33
	Molar	$Y = 0.3810 + 1.8830X$	0.0002	18.33	1,32	0.36

[a] $B{:}H$ values (X) ranged from 0 to 0.075.
[b] $B{:}H$ values (X) ranged from 0.006 to 0.429.

were fed with a filler of lower caloric content (rats or mice), and decreased (retention time increased) when prey were fed with a filler of higher caloric content (sheep meat).

Our findings indicate that a relatively small amount of sheep-meat filler effects a change in digestion. Not until all sheep-meat filler was removed from a meal did recovery of bone and teeth increase significantly. We were unable to detect a significant increase in the mass of bone or teeth recovered when the percentage of sheep-meat filler in a 600-g meal was reduced from 79 to 23% for mice and from 66 to 29% for rats, even though the mass of mice tripled and the mass of rat doubled.

The increase in the number of teeth recovered when prey were ingested over time relative to when they were ingested as a single meal is also consistent with the physiological mechanism of the stomach. When all prey are consumed as a meal, each prey item remains in the digestive acids of the stomach until the IMC is initiated. When the same number of prey are ingested over time, each successive prey item ingested remains in the stomach only until it and the prey ingested after it are digested. As a result, each successive prey item ingested spends less time exposed to the digestive acids of the stomach, and thus is less digested, than if it had been one of the prey ingested as a single meal.

Our results indicate that mice consumed as part of a large meal are less digested than mice consumed as part of a smaller meal. Although larger meals remain in the stomach longer than smaller meals, the increase in gastric retention time is not proportional to meal mass (Van Liere and Sleeth 1938). In other words, each mouse fed as part of a large meal spends less time in the stomach than if it had been part of two small meals. Our inability to show an effect of meal size on the digestion of rat-size prey may be a function of (*i*) rat bones having less surface area relative to their mass than mouse bones and thus possibly being less digestible, or (*ii*) the relative increase in rat meal size (1 versus 2 rats) being only half the increase in mouse meal size (5 versus 20 mice).

Our results support, and conflict with, the results of other research on the digestibility of mammalian prey by carnivores. Meriwether and Johnson (1980) found that digestion of bone and hair by coyotes varied with prey size. Johnson and Alred (1982) found similar results for the bobcat (*Felis rufus*). Gamberg and Atkinson (1988) concluded that ermine (*Mustela erminea*) digest bone but not hair. Based on our results with coyotes, we agree that bone is digestible and that mice are more digestible than rats. With respect to the digestion of hair, however, our data are consistent with the findings of Gamberg and Atkinson (1988). Digestion of bone and teeth was greatest when prey were fed with sheep-meat filler and was least when prey were fed over time. However, we saw no indication that hair was affected in either case. Unlike bone and teeth, when sheep-meat filler was present we detected a significant increase in the mass of hair recovered each time the mass of prey fed increased, and when sheep-meat filler was removed from the diet we were unable to detect a change in the mass of hair recovered.

Gamberg and Atkinson (1988) concluded that ermine digest less bone than coyotes. However, Gamberg and Atkinson ground the prey they fed through a 2-mm screen. Hinder and Kelly (1977) found that ground liver passed from the stomach of the domestic dog faster than unground liver. Therefore, the grinding of prey by Gamberg and Atkinson may have influenced the gastric retention time of bone and may explain why more bone was recovered from ermine than from coyotes fed whole, intact prey (Meriwether and Johnson 1980). Furthermore, Meyer et al. (1985) found that particulates up to 5 mm in diameter passed through the pylorus of the dog independent of the IMC, that is, while digestion of the stomach contents was still occurring. The pylorus of the ermine should be smaller than that of the dog, but because the prey had been ground and then sieved through a 2-mm screen, much of the bone fed by Gamberg and Atkinson was 2 mm in diameter or less, suggesting that some may have been small enough to pass through the pylorus of the ermine independently of the IMC. If bone did pass from the ermine stomach prior to the IMC, it spent less time in the stomach than if it had not been ground, possibly causing less bone to be digested by ermine than by coyotes fed whole, intact prey.

Researchers have noted that the portions of a prey item consumed by a predator affect recovery of that prey item in scats (Lockie 1959; Goszczynski 1974; Liberg 1982; Gamberg and Atkinson 1988; Hewitt 1989; Weaver 1993). Gamberg and Atkinson (1988) felt that this bias should be considered when feeding trials are performed to determine correction factors. We agree, and suggest that our results document the need to consider the influence of the frequency with which predators consume prey on the digestion of prey. Feeding prey over time yielded $B{:}H$ values more consistent with

those from field-collected scats. By altering how prey were consumed, and with what, we were able to increase the percentages of mouse and rat teeth recovered by more than 2400% and almost 400%, respectively. Recovery of bone increased from occurrence in 65% of scats in a trial when prey were fed as in previous feeding trials to 96% when the frequency of prey consumption was more consistent with natural rates. Comparing *B*:*H* values from field-collected scats with those from trial scats may provide a means to test how well correction factors from feeding trials represent actual prey digestion. However, caution should be used with respect to the usefulness of *B*:*H* values obtained in the field. Our *B*:*H* values from feeding trials were derived from all the scats from each meal. It is doubtful that this will ever be the case with scats collected in the field. Furthermore, only the prey, or prey size, of interest must be present in the field-collected scats from which *B*:*H* values are derived.

Meal size, meal composition, and prey-consumption rate are unknown when scats are analyzed, thus it is difficult to correct for their influence. We show that the *B*:*H* value from all the scats produced from a meal explains a significant amount of the variation in the digestion of teeth, variation caused by differences in the frequency with which prey are consumed and the composition of the meal. However, application of this correction factor to a sample of scats when all the scats from each meal represented by the sample may not be present is untested and should be considered unreliable and not applicable to field studies.

Owing to the variability in the recovery of bone and teeth and the lack of variability in the recovery of hair, we recommend the use of teeth or bone to identify the small rodents present in carnivore scats, and then the use of a visual estimate of hair, or a system of sampling hair, to apportion the scat to the prey present. We caution against using the number of teeth or diagnostic bones to determine the number or amount of a prey represented by a scat without addressing the variability in their recovery. If differences in hair characteristics are not sufficient to apportion the prey present in a scat, Kelly (1991) has validated a model that apportions prey on the basis of recovery of teeth. Correction factors that estimate the amount of prey represented by a scat (Ackerman et al. 1984; Kelly 1991; Weaver 1993) can then be used to estimate what the sum of proportions of all scats in a sample represents. An interactive computer program (PROGRAM SCAT) incorporating each of these corrections into a model that provides variance and sample-size estimates (Kelly 1991) is available from the senior author.

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References

Ackerman, B.B., Lindzey, F.G., and Hemker, T.P. 1984. Cougar food habits in southern Utah. J. Wildl. Manage. **48**: 147–155.

Code, C.F., and Marlett, J.A. 1975. The interdigestive myoelectric complex of the stomach and small bowel of dogs. J. Physiol. **246**: 289–309.

Colli, C.W., and Williams, J.F. 1972. Influence of temperature on the infectivity of eggs of *Echinococcus granulosus* in laboratory rodents. J. Parasitol. **58**: 422–426.

Criddle, N.E., and Criddle, S. 1923. The coyote in Manitoba. Can. Field-Nat. **37**: 41–45.

Douglas, T.C., Pennino, M., and Dierenfeld, E.S. 1994. Vitamins E and A, and proximate composition of whole mice and rats used as feed. Comp. Biochem. Physiol. A, **107**: 419–424.

Gamberg, M., and Atkinson, J.L. 1988. Prey hair and bone recovery in ermine scats. J. Wildl. Manage. **52**: 657–660.

Geigy Scientific Tables. 1981. Units of measurement, body fluids, composition of the body, nutrition. Vol. 1. 8th ed. Ciba-Geigy, Basel, Switzerland.

Gier, H.T. 1975. Ecology and behavior of the coyote (*Canis latrans*). *In* The wild canids: their systematics, behavioral ecology, and evolution. *Edited by* M.W. Fox. Van Nostrand Reinhold Co., New York. pp. 247–262.

Goszczynski, J. 1974. Studies on the food of foxes. Acta Theriol. **19**: 1–18.

Hewitt, D.G. 1989. Correcting grizzly bear fecal analysis to observed foods habits. M.S. thesis, Washington State University, Pullman.

Hinder, R.A., and Kelly, K.A. 1977. Canine gastric emptying of solids and liquids. Am. J. Physiol. **233**: E235–E340.

Johnson, M.K., and Alred, D.R. 1982. Mammalian prey digestibility by bobcats. J. Wildl. Manage. **46**: 530.

Johnson, M.K., and Hansen, R.M. 1979. Estimating coyote food intake from undigested residues in scats. Am. Midl. Nat. **102**: 363–367.

Johnson, W.E., and Franklin, W.L. 1994. Role of body size in the diets of sympatric gray and culpeo foxes. J. Mammal. **75**: 163–174.

Kelly, B.T. 1991. Carnivore scat analysis: an evaluation of existing techniques and the development of predictive models of prey consumed. M.S. thesis, University of Idaho, Moscow.

Lewis, L.D., Morris, M.L., and Hand, M.S. 1987. Small animal clinical nutrition. 3rd ed. Mark Morris Associates. Topeka, Kans.

Liberg, O. 1982. Correction factors for important prey categories in the diet of domestic cats. Acta Theriol. **27**: 115–122.

Litvaitis, J.A., and Shaw, J.H. 1980. Coyote movements, habitat use, and food habits in southwestern Oklahoma. J. Wildl. Manage. **44**: 62–68.

Lockie, J.D. 1959. The estimation of the food of foxes. J. Wildl. Manage. **23**: 224–229.

Meriwether, D., and Johnson, M.K. 1980. Mammalian prey digestibility by coyotes. J. Mammal. **61**: 774–775.

Meyer, J.H., Dressman, J., Fink, A., and Amidon, G. 1985. Effect of size and density on canine gastric emptying of nondigestible solids. Gastroenterology, **89**: 805–813.

Murie, O.J. 1946. Evaluating duplications in analyses of coyote scats. J. Wildl. Manage. **10**: 275–276.

Quigley, J.P., and Hallaran, W.R. 1932. The independence of spontaneous gastro-intestinal motility and blood sugar levels. Am. J. Physiol. **100**: 102–110.

Thomas, J.E., and Cridder, J.O. 1939. Inhibition of gastric motility associated with the products of protein hydrolysis in the upper small intestine. Am. J. Physiol. **126**: 28–38.

Todd, A.W., and Keith, L.B. 1976. Responses of coyotes to winter reductions in agricultural carrion. Wildlife Tech. Bull. No. 5, Fish and Wildlife Division, Alberta Recreation, Parks and Wildlife, Edmonton.

Toweill, D.E., and Anthony, R.G. 1988. Coyote foods in a coniferous forest in Oregon. J. Wildl. Manage. **52**: 507–512.

Van Liere, E.J., and Sleeth, C.K. 1938. Studies in gastric motility. The relation of the size of the meal to the gastric emptying time in the dog, using a meal rich in fat and protein. J. Dig. Dis. **5**: 18–19.

Weaver, J.L. 1993. Refining the equation for interpreting prey occurrence in gray wolf scats. J. Wildl. Manage. **57**: 534–538.

Weaver, J.L., and Hoffman, S.W. 1979. Differential detectability of rodents in coyote scats. J. Wildl. Manage. **43**: 783–786.

Zar, J.H. 1984. Biostatistical analysis. 2nd ed. Prentice Hall, Inc., Englewood Cliffs, N.J.