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Abstract: Carnivores exhibit a diverse array of teeth, including peg-like incisors, elongate canines, blade-like carnassials, and rounded, bunodont molars, all of which are presumed to be adapted for particular functions, such as slicing flesh or cracking bones. The validity of these presumed correlations between form and function was explored in a field study of feeding behaviour in four sympatric species of free-ranging African carnivores; African lion (*Panthera leo*), cheetah (*Acinonyx jubatus*), spotted hyena (*Crocuta crocuta*), and wild dog (*Lycaon pictus*). Based on videotapes of feeding behaviour on carcasses of ungulates, the associations among use of teeth, motion of jaw, action of neck, use of paws, and type of food were compiled. There were significant interactions between use of teeth and type of food, and use of teeth and action of neck, in all species. Skin tended to be cut with the carnassials in associations with a slight pull, whereas muscle was more likely to be pulled from the carcass by the incisors. Bones usually were cracked with the premolars in hyenas and the postcarnassial molars in wild dogs. Repeated chewing motions were most common in all species when eating the toughest foods, i.e., skin or muscle in combination with bone. The association between use of teeth and type of food was not perfect; sometimes skin was cut with incisors and bones were cracked with carnassials. This apparent lack of precision in use of teeth suggests that selection will likely favour specializations for particular functions in teeth other than those that are the primary tools for that purpose.

FEEDING BEHAVIOR IN FREE-RANGING, LARGE AFRICAN CARNIVORES

BLAIRE VAN VALKENBURGH

*Department of Biology, University of California, Los Angeles,
Los Angeles, CA 90024-1606*

Carnivores exhibit a diverse array of teeth, including peg-like incisors, elongate canines, blade-like carnassials, and rounded, bunodont molars, all of which are presumed to be adapted for particular functions, such as slicing flesh or cracking bones. The validity of these presumed correlations between form and function was explored in a field study of feeding behavior in four sympatric species of free-ranging African carnivores; African lion (*Panthera leo*), cheetah (*Acinonyx jubatus*), spotted hyena (*Crocuta crocuta*), and wild dog (*Lycaon pictus*). Based on videotapes of feeding behavior on carcasses of ungulates, the associations among use of teeth, motion of jaw, action of neck, use of paws, and type of food were compiled. There were significant interactions between use of teeth and type of food, and use of teeth and action of neck, in all species. Skin tended to be cut with the carnassials in association with a slight pull, whereas muscle was more likely to be pulled from the carcass by the incisors. Bones usually were cracked with the premolars in hyenas and the postcarnassial molars in wild dogs. Repeated chewing motions were most common in all species when eating the toughest foods, i.e., skin or muscle in combination with bone. The association between use of teeth and type of food was not perfect; sometimes skin was cut with incisors and bones were cracked with carnassials. This apparent lack of precision in use of teeth suggests that selection will likely favor specializations for particular functions in teeth other than those that are the primary tools for that purpose.

Key words: feeding behavior, dental function, Carnivora, Africa, *Panthera leo*, *Acinonyx jubatus*, *Crocuta crocuta*, *Lycaon pictus*

The varied shapes of the teeth of carnivorous mammals appear to reflect the different requirements of killing and consuming prey. There are broad, low-cusped molars for cracking and grinding, blade-like carnassial teeth for slicing, pointed premolars for piercing, and dagger-like canine teeth for stabbing (Fig. 1). These functions are largely inferred from broad similarities in the shapes of teeth and kitchen tools, such as knives, mortars, and pestles (Kay and Hiiemae, 1974; Lucas, 1979). Observations on actual use of teeth in free-ranging carnivorous mammals are rare, other than the often-described application of canine teeth in killing bites (Ewer, 1973; Leyhausen, 1979; Van Valkenburgh and Ruff, 1987). Although rather specific roles for particular teeth often are assumed, such as slicing

flesh for carnassials, we do not know how realistic these assumptions are. How precisely do carnivores use their teeth when rapid feeding is at a premium? For example, are bones cracked with teeth that appear adapted for that purpose, or are other teeth frequently involved? Answering such questions is critical to improving our understanding of structure of teeth and the selective pressures that constrain shape of teeth.

I conducted a field study of use of teeth in four large species of free-ranging large carnivores, African lion (*Panthera leo*), spotted hyena (*Crocuta crocuta*), wild dog (*Lycaon pictus*), and cheetah (*Acinonyx jubatus*), living sympatrically in the Masai Mara Reserve of Kenya in the June-July dry seasons of 1989 and 1990. Although it

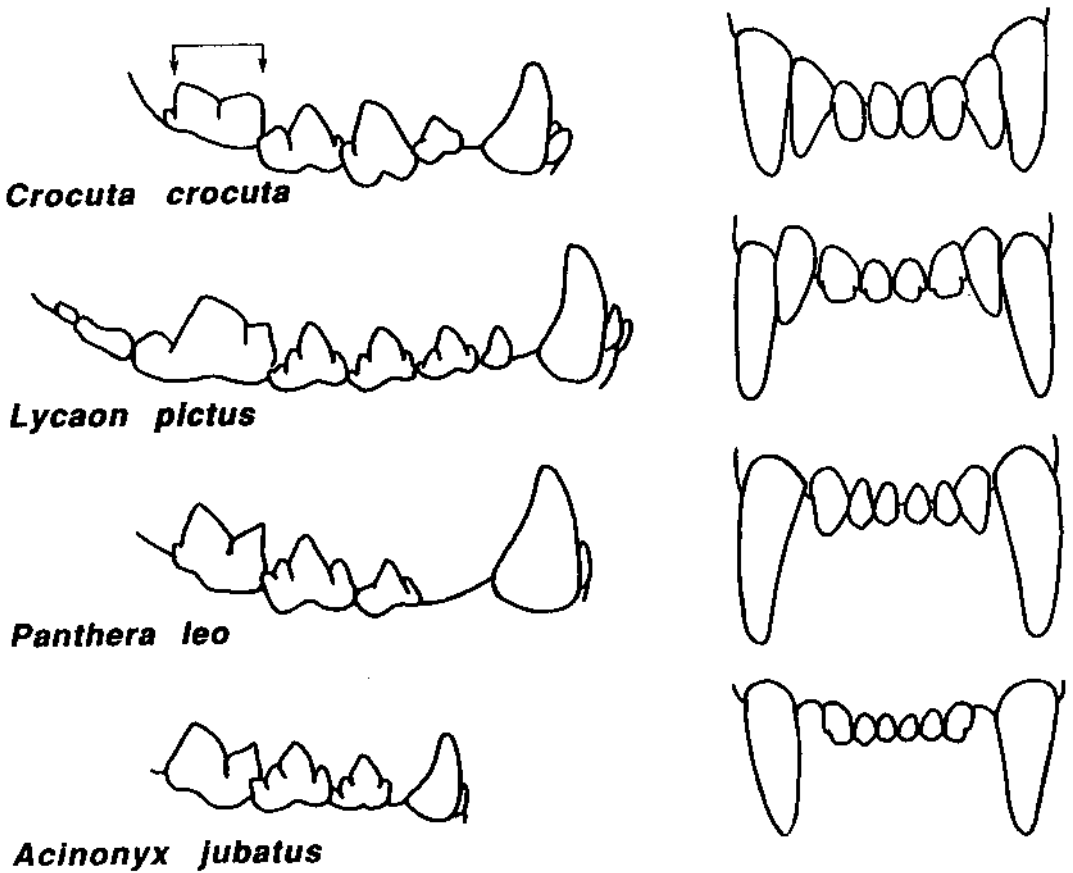


FIG. 1.—Lateral (buccal) views of the lower tooththrows and anterior (buccal) views of the upper incisors and canines of four species of African carnivores. The lower tooththrows are drawn so that the primary slicing, blade-like (trigonid) portions of the first lower molar (as indicated by arrows) are the same length and the anterior views are drawn so that the distances between the outer margins of the two canines are equal.

would have been easier to study animals in a captive situation, feeding behaviors might not be typical of free-ranging carnivores. Even if entire ungulates were fed to captive predators, this would not replicate natural feeding conditions because of an absence or reduction of the need to eat rapidly. In the wild, rapid feeding is advantageous because of competition between species, and within species, in the case of the social lion, wild dog, and hyena. Interspecific competition in the form of theft of carcasses appears to be most significant for cheetahs, and then wild dogs, hyenas, and lions in approximate descending order (Eaton, 1974, 1979; Kruuk,

1972; Schaller, 1972). Teeth likely are used differently when the pressure for rapid ingestion is intense, as opposed to captive situations where food appears predictably in a noncompetitive environment. Thus, despite the shortcomings of field as opposed to captive studies, documenting use of teeth under natural conditions is worthwhile.

There are two generalizations concerning use of teeth in these species that I tested: the carnassials are used primarily for slicing muscle and other pliant tissues and probably little else (Ewer, 1973; Lucas, 1979; Van Valkenburgh, 1989); bone-cracking is accomplished by the premolars in hyenas

and lions, and the postcarnassial molars in wild dogs (Ewer, 1973; Van Valkenburgh, 1989; Werdelin and Solounias, 1991). In addition, I was interested in the function of incisors in feeding because these teeth appear to be relatively small and unimportant in felids relative to canids and hyaenids (Fig. 1; Biknevicius and Van Valkenburgh, 1992).

Comparisons of the skulls and teeth of the four species reveal differences in size and dentition that lead to further predictions concerning feeding behavior (Fig. 1). If the absolute magnitude of bite force that can be produced is positively correlated with body mass and skull size, the lion (mean mass = 160 kg, length of skull = 275 mm) and hyena (mean mass = 54 kg, length of skull = 225 mm) are likely to have much more forceful bites than the wild dog (mean mass = 20 kg, length of skull = 185 mm) and cheetah (mean mass = 65 kg, length of skull = 150 mm; measurements from Van Valkenburgh and Ruff, 1987). Thus, the two larger species might be expected to break up food more rapidly and chew less frequently than the two smaller species. Dental architecture also will affect feeding behavior. Cheetahs and lions have similar dental arrays that differ primarily in the relative emphasis on anterior (canines and incisors) as opposed to more posterior (premolars and molars) teeth (Fig. 1). Cheetahs have much-reduced upper and lower canines associated with well-developed premolars and carnassials. Lions, conversely, have relatively more massive canines and less well-developed anterior premolars (lower p3; Fig. 1). Consequently, lions are likely to rely more heavily on their anterior dentition than are cheetahs.

Spotted hyenas are characterized by massive premolars in association with a cat-like, carnassial tooth and moderately developed canines (Fig. 1). As noted previously, hyenas are expected to use their premolars to crack bone and their carnassials to slice flesh. Because it would seem critical for rapid feeding to maintain a sharp cutting

edge on the carnassial, hyenas are likely to avoid contacting bone with these teeth. Wild dogs differ from hyenas in having molars posterior to the carnassial and a full set of four premolars that are not expanded mediolaterally. Wild dogs are expected to crunch bones primarily with their postcarnassial molars and avoid damage to their cutting blades. The probable function of their premolars is unclear.

MATERIALS AND METHODS

Feeding behavior was documented for four species of large carnivores in the Masai Mara area near Aitong, Kenya (1°15'S, 35°15'E) in summer 1989 and 1990. The Masai Mara is an ideal place to study feeding behavior in large carnivores; the landscape is relatively open, thereby increasing the probability of finding predators on a kill, and the animals are habituated to vehicles and tolerate close observation.

Because it was not possible to predict where or when a kill would be made, all observations of feeding behavior were done opportunistically. Several hours were spent each morning and evening traversing the reserve in a vehicle in search of kills. For wild dogs, my search was facilitated by working with colleagues studying the movements of a pack with the assistance of radiotelemetry. For all species, when one or more individuals were discovered on a carcass, their feeding behavior was recorded on videotape. In general, one individual would be filmed for as long as possible, but it often was necessary to switch among individuals because the original subject stopped feeding or was no longer in view. Because of the opportunistic nature of the study, the number of individuals observed and the duration of tape varies among species (Table 1). For example, only one cheetah was filmed for ca. 2 h on a single carcass, whereas ca. 10-15 spotted hyenas were observed on 15 carcasses for a total of 4.5 h. The samples for lions and wild dogs also represent several individuals and multiple carcasses. In general, the prey, and thus foods, consumed were similar; the cheetah's kill was a Thomson's gazelle (*Gazella thomsoni*) as were most, but not all, of kills by wild dogs. The hyenas and lions fed on zebras (*Equus burchelli*) and wildebeests (*Connochaetes taurinus*) primarily, but also feed on Thomson's gazelles and topi (*Damaliscus lunatus*). The carcasses

TABLE 1.—The approximate duration of videotape acquired, total number of discrete feeding observations, number of individuals observed (n), and the age and numbers of prey species consumed for each of four species videotaped feeding in the Masai Mara area of Kenya, 1989–1990.

Species	Duration of tape (h)	Total observations	Individuals (n)	Prey consumed		
				Species	Adults	Juveniles
<i>Lycan pictus</i> , African wild dog	2.0	363	10–15	<i>Gazella thomsoni</i>	7	3
				<i>Connochaetes taurinus</i>		2
				<i>Aepyceros melampus</i>	1	
<i>Crocota crocuta</i> , spotted hyena	4.5	680	10–15	<i>G. thomsoni</i>	2	
				<i>C. taurinus</i>	7	4
				<i>Equus burchelli</i>	1	
				<i>Damaliscus lunatus</i>	1	
				<i>G. thomsoni</i>	1	
<i>Panthera leo</i> , African lion	4.0	493	5–10	<i>C. taurinus</i>	1	
				<i>E. burchelli</i>	3	
				<i>G. thomsoni</i>	1	
				<i>G. thomsoni</i>	1	
<i>Acinonyx jubatus</i> , cheetah	2.0	352	1	<i>G. thomsoni</i>	1	

varied in their condition when discovered; in most instances, the viscera and hind quarters had been largely consumed prior to filming. I assumed that the ungulates did not differ significantly in the material properties of their skin, muscle, and bone.

Observations were recorded from the videotapes by examining the tapes at slow speed and stopping the tape whenever an identifiable behavior was seen, such as cutting skin with the carnassial. Based on the length of the tapes and total number of observations, an identifiable behavior occurred about once every 30 s. When the tape was stopped, behavioral data were recorded including the teeth used, food being eaten, motion of the jaw and neck, and use of paws. Although it sometimes was difficult to ascertain exactly which teeth were in use, the position of the bite relative to the eye served as a useful landmark. In all four species, the carnassial is located below the orbit and, thus, bites just anterior to the eye could be interpreted as being made between premolars, whereas as those behind the eye, in the case of the wild dog, could be identified as positioned between molars. "Jaw motion" was classified as repeated bites (i.e., chewing) or a single bite. "Neck motion" was defined as either a twist, pull, or none, and use of front paws as one, both, or none.

The five categories of foods were: skin; skin plus other; muscle; muscle plus bone; bone. Skin, muscle, and bone were easily identified. "Skin plus other" was constructed to accommodate various combinations of skin and asso-

ciated connective tissue or muscle. Included in this category was a white, elastic connective tissue most often located between skin and muscle that often was consumed by all four species. "Muscle plus bone" included parts that had both a muscle and bone component such as the ribcage and pelvis, and the category "bone" was reserved for instances where little muscle tissue was apparent.

Using the program STATISTICA for the Macintosh, data were analyzed with nonparametric tests, including chi-square and log-linear analysis of frequency tables. The latter method is appropriate for exploration of the significance of interaction effects in a multi-way frequency table (Sokal and Rohlf, 1969). There were five possible factors; type of food, use of teeth, action of neck, use of paws, and motion of jaw. Using an iterative procedure, the log-linear approach fits a series of models to these data, beginning with no interactions among the factors, then all two-way interactions, and then all three-way, and so on (Bishop et al., 1975). The contribution of each interaction to the model is examined by a comparison of the goodness-of-fit of a model without a particular interaction relative to the fit provided by the complete model. If the difference in fit is significant as determined by the chi-square test, then the interaction is retained in the model. The goodness-of-fit of each model to these data is evaluated relative to all others and ultimately the model that produces the best fit and includes the least number of interactions is identified. The log-linear analysis

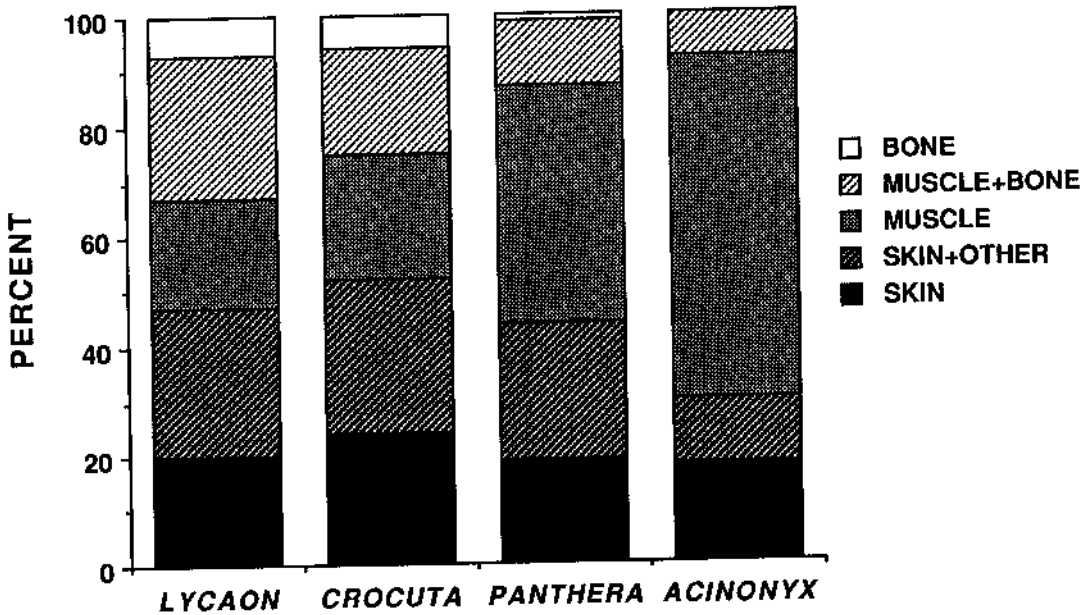


FIG. 2.—Distribution of types of food consumed by each of the four species of African carnivores that were videotaped while feeding in the Masai Mara, Kenya, 1989–1990.

was performed for each species separately because of intraspecific variation in the types of food consumed and types of teeth present (e.g., only wild dogs have postcarnassial molars).

Chi-square tests were used to examine differences in behavior among species. All comparisons were done within types of food because of an expected association between type of food and use of teeth. If particular teeth typically are used for a particular type of food, then overall use of teeth simply will reflect the array of foods eaten rather than the relative importance of different teeth among species. Although all four species consumed skin, connective tissue, muscle, and bone, they varied in both the absolute and relative quantities of the different types of food they ate. Because of the variation, the comparative analyses of use of teeth, neck, and paws were done within food categories, such as skin, muscle, and bone.

RESULTS

Types of food consumed and log-linear analysis.—The distribution of the types of food consumed differed significantly among the four species (Fig. 2; $\chi^2 = 257.42$, $d.f. = 12$, $P < 0.001$). Both felids ate little bone, whereas for hyenas and wild

dogs, bone and muscle plus bone composed 20–30% of all observations.

The log-linear analysis was conducted separately for each species and used only three of the five factors; action of neck, type of tooth, and type of food. Use of paws and motion of jaw were eliminated because their inclusion resulted in too many empty cells, and thus failure to meet assumptions of this analysis. In all four species, models that included a three-way interaction did not produce a significantly better fit to these data than those based on two-way interactions ($P > 0.26$).

The relative importance among species of the three possible two-way interactions was inferred from chi-square values for tests of partial association (Table 2). For example, in *Lycaon pictus* the interactions between type of food and type of tooth ($\chi^2 = 112.39$), as well as that between action of neck and type of tooth ($\chi^2 = 111.55$), contributed more to the model than that between action of neck and type of food ($\chi^2 = 22.24$). A stronger interaction between variables suggested a closer dependence of

TABLE 2.—Results of log-linear analysis of the associations between use of teeth, type of food and action of neck in the four species. Listed are the chi-square values for the tests of significance of partial association for the listed interactions (χ^2), the probability that the interaction is significant (P), and the degrees of freedom for each comparison.

Interaction	χ^2	P	d.f.
<i>Lycaon pictus</i>			
Tooth, food	112.39	<0.001	12
Tooth, neck	111.55	<0.001	8
Neck, food	22.24	<0.001	6
<i>Crocuta crocuta</i>			
Tooth, food	382.54	<0.001	12
Tooth, neck	130.68	<0.001	6
Neck, food	81.79	<0.001	8
<i>Panthera leo</i>			
Tooth, neck	246.85	<0.000	4
Tooth, food	124.68	<0.000	6
Neck, food	39.53	<0.000	6
<i>Acinonyx jubatus</i>			
Tooth, neck	89.05	<0.001	2
Tooth, food	17.54	0.001	3
Neck, food	4.98	0.547	6

one on the other; in this instance, type of food was influencing use of teeth and which teeth were used affected the probable action of neck. Thus, particular teeth were used for specific types of food, and actions of neck, such as pulling, are associated with certain teeth, such as the incisors and canines.

Data for the spotted hyena were fit by a model similar to that used for the wild dog. All two-way interactions were significant, and their relative importance followed the pattern observed for *Lycaon*. The effect of type of food on use of teeth was most important, followed by type of tooth on action of neck and then type of food on action of neck (Table 2). The best-fitting models for data on the two felids differed from those of the hyena and wild dog. Although the weakest interaction was still between type of food and action of neck, the interaction between use of teeth and action of neck dominated that between type of food and use of teeth in both cats. Notably, in the

cheetah, the effect of type of food on action of neck was not significant.

Type of food and feeding behavior.—Eating of skin composed 17–24% of all feeding observations (Fig. 2). Although there were significant differences among species in the proportional use of different teeth in cutting skin ($\chi^2 = 231.24$, $d.f. = 12$, $P < 0.001$), there were broad similarities. In all four species, the carnassials alone or the carnassials in company with the adjacent premolar were used to cut skin in 67–83% of all instances (Fig. 3). Lions rarely used the carnassial alone and the cheetah never did. By contrast, hyenas almost never applied the premolars alone to cut skin. Over all species, the second most likely teeth to be involved were the incisors and canines. Wild dogs were the most distinct of the four species in spreading the function of skin-slicing fairly evenly among three regions of teeth, incisor plus canine, premolar plus carnassial, and carnassials alone.

All four species were likely to use repeated jaw movements (i.e., chewing) rather than a single bite to cut skin. The frequency of chewing during skin processing ranged from 73 to 90% across the four species, but was not significantly different (Table 3 $\chi^2 = 7.17$, $d.f. = 3$, $P = 0.07$). Actions of the neck also were common when eating skin; in lions, hyenas, and wild dogs, pulling was the predominant motion, whereas in cheetahs, twisting behavior (both pull-twist and twist) occurred more often than pulls (Table 4).

Together, the information on use of teeth, chewing, and action of the neck indicates that skin usually is cut with a repeated action of the carnassials and perhaps adjacent premolars in association with short pulls that separate the skin from underlying tissue. Of the four species, the cheetah is distinct in exhibiting a relatively greater frequency of twisting actions when feeding on skin.

Skin plus other.—The consumption of connective tissue and muscle in association with skin composed 12–27% of the types

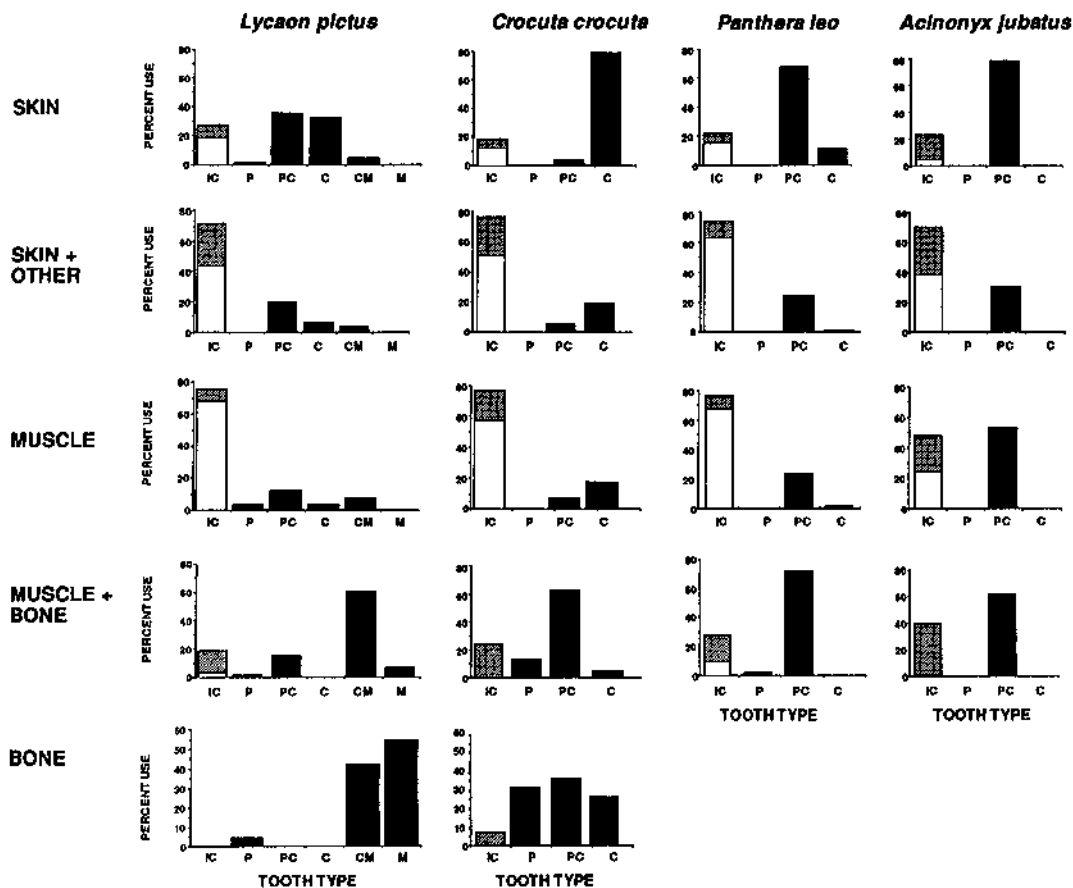


FIG. 3.—Relative use of different teeth by four species of large carnivores when eating different foods, Kenya, 1989–1990. The percentage use represents the relative proportion of the total observations of feeding on each food type for each species in each tooth category: IC, incisors + canines; P, premolars; PC, premolars + carnassials; C, carnassials; CM, carnassials + molars; M, post-carnassial molars. Within the IC category, the proportion of bites that were made by incisors alone is shown by the unshaded portion of the bar. Across types of teeth, the shading is darker for more posterior teeth.

TABLE 3.—Percentage of all observations (n) where chewing behavior (repeated closure of jaw) was observed by type of food for each species, Kenya, 1989–1990.

Type of food	<i>Lycaon pictus</i>	<i>Crocuta crocuta</i>	<i>Panthera leo</i>	<i>Acinonyx jubatus</i>
Skin	90 (71)	83 (169)	80 (95)	73 (62)
Skin + other	71 (99) ^a	51 (187)	43 (123)	51 (42)
Muscle	79 (74) ^a	56 (162)	48 (211)	62 (221) ^b
Muscle + bone	92 (93) ^a	55 (120)	67 (60)	57 (27)
Bone	100 (26) ^a	69 (42)	0 (4)	0

^a Significantly different from the other three species ($P < 0.05$).

^b Significantly different from *Panthera leo* ($P < 0.01$).

TABLE 4.—*Crosstabulation of percentage of neck motions associated with food types by species from Kenya, 1989–1990. Table 3 provides the total numbers of observations in each food category.*

Type of food	<i>Lycan pictus</i>	<i>Crocuta crocuta</i>	<i>Panthera leo</i>	<i>Acinonyx jubatus</i>
Skin				
Pull	69	54	53	25
Twist	1	16	15	32
None	30	30	33	43
Skin + other				
Pull	92	76	64	40
Twist	0	15	15	45
None	8	9	21	14
Muscle				
Pull	89	78	67	37
Twist	1	16	10	29
None	10	6	23	33
Muscle + bone				
Pull	24	19	24	21
Twist	11	55	15	39
None	65	26	61	39
Bone				
Pull	15	0	0	0
Twist	31	43	0	0
None	54	57	100	0

of food consumed, a proportion similar to that for skin (Fig. 2). The pattern of use of teeth, however, was different from that observed for eating skin. In all four species, incisors and canines were used to separate subcutaneous tissue and muscle from the carcass in >67% of all observations, with carnassials and premolars used much less often (Fig. 3). Chewing behavior was not as common as when eating skin, with repeated bites occurring 43–71% of the time (Table 3). The wild dog exhibited significantly more chewing behavior for this type of food than did the other species ($\chi^2 = 18.38$, $d.f. = 3$, $P < 0.001$). Movements of the neck were associated with eating subcutaneous tissue and skin-muscle combinations in >75% of all instances (Table 4). As was true for ingestion of skin, short pulls appeared to be most useful in all but the cheetah, where twisting actions were

more important (Table 4). In sum, skin associated with connective tissue or muscle typically was ripped from the carcass by short pulls (lions, hyenas, wild dogs) or twists (cheetahs) with the incisors and canines.

Muscle.—Feeding on muscle made up ca. 20% of all observations in hyenas and wild dogs, and 40–60% in the two felids (Fig. 2). The difference largely reflects the more diverse array of types of food consumed by the canid and hyaenid. With the exception of the cheetah, the pattern of use of teeth was similar to that documented for skin plus other. Incisors and canines were the most common teeth used, and far exceeded any other type of tooth (Fig. 3). In the cheetah, however, the function of eating muscle was nearly evenly split between anterior (incisors, canines) and posterior teeth (premolars, carnassials). Examination of the frequency of chewing behavior reveals that the cheetah chewed significantly more often than the lion ($d.f. = 1$, $P < 0.01$, $\chi^2 = 8.147$), but less than the wild dog, which chewed muscle significantly more than all three other species ($P < 0.01$; Table 3).

Because of the similarity in patterns of use of teeth for eating muscle and skin plus other, it was not surprising to see a parallel in data for action of the neck. Similar to eating skin plus other, pulls with the anterior teeth predominated in all but the cheetah, where twists were almost as common as simple pulls (Table 4), and cheek teeth were used nearly as often as anterior teeth.

Muscle plus bone.—All four species ate some bone in combination with muscle, but the proportion was greater in the wild dog and hyena (24% and 18%, respectively), than the lion and cheetah (12% and 8%, respectively). For all but the wild dog, the distribution of bites among tooth types was similar to that observed for eating skin; >60% of all bites were made with the carnassials and adjacent premolars (Fig. 3). In the cheetah and lion, the remaining bites involved incisors and canines, and premolars alone occasionally in the lion. In the

spotted hyena, the premolars alone were used relatively more frequently than in the felids.

The wild dog was similar to the other species in emphasizing the posterior teeth over the anterior teeth in processing muscle plus bone. Wild dogs, however, used their carnassials in combination with their postcarnassial molars most often, rather than premolars. In association with this, wild dogs chewed significantly more frequently than the other species ($\chi^2 = 36.18$, $d.f. = 3$, $P < 0.001$). Ninety-two percent of all bites on muscle plus bone were repeated actions as opposed to a relative frequency of 55–67% in the other three species (Table 3).

The pattern of neck motions that occurred when eating muscle plus bone differed markedly from the three previous types of food. In the wild dog and the lion, most bites were made without a concurrent pull or twist, but in the cheetah and hyena, bites on muscle plus bone were characterized by a greater proportion of neck motions, especially twisting in the hyena (Table 4). There was no single combination of use of teeth and motion of neck that was typical of all four species. The wild dog usually was observed to process muscle plus bone with repeated bites of its carnassial and postcarnassial molars and rarely pulled or twisted such foods from the carcass. In the other three species, carnassials and premolars were the most common teeth used, chewing was less frequent than in the canid, and pulling and twisting often were employed by the hyena and cheetah.

Bone.—Because the cheetah was never observed to eat bone and <1% ($n = 4$) of all observations on lions represented eating of bone this activity was not analyzed for the felids. In the hyena and wild dog, the number of observations were sufficient to make reasonable comparisons (Table 3). The two exhibited nearly nonoverlapping distributions in use of teeth (Fig. 3). Whereas, wild dogs depended on the combined use of carnassials and postcarnassial molars for bone cracking, hyenas used premolars

along with carnassials. In addition, hyenas were observed to apply their incisors and canines to bones occasionally. As was true of muscle-plus-bone consumption, wild dogs chewed bones more often than did hyenas. All observed bone-eating events involved repeated jaw closure in the wild dog as opposed to only 69% in the hyena (Table 3). Both species were unlikely to use their necks when feeding on bone. When motion of the neck occurred, it was usually a twist (Table 4).

Action of neck.—In all four species, some action of the neck was involved in >65% of observed feeding behaviors (Table 5). Pulling actions occurred much more frequently than twisting actions in all except the cheetah where both were observed at near equal frequencies. As noted previously, the cheetah tended to use twisting actions more often than the other species when feeding on all types of food.

The log-linear analysis indicated that in all species, there was a significant interaction between action of neck and use of teeth, and in all but the cheetah, there was a significant but weaker interaction between action of neck and type of food (Table 2). The associations between particular actions of neck and type of food were noted previously (e.g., pulling with feeding on muscle and connective tissue; Table 4). Actions of neck also correspond somewhat to use of teeth, although the patterns were not the same for all four species. For example, in all four species, a bite with the incisors and canines was likely to be associated with pulling behavior, but bites with the premolars and carnassials were accompanied most often by no action of the neck in the felids and pulling in *L. pictus* (Table 5).

Use of paws.—Both hyenas and wild dogs placed one or both front paws on the carcass when feeding in more than one-half of all observations, whereas the lions did so only 35% of the time, and the cheetah never used its paws in feeding (Table 6). Hyenas and wild dogs neither differed significantly in the overall frequency of use of paws (χ^2

= 2.683, *d.f.* = 1, *P* < 0.10) nor in the frequencies observed when eating skin (*P* = 0.27, χ^2 = 1.2, *d.f.* = 1) or bone (χ^2 = 0.119, *d.f.* = 1, *P* = 0.73; Table 6). Lions used their paws less than hyenas or wild dogs, regardless of type of food. Relative to action of neck, wild dogs were more likely to use their paws if they were pulling or twisting food from the carcass, but there was no apparent relationship between these two variables in lions and hyenas.

DISCUSSION

Use of teeth was not random with respect to type of food in the four species of large carnivores. There were clear associations between particular teeth and foods, such as carnassials and skin, in all species. Nonetheless, the associations were not always as expected and they varied. Most foods were separated from the carcass with teeth that represented at least two different regions of the tooth row, although those of one region predominated. For example, muscle was cut most often with the incisors and canines, and secondarily with the carnassials. Because of their relatively small size, incisors were not expected to figure prominently in feeding. Incisors and canines as a unit, however, made up >66% of observations of feeding on skin plus other and muscle, in all species except the cheetah, where cheek teeth were used most often when eating muscle (Fig. 2). Moreover, well over one-half of all observations in the incisor-plus-canine category were incisors used alone; it is clear that these relatively small teeth are important in feeding.

Across species, feeding behavior on muscle and skin plus other was relatively similar and contrasted markedly with that observed for skin and the combination of muscle plus bone. Whereas, the anterior dentition was emphasized when eating muscle or skin plus other, the more posterior teeth (carnassials, in particular) were emphasized when eating skin or muscle plus bone. A greater reliance on posterior as opposed to anterior teeth suggests a need for

TABLE 5.—Crosstabulation of percentage of neck motions associated with types of teeth by species from Kenya, 1989–1990: IC, incisors and canines; P, premolars; PC, precarnassial premolars and carnassials; C, carnassials; CM, carnassials and postcarnassial molars; M, postcarnassial molars; Total, all tooth types combined; n, total number of observations of feeding for each type of tooth.

Species	n	Percent- age pull	Percent- age twist	Percent- age none
<i>Lycaon pictus</i>				
IC	156	97	1	2
P	5	20	0	80
PC	68	57	6	37
C	31	77	0	23
CM	81	8	11	81
M	20	20	25	55
Total	361	63	6	31
<i>Crocuta crocuta</i>				
IC	319	80	18	1
P	28	4	71	25
PC	121	19	46	35
C	212	45	16	39
Total	680	56	25	19
<i>Panthera leo</i>				
IC	289	81	15	4
P	1	0	100	0
PC	189	24	9	67
C	14	36	0	64
Total	493	58	13	29
<i>Acinonyx jubatus</i>				
IC	156	52	40	8
PC	196	19	27	54
Total	352	34	32	34

a stronger bite because the mechanical advantage of muscles that close the jaws improves as the bite point nears the jaw joint (Maynard-Smith and Savage, 1959; Radinsky, 1981). Skin and muscle plus bone, respectively, are likely more difficult to cut than either muscle or skin plus other. Although the latter category included some skin, many of the observations placed in this category were of feeding on subcutaneous connective tissue. Data on use of teeth and action of neck indicate that muscle and skin plus other usually were pulled

TABLE 6.—Crosstabulation of percentage of all observations where paws were used within food types by species from Kenya, 1989–1990. Data for the cheetah are not included because paws were not observed to be used in feeding. Table 3 provides the total number of observations in each food category.

Type of food	Percentage of use of paws		
	<i>Lycaon pictus</i>	<i>Crocuta crocuta</i>	<i>Panthera leo</i>
Skin	48	56	21
Skin + other	62	76	44
Muscle	79	54	37
Muscle + bone	46	67	32
Bone	60	62	75
Total	53	63	35

from the carcass with incisors and canines, rather than cut with cheek teeth as was typical when carnivores were eating skin.

Instead of being most important in cutting muscle, the carnassial teeth appear to be critical for processing tough foods such as skin and muscle plus bone, respectively. The ability to cut skin is not trivial; it allows access to deeper parts of the carcass and made up 17–24% of all feeding observations. In most instances, skin was not simply cut and removed, but was chewed and swallowed. The consumption of skin was greater than expected given that skin was assumed to be of relatively poor nutritional value and has a high work of fracture (Vogel, 1988). Individuals were observed to feed on skin even when muscle was exposed, suggesting that skin sometimes was preferred. Eating of skin usually was associated with repeated movements of the jaw (i.e., chewing), further supporting the notion that skin is difficult to slice. Chewing behavior was less frequent when feeding on muscle plus bone (e.g., ribcage, skull), in all but the wild dog. Nevertheless, the tendency to use the rearmost teeth when feeding on muscle plus bone suggests that, like skin, this combination was significantly more difficult to separate from the carcass than muscle alone.

Bone cracking usually was accomplished with teeth assumed to be built for the task, premolars in hyenas and postcarnassial molars in the wild dog. Recent work on mandibular strength in these species demonstrated a parallel difference in the pattern of cortical thickness of bone along the length of the mandible. The mandibles of spotted hyenas are buttressed beneath the premolars, whereas those of wild dogs are buttressed beneath the carnassials and molars (Biknevicius and Ruff, 1992). Despite the apparent regional specializations in their jaws and teeth for cracking bones, hyenas occasionally break bones, such as ribs and scapulae, with their incisors or carnassials, and wild dogs appeared to rely on their carnassials as well as their molars. In hyenas, the relatively heavy use of the carnassials alone and in concert with the premolars (C, PC; Fig. 3) does not necessarily indicate application of the blade-like part of the carnassials in cracking bone. The anterior-most aspect of the upper carnassial (fourth premolar) has a large, blunt internal cusp, the protocone, which occludes with the posterior cusp of the lower fourth premolar. This portion of the upper carnassial is not blade-like and hyenas may confine most bone-cracking to both this region and the more anterior premolars to limit damage to the scissor-like blades.

The lions I videotaped rarely ate bone and the single cheetah in this study was not observed to do so. Lions are known to be capable of consuming all but the largest limb bones of their ungulate prey (Schaller, 1972), but were seen to bite on bones that had little muscle attached in only four instances in this study. In all four instances, they used their premolars and carnassials in combination. The limited amount of consumption of bone observed in the lions during the study period should not be taken as indicative of typical behavior. During the summer of 1989 and 1990, prey were relatively abundant in the Masai Mara and lions likely were less compelled to fully consume carcasses. The absence of eating of

bone in the observed cheetah is consistent with some previous studies of feeding behavior of cheetahs (Brain, 1981) and dental microwear (Van Valkenburgh et al., 1990a). Brain's (1981) studies of cheetahs feeding on small antelopes and baboons revealed limited consumption of bovid skeletons, and microwear analysis of the carnassial-wear facet indicated little eating of bone relative to other large predators, such as lions. Nonetheless, in a study of free-ranging and captive cheetahs, Phillips (1993) observed substantial consumption of ribs and vertebrae of small antelopes by the cats. Cheetahs do not avoid bone entirely, but appear to eat fewer, smaller bones than the other three species studied here.

I hypothesized that the larger skull and jaw muscles of the spotted hyena and lion would result in greater bite forces in these species relative to the wild dog and cheetah. Because all four species feed on the same foods (skin, muscle, bone), those with stronger bites likely are able to comminute food more quickly, and thus chew less, than those with weaker bites. This follows from experimental studies of mastication in the domestic cat, which showed that the duration of chewing cycles prior to swallowing increased with hardness of food (Thexton et al., 1980). In my study, the wild dog chewed its food significantly more often than all three other species, except when feeding on skin (Table 3). All species relied heavily on repeated movements of the jaw to slice skin. Relative to the larger lion, the cheetah was observed to chew significantly more often only when consuming muscle. These data suggest that there is a negative relationship between size of predator and the need to chew, and that an advantage of large body mass in carnivores might be the ability to consume large prey more rapidly. The species that chews most often, the wild dog, is the smallest of the four in body mass and has the least mechanical advantage of its major jaw-closing muscles (temporalis) for bites at the canines and incisors due to

its relatively long snout (Van Valkenburgh and Ruff, 1987).

The two felids have similar dental arrays that differ in their emphasis on anterior (canines, incisors) and posterior (premolars, carnassials) teeth. Relative to lions, cheetahs appear to have a weaker anterior dentition and larger premolars (Fig. 1) and, thus, might be expected to rely more heavily on their cheek teeth in feeding. A comparison of use of anterior versus posterior teeth in which all cheek teeth are considered as posterior teeth reveals no significant differences among all four species when feeding on skin or skin plus other. The cheetah, however, relied significantly more on its cheek teeth in cutting muscle than the other species ($P < 0.001$). The cheetah also differed significantly from the wild dog, but not the other two species, in using its anterior teeth relatively more frequently in feeding on muscle plus bone. Given the small number ($n = 28$) of observations of muscle plus bone for the cheetah, this result should not be taken as conclusive.

The log-linear analysis of the interactions among use of teeth, type of food, and action of neck demonstrated significant associations between each of these factors; the neck and teeth work together to separate tissues from the carcass, and the use of teeth vary according to type of food. Pulling or twisting with the neck is more likely to be associated with bites made by anterior teeth, whereas no action of the neck was typical of bites made by the cheek teeth. Among the four species, some differences existed in the relative importance of the three interactions, use of teeth versus type of food, use of teeth versus action of neck, and action of neck versus type of food. For example, the association between action of neck and type of tooth was less important in the hyenas than in the wild dogs. This appears to be a result of the greater tendency of hyenas to use their necks in feeding; they used pulls or twists in 81% of observations, whereas the other three species did so 66–71% of the time.

Both cats differed from the wild dog and hyena in that the most significant interaction was that between use of teeth and action of neck, rather than type of food and use of teeth. The greater emphasis on the interaction between action of neck and use of teeth in the felids is likely because of both a stronger association between these two variables, and a less well-defined effect of type of food on use of teeth in the felids relative to the hyena and wild dog. The diminished effect of type of food on use of teeth in felids is probably a result of the more limited sample of types of food consumed by the cats (Fig. 2) and their relatively reduced postcanine dentition that was applied similarly to many types of food. The cheetah was the only species in which the association between action of neck and type of tooth was not significant. This follows from the greater and more nondiscriminant use of twisting action by the cheetah in feeding on all types of food (Table 4).

In addition to its unusual emphasis on twisting actions of the neck, the cheetah was unique among the four species in not using its paws to stabilize the carcass while feeding. These two behaviors likely are causally related; i.e., rather than relying on paws to hold the carcass while pulling tissue with the teeth, the cheetah uses rapid twists of the head to rip tissue free. Whether the avoidance of use of paws in feeding seen in the single cheetah studied is a characteristic of the species is unknown; when feeding in groups, cheetahs are known to place their paws on the carcass between themselves and adjacent individuals in an apparently possessive gesture (T. Caro, pers. comm.). The use of the paws to hold the carcass while pulling tissue away seems an effective technique for more rapid feeding; it was observed frequently in the other three species and is considered to be a primitive characteristic among mammals (Eisenberg, 1981). Leyhausen's (1979) extensive studies of behavior in a variety of feline species indicated that mountain lions (*Puma concolor*), cheetahs, and small cats

were all similar in not using their paws when feeding and differed in this feature from species of *Panthera*. Like the domestic cat, mountain lions and cheetahs crouched next to their kill and used only teeth, jaws, and neck in feeding (Leyhausen, 1979). If future studies reveal that cheetahs never use their paws in feeding, it would seem to be a peculiar feature that may reflect ancestry more than function; recent morphological and molecular studies have suggested that mountain lions and cheetahs may be sister taxa (Herrington, 1986; Janczewski et al., 1995; Van Valkenburgh et al., 1990b).

In addition to revealing a potential oddity in the cheetah, this study of feeding behavior has suggested several further avenues for study. The surprising importance of incisors in feeding highlights the need for more study on the form and function of arcades of incisors in carnivores. Motions of the neck varied in frequency and type among species and might be associated with parallel variations in occipital and cervical musculature and osteology. The unexpected frequency of consumption of skin in all four species, despite its toughness, suggests that skin may harbor a critical resource such as fat. African ungulates are well known to be extremely lean, with fat usually making up <5% of their body mass, as opposed to 15–35% in cattle (Ledger, 1968). This small quantity of fat is distributed throughout the body, within muscles and bones, below the skin (subcutaneous), and within the mesentery. Perhaps carnivores are eating the skin to obtain the subcutaneous fat attached to the inner surface. In addition, the high protein content of skin might explain its desirability, but it is unclear how much of the skin actually is digested in any of the four species.

The lack of a perfect association between a particular type of tooth, such as the carnassial, and a particular function, such as cutting skin, may not be surprising; mammals are not machines and their behavior is readily altered according to circumstance. If

there is pressure to eat rapidly, which often may be the case in socially feeding carnivores, precision in use of teeth may be compromised for speed of ingestion. Speed certainly seemed important in the observed hyenas and perhaps wild dogs, where feeding was much more rapid than in the two cats and appeared highly competitive. The lack of precision in use of teeth suggests that selection should favor specializations for particular functions in teeth other than those that are the primary tools for that purpose. For example, the premolars of hyenas were the primary bone-crackers, but the carnassials also were important. Consequently, the carnassials are likely to show structural adaptations to resist fracture. Indeed, recent work on microstructure of enamel in teeth of hyenas has shown that the canines, premolars, and carnassials all share a similar, complex internal architecture that resists fracture (Rensberger, 1995). Because hyenas appear to use all of their teeth to crack bones, the distribution of this specialization among all the tooth types is understandable.

The observed lack of precision in use of teeth also might explain the tendency of carnivores to fracture their teeth. Recent studies of the frequency of teeth fractured in life among 10 species of large predators, including the four examined here, demonstrated that breakage of teeth occurs regularly, and the teeth most likely to have been broken are canines (Van Valkenburgh, 1988; Van Valkenburgh and Hertel, 1993). Teeth are probably most vulnerable when they contact bone, but this was not easily reconciled with the greater number of broken canine teeth, as these teeth were assumed not to be used in eating bone. Nonetheless, this study of free-ranging carnivores has revealed a substantial use (19–40%) of the anterior dentition when feeding on muscle plus bone in all four species, and thus potentially injurious contact between canines and bone occurred regularly. Future studies of feeding behavior in free-ranging predators should focus on rates of feeding relative to precision of use of teeth within

a species. If rates of ingestion increase when individuals share a carcass, and if this also results in greater variation in use of teeth relative to type of food, then it could be argued that selection for dental and cranial strength should be greatest among large predators that are social. The increased risk of fracture of teeth could then be viewed as a cost of sociality that must be met by enhanced strength of the jaws and teeth.

Despite the variation in use of teeth relative to type of food, some of my assumptions concerning shape and function of teeth were upheld by this study. Carnassials were important in all species in slicing function (primarily skin), and the postcarnassial molars of wild dogs and premolars of spotted hyenas, respectively, were the primary bone-cracking tools. Thus, studies of the evolution of dental form and function in mammalian predators can continue with some additional measure of confidence in our assertions.

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