Paleobiology, 9(2), 1983, pp. 164–172

A guide for differentiating mammalian carnivore taxa responsible for gnaw damage to herbivore limb bones

Gary Haynes

Abstract.—Large cats, canids, bears, and hyenas create distinctive types of damage when they gnaw bones. This paper describes the diagnostic characteristics of damage done by each taxon to femora and tibiae of herbivores whose body weights are 300 kg or more. Pleistocene and Recent fossil collections that include gnawed bones might provide data on the presence of carnivores whose own remains are not found in the collections. Information might also be gained about predator and scavenger utilization of prey carcasses, often a reflection of prey vulnerability or availability in past communities.

Gary Haynes. National Museum of Natural History, Department of Anthropology, Smithsonian Institution, Washington, D.C. 20560

Accepted: May 13, 1983

Introduction

During the late Pleistocene, North America was inhabited by more taxa of mammalian carnivores than in Recent times. These taxa include *Arctodus,* an enormous bear that has no modern counterpart (Kurtén 1967); *Panthera leo atrox,* a lion larger than modern African relatives; and *Canis dirus,* a wolf with massive, hyena-like dentition (Kurtén and Anderson 1980; Martin and Guilday 1967).

Because modern carnivores can inflict recognizable gnaw damage to bones of large prey animals (Buckland 1824; P'ei 1938; Zapfe 1939; Miller 1969; Bonnichsen 1973; Haynes 1980, 1981, 1982; Binford 1981), we can reasonably expect that related extinct species were also capable of modifying prey bones with their teeth. The end effects of carcass utilization and bone damage by specific kinds of Recent carnivores can be distinguished (Buskirk and Gipson 1978; Haynes 1980, 1981, 1982; Magoun 1976), and similar damage by related Pleistocene species should also be distinguishable. The existence of certain carnivores in the past might be concretely reflected by gnaw damage to prey bones, even in fossil assemblages that lack remains of predators and scavengers.

I describe here some of the diagnostic attributes of bone modifications due to various carnivores, so that similar damage types might be distinguished in fossil bone collections.

The characteristics described and illustrated here are considered to be reliably diagnostic and have been found to be unambiguous indicators of carnivore taxa responsible for gnaw damage. I must emphasize that the types of damage described here need not always occur on bones gnawed by any particular carnivore taxon, since the degree of carcass and bone utilization can vary greatly for numerous reasons, most of which reflect the ease of food procurement. The presence and exact degree of gnaw damage due to carnivores can never be predicted by taxon without prior knowledge of the local conditions of hunting and feeding. However, when the types of damage that I have described do appear on bones, they can be confidently assigned to particular carnivore taxa. Yet other types of gnaw damage are possible, and need not always be diagnostic. For example, very light gnaw damage by all taxa of carnivores might look identical. Bones that have been only lightly gnawed by lions will never be distinguishable from bones that have been lightly gnawed by bears or any other taxon.

Materials and Methods

Published field studies of carnivores often provide data on feeding behavior. To enlarge on these observations, I carried out my own long-term studies, beginning with projects involving zoo animals. Captive bears, wolves, large cats, and hyenas in three zoological parks were experimentally fed fresh limbs or limb bones of domestic cattle (*Bos taurus*) in order to record sequences of bone damage, lengths of time re-

0094-8373/83/0902–0008/$1.00

TABLE 1. Numbers of bones examined after carnivore feedings (captive and wild). Sample includes only femora and tibiae of *Bos, Bison, Alces, Cervus, Equus, Loxodonta* (elephant), *Synceros* (African buffalo), and *Giraffa* (giraffe).

Carnivore species	Number of bones
Canis lupus	205
Helarctos malayanus (Malay Sun Bear)	3
Tremarctos ornatus (Spectacled Bear)	2
Ursus arctos	13
U. americanus	7
U. maritimus	2
Crocuta crocuta	65
Panthera leo	23
P. tigris	3
P. onca	3

quired for specific types of damage, lengths of time the bones were of interest, types of damage when several animals gnawed, and so forth. In addition I carried out field studies of wild wolves, bears, and their prey in northern North America (Haynes 1980, 1981, 1982), lions and their prey in southern Africa, and hyenas and their victims (both prey and scavenged carcasses) in Africa (Haynes, in prep.). Fresh carcasses and skeletons were located that have undergone documented processes of natural modifications, such as carnivore feeding or weathering, and changes were monitored in the condition and distribution of bones (Table 1).

Results

Carcasses are utilized by large carnivores in surprisingly patterned, predictable sequences (Haynes 1980, 1981, 1982). For purposes of classification, I have arbitrarily broken down the sequences of gnaw damage to single elements into "stages"; more detailed descriptions of the stages seen when wolves feed are in Haynes (1981, 1982). Basically, with prey that weighs over 300 kg, the sequences include light, medium, and heavy damage reflecting similar degrees of utilization of entire carcasses. It must be emphasized that the damage done by each taxon of gnawing animals varies significantly from stage to stage. In this report, attributes of all utilization stages will be described, but it is in the medium to heavy stages that the distinctions between gnawing animals are easiest to isolate and identify.

Tooth marks.—When an animal bites down hard on bone, which deforms under pressure only up to a point, the teeth leave impressions as pits in the bone surface (Fig. 1). When the animal moves its teeth on the bone, the impressions may be in the form of furrows, scratches, or incisions (Fig. 2). Gnaw marking is usually most apparent near the ends of the remaining bone or bone fragments, especially on shaft fragments from near epiphyses. On epiphyses, cheek teeth may be used to grind or shear off cancellous or thin compact tissue, creating grooves where the cusps pressed deep into, and moved through, the tissue (see Haynes 1980, figs. 6, 7). Such furrows may appear similar to chopping damage done by stone, metal, or bone implements which have relatively low-angled edges.

FIGURE 1. Pit impressions of wolf (*Canis lupus*) teeth on larger trochlear rim of *Bison* femur.

As teeth scrape compact bone, concentric layers of tissue (bone lamellae) are broken through, and the groove produced is seldom flat-walled and smooth, like a true tool cut, unless the mark

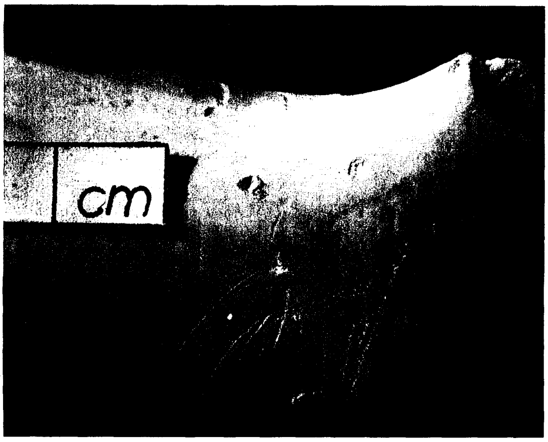

FIGURE 2. Scratches and pits left by wolf (*Canis lupus*) teeth on shaft of *Bison* humerus.

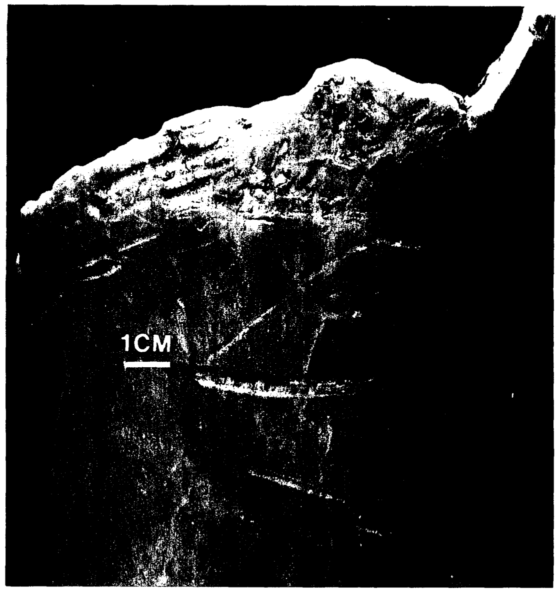

FIGURE 3. Marks of wolf (*Canis lupus*) teeth on *Bison* femur shaft. Largest scratch mark shows several layers of lamellar tissue unevenly broken through.

is a deformation rather than an incision. Cutlike marks produced by very sharp carnivore teeth usually do not occur as single, isolated marks, and other, less equivocal tooth marks may be apparent on the same specimens. Many carnivore tooth marks are made by the teeth of adult animals, which have relatively blunt or large cusps. These marks are characterized by uneven edges and incomplete slicing through bone lamellae (Fig. 3).

Observations of Tooth-inflicted Damage

Hyena (Crocuta crocuta).—Hyena gnaw damage to large bovid femora: In the early stages, tooth scoring of compact bone surfaces generally consists of scrapes and impact depressions averaging 1 × 2 cm, about the size of moderately worn cusps of hyena cheek teeth. In the stage of medium utilization, the greater trochanter is half removed, compact tissue of the shaft is ground and crushed, and the trochlear area is well gouged (Fig. 4). In later stages the proximal epiphysis is removed and the diaphysis is pulled apart fragment by fragment. Variably sized shaft pieces may be ignored, bolted down outright, or well chewed. One distal condyle, usually medial, may remain uneaten. If the femur is located at a killsite, it is usually abandoned before reaching this stage. However, if it has been carried to a den or fed to a captive hyena, it will probably be gnawed again from time to time, and this stage may be reached within 1 hr.

In the final stages, the bone may be entirely eaten or abandoned when only short segments of the shaft remain. These segments may be 15 cm long or longer. Surviving fragments may have numerous tooth scratches on the surfaces, as well as many single tooth-cusp impressions. Parts or all of fractured edges may be well rounded from chewing abrasion, repeated licking, or rubbing against ground surfaces. Trabecular bone inside the shaft may have numerous furrows and impressions inflicted by single hyena teeth. These are generally cone-shaped and round bottomed, measuring about 3–5 mm wide at the widest point and 3–5 mm deep if made by adult hyenas.

Hyena gnaw damage to large bovid tibiae: In the early stages the proximal anterior crest is gouged out and tooth furrows are visible in the exposed cancellous bone. When utilization increases, the entire proximal end is removed, and the shaft shows jagged fracture edges that are mostly not rounded. Tooth marks on the central shaft are left by incisors used to peel periosteum and by cheek teeth used to carry the bone crossways in the jaws.

In medium utilization the shaft is pulled apart, each fragment measuring up to 5 cm long or longer, and possibly terminating as might a stone

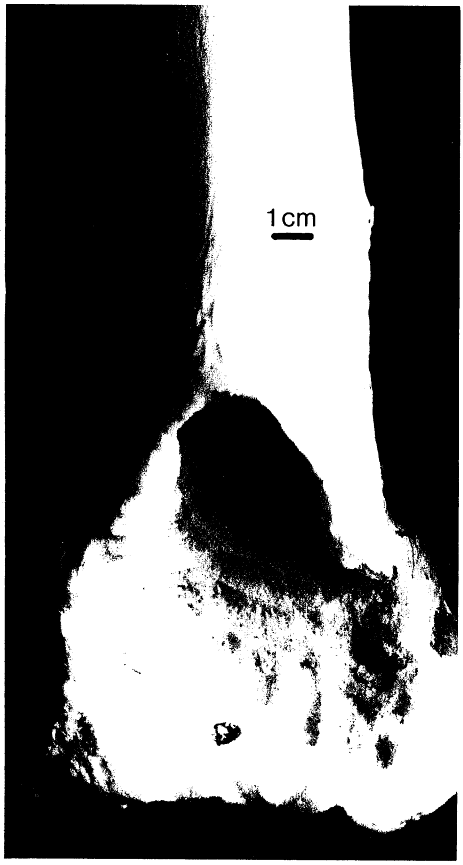

FIGURE 4. Frontal view of *Bos* femur distal end, showing gouging by hyena (*Canis crocuta*). Note tooth furrows in cancellous bone.

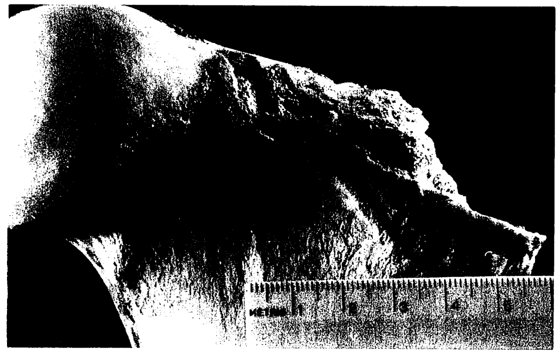

FIGURE 5. Proximal end of *Bison* femur partly eaten by wolves (*Canis lupus*). Greater trochanter is gone, but a rim of compact bone remains at the stump, to right.

flake, with so-called feather termination. The broken edges of the shaft may be rounded by gnawing, and there is heavy tooth marking of compact bone surfaces, sometimes leading to exfoliation of thin layers of bone tissue in patches crushed between teeth. There is a great deal of scoring on the shaft perpendicular to the long axis. Tarsals will have been disarticulated by this stage.

In a final stage of utilization, less than one-third of the shaft remains, with the edges well rounded and the surfaces very tooth-marked. The extreme distal end often survives practically unmarked by teeth.

Wolf (Canis lupus).—Wolf gnaw damage to large bovid femora: Damage in the early stages is the result of cheek teeth penetration of the outer bone surfaces of epiphyses, exposing trabecular tissue (see Haynes 1980). The stump of the greater trochanter may consist of a 5-mm-high rim of compact bone encircling cancellous bone (Fig. 5). The larger distal trochlear rim, about 60–70 mm of its length, will have been removed to expose cancellous bone about 20 mm in width. The damage may consist of isolated tooth punctures through outer compact bone into cancellous tissue or sets of single tooth punctures that run together.

Individual tooth furrows may be visible, and thin compact tissue is further gouged out during heavier utilization. Compact tissue near or at articular surfaces is removed in patches about 1 mm in diameter, and the exposed cancellous tissue shows tooth furrows and impressions. In the final stages of utilization, the shaft survives as a hollow cylinder with most tooth scratches at right angles or diagonal to the long axis. The scratches may be up to 3 cm long or longer and may be 1 mm deep and up to 2–3 mm wide. These scratches are most abundant near the ends of diaphyses. Broken edges of the shaft may be somewhat polished in a few places, possibly due to repeated chewing and licking or to abrasion on ground surfaces. The femoral head and one or both distal condyles may also remain. Impressions from individual teeth in trabecular bone are about as wide and deep as those left by hyenas, but the bottom may not be as rounded.

The basic differences between damage to femora due to hyenas and to wolves is in degree of tooth crushing and scratching. Wolves do not normally mark up compact bone as heavily as do hyenas, although in dens and homesites

FIGURE 6. Frontal view of proximal end of moose (*Alces*) tibia partly eaten by wolves. "Crest" has been removed.

FIGURE 7. Remaining proximal end of *Bison* tibia partly eaten by wolves (*Canis lupus*).

wolves will spend much more time chewing on bones than at killsites, leading to characteristically differential tooth marking.

Wolf gnaw damage to large bovid tibiae: After wolves have successfully disarticulated the tibia from the femur, the proximal crest has been removed on the anterior side of the element (Fig. 6), and distinct furrows and tooth impressions are noticeable in the medullary cancellous tissue. A small number of tooth scratches may be present on the shaft perpendicular to the long axis. In the final stages of utilization, the proximal end is gone, and the edges of the remaining shaft are partly polished and irregular, with scrapes, scratches, and pitting near the edges as well as on the rest of the shaft (Fig. 7). When scavenging is heavy, the shaft is broken apart.

Because uneaten or partially eaten carcasses and body parts may be covered by snow or freeze solidly during winter, paired long bones may not be equally damaged. Utilization and damage to whole carcasses is described in Haynes (1982).

Bears (Ursus arctos, U. americanus *mainly; other species listed in Table 1*).—Bear gnaw damage to large bovid femora: Most bears will usually not gnaw heavily on bones after the soft tissue has dried or been removed, although there are wide behavioral differences between individuals and species.

Damage from bear gnawing is distinct from damage caused by canids and hyenas, in that the broader cheek teeth of bears grind down and crush cancellous bone as well as plane or shear it off. However, bear gnawing, like hyena or wolf gnawing, may leave distinct furrows or score marks across cancellous tissue.

In the early stages the cheek teeth grind off most of the greater trochanter (Fig. 8) and the larger trochlear rim, with the jaws aligned parallel to the rims.

In the later stages the stump of the greater trochanter is faceted or flattened, and the exposed cancellous bone may be gouged into fewer than 5 pits that are 6 mm deep and 10–20 mm long, each corresponding to and about the size of individual cheek teeth of large bears. There is rarely a rim of compact bone higher than the cancellous bone of the trochanter stump. The trochlear rims also appear to have been crushed or ground off between teeth, rather than chopped off (Fig. 9). There may be no tooth marks or scratches on the shaft surfaces. The occasional tooth marks on compact bone appear as short

FIGURE 8. Proximal end of *Bos* femur partly eaten by Kodiak bear (*Ursus arctos*). Greater trochanter has been removed.

FIGURE 9. Frontal view of distal end of *Bos* femur partly eaten by Kodiak bear (*Ursus arctos*). Trochlear rims have been furrowed by cheek teeth.

and wide sets of parallel scrapes, each seldom wider than 1.5 mm or longer than 9 mm, or they may appear as roughly circular pits no deeper than 0.5 mm.

Bear gnaw damage to large bovid tibiae: Black and brown bears (*U. americanus* and *U. arctos*) do not often severely damage tibiae of large herbivores such as *Bison bison* unless wolves have first gnawed off epiphyses. Bears seldom inflict the full range of damage of which they are capable, except when other sources of food are in short supply.

Typical damage due to gnawing by bears appears as a rounding of edges and a grinding with crushing of compact bone surfaces, exposing cancellous tissue and leaving it with a mashed look. There may be occasional tooth cusp impressions in the proximal end of the bone, consisting of single, nearly flat-bottomed holes entering cancellous tissue. There may also be sets of parallel furrows on the crest, resulting from the filing away of bone by separate tubercles on the cheek teeth. The cheek teeth may produce a few short scratches on the shaft. These scratches actually appear similar to rodent gnaw marks: short and parallel, shallowly etched, straight score lines.

Lion, tiger, and jaguar (Panthera leo, P. tigris, *and* P. onca).—Large cat gnaw damage to large bovid femora: African lions, Bengal tigers, and jaguars will not often sustain gnawing on large bones, although captive cubs and adults may mouth bones and gnaw briefly from time to time.

The main damage from large cats consists of the biting off of the greater trochanter, undercut biting of the femoral head (Fig. 10), and scraping off of trochlear rims by use of the carnassials and other cheek teeth, leaving a few, relatively deep, identifiable grooves from individual tooth cusps running perpendicular to the larger trochlear rim (Fig. 11). The grooves, if clearly produced, will usually be larger than grooves created by the teeth of hyenas or wolves, and may be fewer in number.

Lion cubs may gouge out only some of the greater trochanter, leaving a discontinuous 3–7-mm-high rim of compact tissue around the internal cancellous tissue, similar to gnaw damage created by adult wolves.

Adult lions sometimes leave tooth scratches on the compact tissue of the diaphysis. Most of these marks are nearly perpendicular to the element's long axis, and all are shallow but rather sharply incised. The outline of the greater trochanter may be irregularly gnawed into deep round pits. The basic identifying characteristic of large cat gnawing is the rough and irregular marking left by biting on or through cancellous bone of the epiphyses. These marks are wide, deep, and countable, and are inflicted by the large cheek teeth.

Large cat gnaw damage to large bovid tibiae:

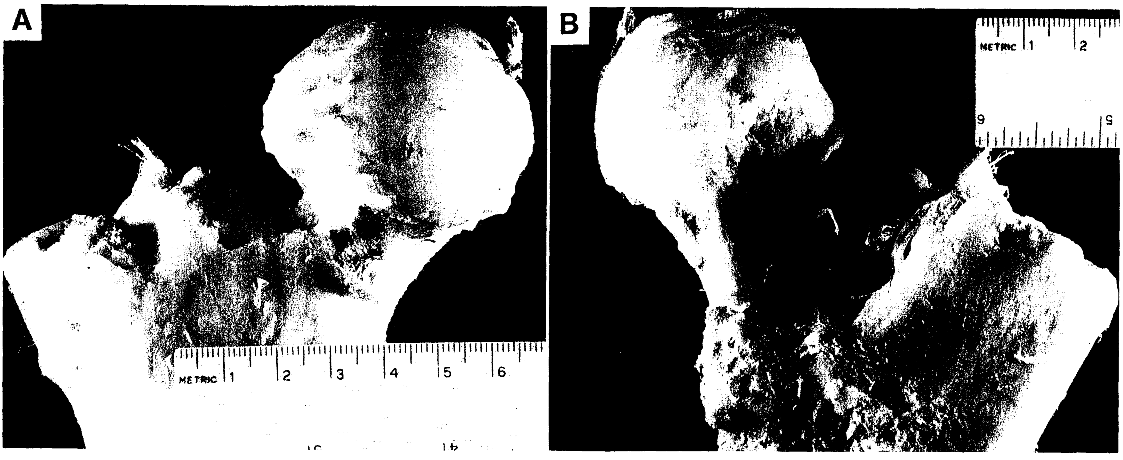

FIGURE 10. Front and rear views of proximal end of *Bos* femur partly eaten by African lion (*Panthera leo*).

The main damage that I have recorded from large cats gnawing on tibiae has been moderately deep and isolated scoring of parts of the proximal articular edges on medial and lateral sides. The cranial proximal end (or "crest") is also occasionally furrowed perpendicular to the element's long axis, probably during consumption of the muscle and soft tissue around the patella. The crest may also be bitten off.

Discussion

In studying Pleistocene bone specimens from Alaska and the Yukon (curated in the Smithsonian Institution and the University of Alaska Museum), I have found that much of the gnaw damage to bison bones is patterned and compares closely with the predictable kinds of damage that modern northern wolves (*Canis lupus*) inflict on bones of modern bison (Haynes 1981, 1982). The damage seems similar to patterns that I define as a result of moderate to full utilization of prey carcasses by carnivores. This signifies that: (1) the local prey populations were providing adequate food for local predators, due to the existence of an optimal number of vulnerable and available individuals in the herd; (2) scavenger species or individuals were relatively uncommon (as in modern northern communities); and (3) the dynamics of Pleistocene predator-prey relationships were probably quite similar to modern dynamics, at least where bison and wolves are concerned.

As in modern assemblages of bones from wild moose (*Alces*) or bison, a few fossil elements from Pleistocene bison and moose in the collections exhibit damage inflicted by brown bears, but the greater proportion of bones that are damaged have been modified by large wolves. I have not seen damage that clearly appears to be caused by large cats, but I have examined only small samples from any collecting locale. I have examined less than 100 femora and tibiae from late Pleistocene bison and moose, compared to several hundred modern (Holocene) specimens.

Unless prey animals were unusually scarce or difficult to kill, Pleistocene lions would probably not have inflicted heavy gnaw damage on the larger bison bones. It is possible that scavenging wolves in fact might have gnawed over lion-inflicted damage, thereby obscuring it. But it is my opinion (and only speculation) that few wolves would have habitually scavenged, or have been hungry enough to eat bones; healthy wolves who are members of packs are more inclined to hunt live prey than to spend time most of the year seeking carcasses. There are no unquestionable remains of Dire wolves from Beringia, and scavenging specialists larger than wolverine (*Gulo* sp.) seem to be absent from the late Pleistocene fauna; therefore, lion gnaw damage ought to remain recognizable in the Pleistocene collections.

Guthrie (1980) postulates that *Panthera leo atrox* and *Arctodus* were the main predators on *Bison priscus* during the Late Pleistocene in

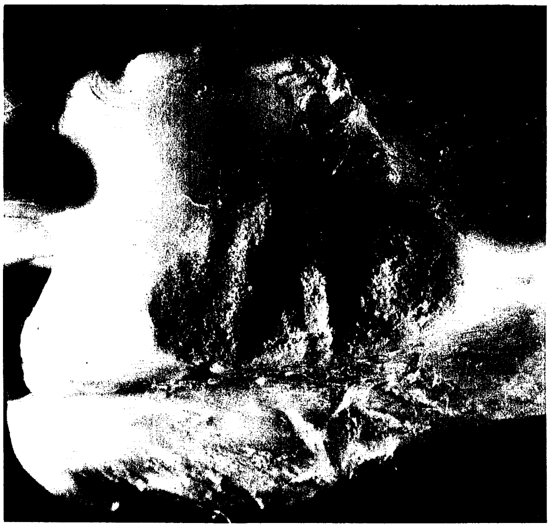

FIGURE 11. Frontal view of distal end of *Bos* femur partly eaten by African lion (*Panthera leo*).

Beringia, although he provides no concrete evidence in support. I suggest that support (or contradiction) may be found from examination of large samples of Pleistocene bison limb bones, because the gnaw damage characteristic of large cats and bears ought to be discernible.

I have described typical canid gnaw damage seen on Pleistocene bones from Alaskan collections (Haynes 1980). Canid gnaw damage is common on specimens in many collections from south of Beringia, too, even from archaeological assemblages. Collections from archaeological sites that contain numerous bison bones, such as mass kill sites, sometimes show very heavy gnaw damage from medium-sized and small canids. I called such damage a kennel pattern (Haynes 1981), indicative of homesite gnawing by animals too preoccupied or unable to hunt live prey. The logical animals to blame for the damage are domesticated dogs. This kind of gnaw damage appears in the High Plains fossil record early in the Holocene but seems to be present in Beringia even earlier. Many bones from the Bluefish Caves archaeological site in the Yukon (Cinq-Mars 1979) show a kennel gnawing pattern (Haynes 1981); the bones date to the late Pleistocene, about 13,000–14,000 years BP.

Conclusion

The proportion of prey bones that show gnaw damage due to feeding by any carnivorous species is complexly dependent on relative prey vulnerability to predation, size of feeding group, and other variables that affect an individual predator's behavior. Hence, it is possible that under certain conditions no identifiable gnaw damage may be found in particular assemblages of prey bones, just as it is possible that a large proportion of prey bones may show clear gnaw damage. The purpose of this paper is to point out the specific diagnostic characteristics of gnaw damage due to different carnivores so that information on animal communities can be derived from examination of those elements in bone collections thought to have been gnawed. Table 2 provides a comparison of general characteristics of damage caused by the four carnivore taxa discussed in this paper.

There might be carnivore taxa that do not coexist well because of intolerance or competition, and some bone assemblages need not con-

TABLE 2. Comparisons of damage characteristics.

	Canids	Hyenas	Bears	Felids
Presence of tooth marking on compact tissue:				
5 = most expectable				
1 = least expectable	3	5	2–1	1–0
Grinding off prominences vs. biting through:				
5 = mostly grinding with teeth (leaves smooth stump)				
1 = mostly biting through (leaves a rough stump, usually an irregular rim of compact bone)	2	2–3	5	1
Shape of tooth impressions in trabecular bone:				
5 = square or rectangular				
3 = cone or truncated cone				
1 = "Axe-edge" or elongated V shape	3	3	5	1

tain prey bones damaged by certain carnivores whose tolerance of competing taxa was very low. However, lions, leopards, cheetahs, and hyenas share much of their range in Africa, and bears and wolves share much of their range in North America; all these species are even known to feed from the same carcasses when opportunities arise in their respective ranges (Bromlei 1973; Coutourier 1954; Herrero 1978; Kruuk 1972; Magoun 1976; Mech 1970; Schaller 1972). Therefore, in Africa as well as in North America, carnivores create and modify bone assemblages in compound and multilevel ways that cannot be interpreted more fully without very detailed taphonomic observations such as reported here.

Acknowledgments

This research was made possible by the assistance and cooperation of Miles Roberts, Daryl Boness, and keepers at the National Zoological Park; the Superintendent and wardens of Wood Buffalo National Park; Sebastian Oosenbrug and Lu Carbyn in Canada; Rolf Peterson and David Mech in Michigan and Minnesota; David Cumming and Eugene Joubert in southern Africa; and Dennis Stanford at the Smithsonian Institution. I am especially grateful to the late John Guilday, who read an earlier draft of this paper. He was a kind source of encouragement, advice, and editorial assistance over the years.

Literature Cited

BINFORD, L. 1981. Bones: Ancient Men and Modern Myths. Academic Press, New York.

BONNICHSEN, R. 1973. Some operational aspects of human and animal bone alteration. Pp. 9–25. In: Gilbert, B. M., ed. Mammalian Osteo-Archeology: North America. Archeol. Soc., Columbia.

BROMLEI, F. G. 1973. Bears of the South Far-East of the USSR. Indian Nat. Sci. Documentation Centre, New Delhi.

BUCKLAND, W. 1824. Reliquiae Diluvianae; or, Observations on the Organic Remains Contained in Caves, Fissures, and Diluvial Gravel, and on Other Geological Phenomena, Attesting the Action of a Universal Deluge. John Murray, London.

BUSKIRK, S. W. AND P. S. GIPSON. 1978. Characteristics of wolf attack on moose in Mount McKinley National Park, Alaska. Arctic. *31*(4):499–502.

CINQ-MARS, J. 1979. Bluefish Cave I: a late Pleistocene eastern Beringian cave deposit in the northern Yukon. Can. J. Archaeol. *3*:1–32.

COUTOURIER, M. A. J. 1954. L'Ours Brun. Grenoble. Publ. by author. 904 pp.

GUTHRIE, R. D. 1980. Bison and man in North America. Can. J. Anthropol. *1*(1):55–73.

HAYNES, G. 1980. Evidence of carnivore gnawing on Pleistocene and Recent mammalian bones. Paleobiology. *6*(3):341–351.

HAYNES, G. 1981. Bone modifications and skeletal disturbances by natural agencies: studies in North America. Unpublished Ph.D. thesis, Catholic Univ. America, Washington, D.C.

HAYNES, G. 1982. Utilization and skeletal disturbances of North American prey carcasses. Arctic. *35*(2):266–281.

HERRERO, S. 1978. A comparison of some features of the evolution, ecology, and behavior of black and grizzly/brown bears. Carnivore. *1*(1):7–17.

KRUUK, H. 1972. The Spotted Hyaena. Univ. Chicago Press, Chicago.

KURTÉN, BJ. 1967. Pleistocene bears of North America. II. Genus *Arctodus,* Short-faced bears. Acta Zool. Fennica. *117*.

KURTÉN, BJ. AND E. ANDERSON. 1980. Pleistocene Mammals of North America. Columbia Univ. Press, New York.

MAGOUN, A. 1976. Summer scavenging activity in northeastern Alaska. Unpublished M.Sc. thesis, Univ. Alaska, College, Alaska.

MARTIN, P. S. AND J. E. GUILDAY. 1967. A bestiary for Pleistocene biologists. Pp. 1–62. In: Martin, P. S. and H. E. Wright, eds. Pleistocene Extinctions: The Search for a Cause. Yale Univ. Press, New Haven.

MECH, L. D. 1970. The Wolf: The Ecology and Behavior of an Endangered Species. Natur. Hist. Press, Garden City, N.Y.

MILLER, G. J. 1969. A study of cuts, grooves, and other marks on recent and fossil bone. I. Animal tooth marks. Tebiwa. *12*(1): 20–26.

P'EI, W.-C. 1938. Les rôles des animaux et des causes naturelles dans la cassure des os. Palaeontologica Sinica, N.S. D. No. 7.

SCHALLER, G. B. 1972. The Serengeti Lion: A Study in Predator–Prey Relations. Univ. Chicago Press, Chicago.

ZAPFE, H. 1939. Lebensspuren der eiszeitlichen Hohlenhyane. Die urgeschichtliche Bedeutung der Lebensspuren knochenfressender Raubtiere. Palaeobiologica. *7*:111–146.