

Utilization and Skeletal Disturbances of North American Prey Carcasses

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ABSTRACT. More than 125 carcasses and skeletal remains of wild bison, moose, and whitetail deer were examined in the field. Most were from closely documented episodes of predation, mass drownings, or other natural causes of death. Predictable and unusual kinds of bone and carcass utilization by timber wolves and bears are described. The variables emphasized include sectioning of carcasses by feeding predators, distribution and dispersal of bones at kill sites, gnaw damage to bones in homesites, kill sites and scavenge sites, potential or observed survival of bones at sites of prey carcasses, and the patterns of scatter or accumulation of skeletal remains in moose and bison ranges due to predation or other natural causes of death. Variations in gnaw damage to bones and utilization of carcasses by carnivores reflect significant aspects of predator-prey interactions, and can be deciphered by ecologists interpreting either fossil or modern assemblages of bones.

Key words: carnivores, prey carcasses, taphonomy, North America, paleoecology, archeological interpretation

RÉSUMÉ. Plus de 125 carcasses et ossements de bisons, d'orignaux et de cerfs de Virginie ont été examinés sur le terrain. La plupart représentaient des cas bien documentés d'attaques de prédateurs, de noyades en masse, ou d'autres causes de mort naturelles. Des utilisations curieuses et prévisibles d'ossements et de carcasses de la part de loups et d'ours sont décrites. Les variables soulignées comprennent le sectionnement de carcasses par des prédateurs en quête de nourriture, la distribution et la dispersion d'ossements aux lieux d'abattage, les traces de rongement d'os dans les repaires, aux lieux d'abattage et aux sites d'activité nécrophage, les vestiges potentiels ou observés d'ossements aux sites de carcasses de proies, et la distribution ou l'accumulation de restes squelettiques dans les habitats de bisons et d'ours, suivant les attaques prédatrices ou d'autres causes de mort naturelles. Les variations dans les dommages aux ossements causés par le rongement et l'utilisation des carcasses par les carnivores reflètent des aspects importants dans les rapports prédateur-proie, qui peuvent être interprétés par des écologistes étudiant des collections d'ossements modernes ou fossiles.

Mots clés: carnivores, carcasses de proies, taphonomie, Amérique du Nord, paléoécologie, interprétation archéologique

Traduit pour le journal par Maurice Guibord.

INTRODUCTION

Most paleoecologists realize that misrepresentation of animal bones or body parts in fossil assemblages can result from decay, weathering, geomorphic processes, or feeding by carnivores. Lack of detailed knowledge concerning such biases could cause serious mistakes in paleoecological interpretations. In an effort to address this problem, I have studied the nature and extent of some potential biasing agencies in the field and under controlled conditions (Haynes, 1978, 1980a, b, 1981, in press a, b). The basic operating principle for the research is that bones damaged or otherwise modified by natural processes bear the distinguishing effects of those processes.

Observational research on natural processes of bone modification has been undertaken by other scholars with various perspectives and goals. Sutcliffe (1970), a vertebrate paleontologist, described the damage to bones and the kinds of bone accumulations made by spotted hyenas, partly to demonstrate that not all bone hoards are created by humans. Hill (1975), an anthropologist, described the order in which mammalian skeletons naturally come apart in east Africa when scavengers are active, in order to compare human processes to natural processes of disarticulation. Toots (1965), a geologist, described the sequence of skeletal disarticulation in Wyoming, to achieve an understanding of how specific environmental factors affect the process. Behrensmeyer (1978), a paleozoologist, described the sequence of bone deterioration (weathering) in east

African environments, correlating past weathering environments with end effects on bones.

My own field studies are concerned with the same variables in northern North America. This report describes modifications to bones caused by some large North American carnivores and scavengers, with an emphasis on timber wolves.

The timber wolf (*Canis lupus*), when minimally disturbed by humans, utilizes prey carcasses in patterned and predictable ways according to a number of influential factors that are mostly related to ease of the hunt (Carbyn, 1974; Mech, 1970; R.O. Peterson, 1977; R.O. Peterson and Allen, 1974). When killing is comparatively easy, prey carcasses are not as fully utilized as when hunting is difficult (Mech and Frenzel, 1971; Pimlott *et al.*, 1969). When a large proportion of prey is highly vulnerable, as when many old and subadult animals are available, the predators utilize their carcasses only lightly. During unusually severe winters a greater proportion of prey animals normally thought least vulnerable to predation are killed by wolves (R.O. Peterson, 1977), and the carcasses are not fully consumed. The most vulnerable animals probably die without predation during unusually severe winters and their carcasses are little utilized, if at all, since hungry wolves in packs are more inclined to hunt and kill living prey than to seek frozen carrion for the bulk of their food. Wolves and other carnivores do scavenge frozen carcasses, but normally feed on and disturb such remains less than those of freshly-killed prey.

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Wolves ordinarily hunt in packs during the winter, and pack size affects carcass utilization. There are seemingly optimal size ranges for wolf packs that prey selectively on particular prey species: for example, bison may be most efficiently hunted, killed, and utilized by packs with no fewer than 8-10 nor more than 16 members, moose by packs containing no fewer than 6-8 nor more than 12 wolves, and so on (Carbyn, 1974; Mech, 1970; Oosenbrug and Carbyn, in press; R.O. Peterson, 1977). Packs of different sizes exist where alternative prey species are available or where there is human disturbance such as fur trapping and hunting. Pack sizes also vary when prey populations are adjusting their local distribution or their numbers, in response to climatic or vegetative changes. Ecosystemic stresses are concretely reflected by the degree of bone damage inflicted by wolves.

Some carcasses may be utilized by wolverines, foxes, mustelids and bears in addition to wolves, and the potential ecologic meaning of the skeletal material will not be directly decipherable if compared to remains fed on only by wolves. Fortunately it is often possible to distinguish the end effects of feeding by various species, in the absence of visual documentation or observations of tracks, by examination of gnaw damage to bone elements (Haynes, 1981, in prep.). Wounds in soft tissue also may indicate predator species (Buskirk and Gipson, 1978).

The data to be gained about fossil or modern ecosystems from a study of bones and bone sites are not entirely self-evident or straightforward, but such studies clearly are of value. More simple observations are necessary, as is more work in interpretation and theory.

METHODS

Field studies of predators and prey were performed in Superior National Forest in northeastern Minnesota where timber wolves prey on whitetail deer (*Odocoileus virginianus*) and moose (*Alces alces*), and where fishers (*Martes pennanti*), foxes (*Vulpes vulpes*), and bears (*Ursus americanus*) may scavenge carcasses (Haynes, in press a); in Isle Royale National Park in Lake Superior, where wolves prey on moose, and foxes may scavenge carcasses; and in Wood Buffalo National park in north central Canada, where wolves prey on bison (*Bison bison*), moose, deer, and occasionally on caribou (*Rangifer tarandus*), and where a number of species such as fox and bear may scavenge carcasses. Biologists in these three locales regularly monitored the winter activities of wild wolves, and examined fresh kills or scavenged carcasses from the ground after carnivores completed feeding (Fig. 1). Less intensive summer observations of wolves and prey activity were also carried out in each locale. In addition, bones of animals fed upon by wolves, black bears, and brown bears (*Ursus arctos*) have been collected from a number of other parks and preserves in North America.

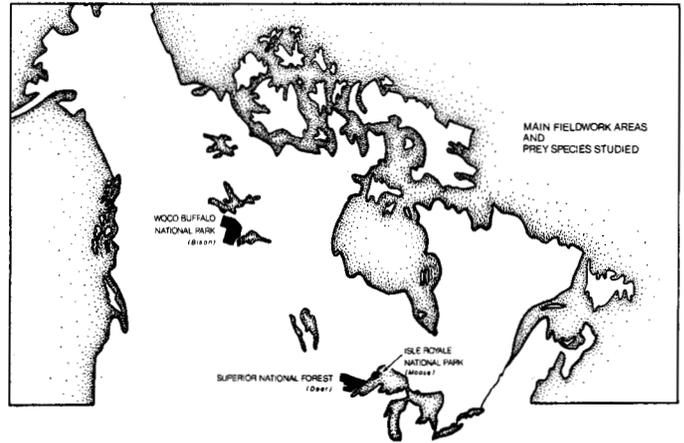


FIG. 1. Main study areas.

The sample of carcasses includes 30 bison killed in a dated flood, 26 bison killed by known numbers of wolves on known dates, 30 bison dying of disease or other causes (including poaching) and scavenged by wolves, 10 moose and 15 deer killed by known numbers of wolves on known dates, and several dozen other animals including wapiti (*Cervus canadensis*) (known as elk in North America) and pronghorn (*Antilocapra americanus*) (usually called antelope in North America) with unconfirmed dates and causes of death. Complete records on over 800 other animal remains have been studied. Most carcasses and skeletons in this study had not been modified by human activity, and were selected for the sample because of their remote locations. All skeletal sites have been inspected more than once, and will be re-inspected over the next two decades to monitor natural modifications to bones and body parts.

BONE SITES

Prey bones are found at several different kinds of sites other than kill sites. The end effects of carnivore gnawing behavior vary at each type of site.

Homesites

Timber wolves raise their young in dens, which may be underground burrows dug out and abandoned by other animals, or hollow logs, rock shelters, or chambers excavated or enlarged by the denning wolves themselves. One or more nursery den sites are occupied from whelping season (spring) until the young are weaned (Mech, 1970), at which time the wolf "family" (breeding pair, pups, and any other associated adults) moves to sites that do not necessarily provide subterranean shelter. Pups remain at these so-called rendezvous sites (Joslin, 1967; Murie, 1944) while all or some of the adults hunt or forage for food to bring back to the young. Sometimes meat is brought back in the adults' stomachs, to be regurgitated for the pups, and sometimes carcass parts that include bones are brought back. By fall and winter, pups are able to accompany

adults on their nomadic hunting travels through the prey catchment territory, and can feed at actual kill sites.

In geographic regions where there is an abundance of natural shelters or excavations made by other denning animals, or where dens can easily be excavated, each burrow or den chamber complex may be used for only a single season (Mech, 1970; Pulliainen, 1965). Where prey are annually abundant due to migration, or annually more vulnerable due to local changes in proportion of age and sex categories of herds, den re-use by wolves many extend over several decades. In these situations, a large number of prey animals may be represented by bones at the sites (Binford, 1981; Haber, 1977; Kuyt, 1972).

Bones at homesites characteristically have been gnawed much more than bones found at kill sites. Elements may be carried from carcasses to dens or rendezvous sites to be gnawed at leisure, and may become play items for pups (R.O. Peterson, 1977). If carcasses or body parts are too bulky for adult wolves to transport to pups or to rendezvous sites, the wolf group may relocate itself close to certain carcasses, which become temporary rendezvous sites (L. Carbyn, pers. comm.; S. Oosenbrug, pers. comm.). Bones at such sites exhibit significantly more tooth scoring and scratching on compact bone tissue, fracture-edge rounding (produced by abrasion against teeth, paws, tongue, and the ground) and gouging and furrowing of cancellous tissue caused by teeth (Fig. 2), than do bones found at kill sites.

Scavenge Sites

The carcasses of freshly-dead bison and moose scavenged by wolves are abandoned more intact than the remains of kills (Allen, 1979; Haynes 1980a, 1981, in press b; Mech, 1966; R.L. Peterson, 1955). In winter, wolf packs prefer hunting fresh meat on the hoof to feeding very long on frozen carrion (pers. obs.). During the spring denning season, wolf feeding groups are smaller, and thus damage carcasses less at any one feeding session than during the rest of the year, when denning groups aggregate into packs. Previously (Haynes, 1980b:34) a summer carcass was thought to be more fully used than a winter carcass, but recently correlated data are inconclusive regarding the degree of utilization of summer carcasses, even though single bones may be severely gnawed (Fig. 2).

If wolves encounter remains of bison or moose dead more than six months, efforts to gnaw bones generally are relatively slight. When food is scarce, the bones may be partly consumed and fragmented, and spiral, longitudinal, and transverse fractures will occur on long bone shafts. This linear fracturing is caused by drying cracks in the compact tissue and by increased brittleness (Fig. 3). After remains have weathered over a full summer there is usually not enough marrow, grease, or periosteal connective tissue to provoke more than brief mouthing of bones by wolves.

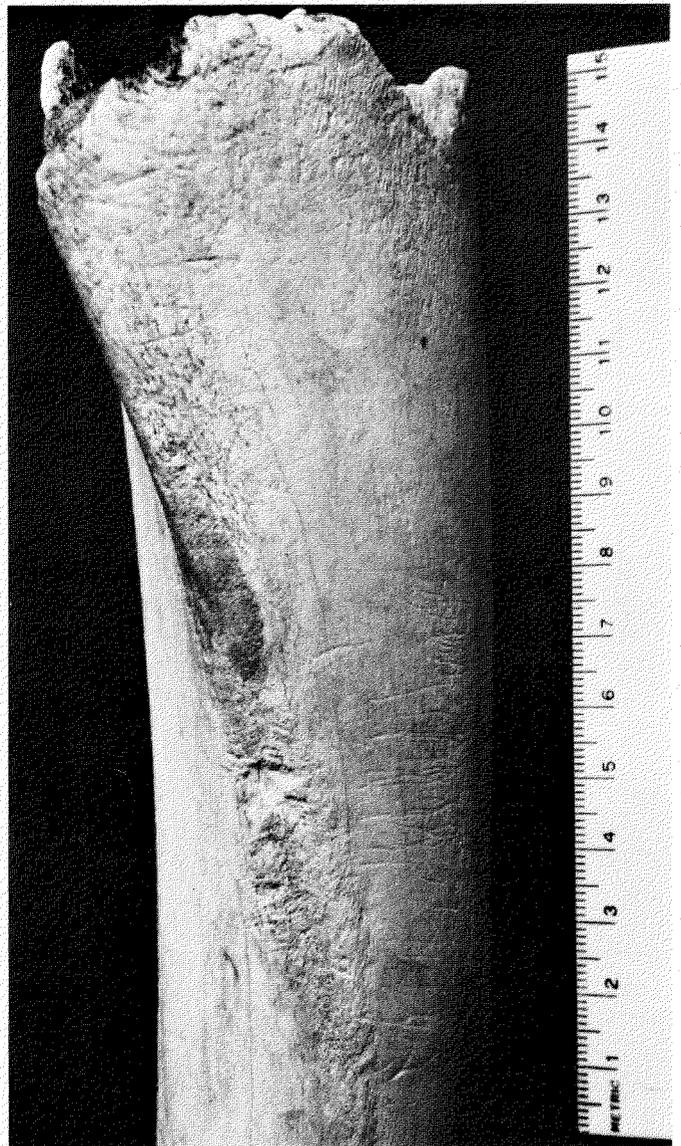


FIG. 2. Proximal end of tibia shaft from adult female bison, whose carcass was a rendezvous site in Wood Buffalo National Park, 1978.

Carcasses may be locally abundant after mass drownings, not uncommon in Wood Buffalo National Park (Haynes, 1981), and wolf-inflicted gnaw damage to bones is slight at the skeletal sites. Many bison bones may be cached elsewhere by scavenging bears and wolves, so that remaining skeletons are incomplete but very slightly gnawed, if at all. However, isolated remains of prey animals smaller than caribou may suffer a great deal of dispersal and fragmentation by scavenging carnivores, even after months of aging.

"Kennel" Sites: Captive Wolf Studies

In connection with the wild animal studies discussed here, I observed a number of colonies of captive wolves feeding on ungulate carcasses and bones. These observations are reported in detail in Haynes (1981, in press a).

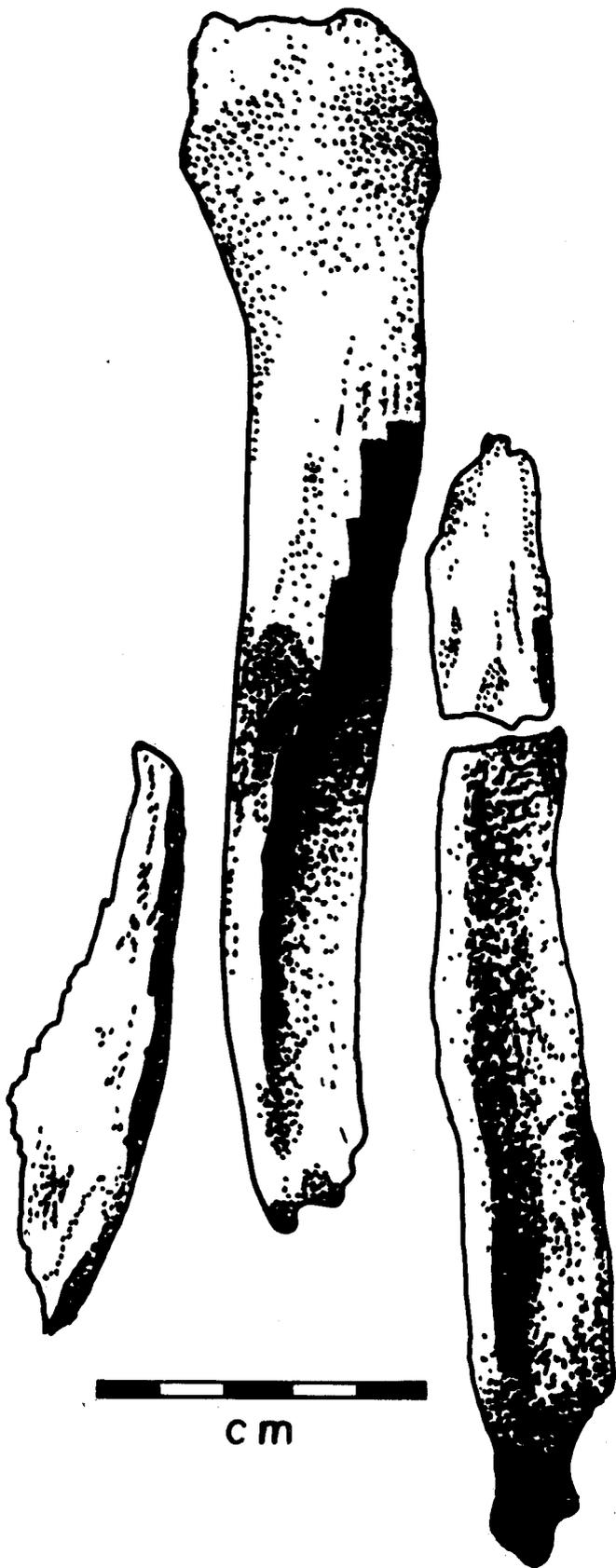


FIG. 3. Fractured moose tibia, oblique view from the proximal end looking into the shaft. The bone was fractured by scavenging wolves six months after the date of death. (Isle Royale National Park)

In most cases, when single limb bones or carcasses of *Equus* or *Bos* were fed to captive wolves, one or both epiphyseal ends of long bones were gnawed away, producing open-ended diaphyseal cylinders. Nearly 75% of hundreds of recovered bones and fragments were marked by teeth scratches, furrows, or crushed tissue. Many long bones of *Equus* or *Bos* had been broken into spiral and other types of fractures. In tibiae, fracturing begins at the proximal end, following destruction of the epiphysis (Haynes, in press b). Femora are fractured from either end, following removal of epiphyses; humeri are fractured first from the proximal end. Fracture margins are mixtures of rounded and sharp edges. Edges of levered-off fragments are initially sharp until abraded by rubbing against the ground, teeth, paws, and tongue.

I term this kind of damage a kennel pattern (Haynes, 1981), mostly diagnostic of sustained gnawing by sedentary animals that need not hunt often or for most of their diet. Bison or moose bones found at rendezvous sites in the wild are occasionally damaged in a kennel pattern (Fig. 2; Haynes, in press b), but evidently such sites are less common than those with less-scarred bones. Thus, a kennel pattern is typically inflicted by captive animals, but much less commonly by wild animals.

BODY DISMEMBERMENT AND DAMAGE TO BONES OF DEER

The following information is extracted from Haynes (1981, in press a).

Some kill sites may contain nothing more than a few dozen pieces of broken long bones (Fig. 4), fragments of vertebral processes, and segments of rib shafts. Long bone fragments may exhibit no tooth markings (such as linear scoring of compacta, produced by the forceful drawing of cheek teeth across bone surfaces). Occasionally a fracture edge is notched by teeth, exhibiting damage that resembles impact-fracture scars caused by a blow from a hard implement, as for example by humans splitting long bones to extract marrow. Bears and wolves produce such damage on bones of prey as large as bison and moose (Fig. 5).

The following body parts of deer are fed upon and abandoned as units by wolves.

(1) Head and neck: when wolves lightly utilize deer carcasses, undamaged heads and necks remain articulated to the body. The edges of nasal bones may be scratched by the teeth or splintered. The angle of one or both mandibles may be broken off if the throat is opened and the tongue is eaten. Mandibles may be broken apart at or posterior to the symphysis when utilization is fuller. There may be small depressed fractures (punctates) on rami, and lower borders may be broken off, exposing marrow cavities. When carcasses are heavily utilized, only upper and lower tooththrows may remain from the head.

(2) Thoracic cage: the sternum is usually completely consumed. The proximal ends of six or eight ribs remain

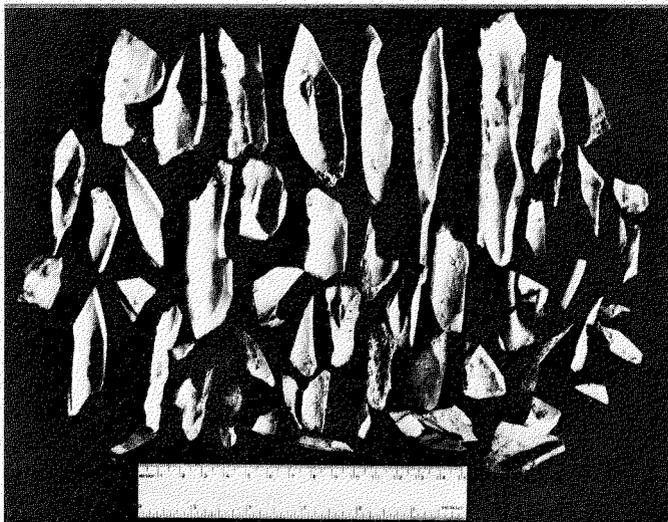


FIG. 4. Complete assemblage of bone remains, collected from kill site of a whitetail deer one week after date of death. (Minnesota, 1976).

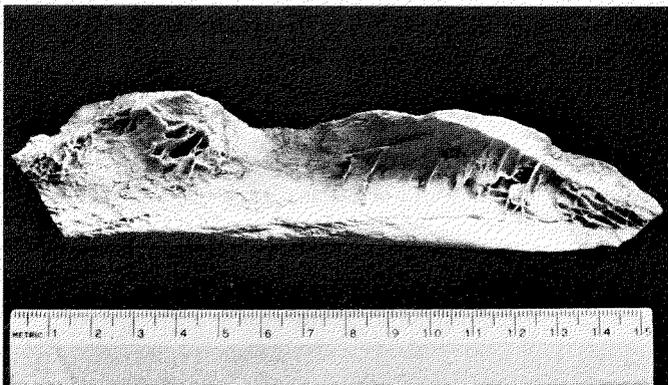


FIG. 5. Notches and flake scars on inner surface of a fragment of a bison femur gnawed by wolves in Wood Buffalo National Park.

articulated to vertebrae, their sternal portions having been eaten. The thoracic cage is separated from the head and from most cervical and lumbar vertebrae by feeding wolves (Fig. 6). Spines and most lateral processes are broken or splintered on vertebrae of fully utilized carcasses, and vertebral bodies may show isolated tooth marks, usually round-bottomed depressions the size of tooth cusps.

(3) Scapula: one or both scapulae are detached from the carcass early in carnivore feeding. Only the vertebral borders show damage when remains are lightly utilized. With a well utilized kill, only the glenoid portion will remain.

(4) Lumbar vertebrae/sacrum/pelvis: the pelvis may remain attached to the sacrum and to several or all lumbar vertebrae, the lateral processes of which have been destroyed. Tuberosities and edges of the pelvis are always gnawed, and the pelvis is often split asymmetrically into right and left portions. When utilization is heavier, both halves may be destroyed down to the thicker bone surrounding the acetabulum.

(5) Legs: all legs may eventually be detached from the body, though on lightly utilized carcasses only a single limb is separated. The remaining legs at any kill site contain articulated elements, specifically third phalanges still in the hoof sheaths, and often including the metapodial and continuing to the midshaft of the tibia, the distal end of the femur, or the distal end of the humerus (Fig. 6). The upper long bones of all limbs are usually broken. If the carcass is lightly utilized the olecranon is bitten or broken off, the proximal tuberosities and head of the humerus are slightly damaged, and the greater trochanter and trochlear rims of the femur are damaged. The damage consists of tooth scoring and scratching on compact tissue, removal of epiphyseal tissue, and gouging and furrowing of cancellous tissue.



FIG. 6. Rear limb and thoracic cage segment of whitetail deer killed within previous 24 hours by wolf pack on a frozen Minnesota lake, 1979.

BODY DISMEMBERMENT AND DAMAGE TO BONES OF LARGER PREY

A pack of 10-15 wolves feeding on the carcass of a freshly-killed adult bison or moose can consume nearly all edible soft tissue and half of the hide within four days of bringing down the animal. The first bones damaged by feeding wolves are the pelvis, femora, and the ribs and vertebrae (Table 1). Some or all ribs are snapped off in segments averaging 30 cm long, the break occurring close to the articular ends in most cases. One half or more of the spinous processes of most thoracic vertebrae are broken, rather than being ground off by hard gnawing. The vertebral border of one or both scapulae may be ragged, and the blade may show a few punctures from teeth.

In late winter when prey animals are weakened by the cumulative effects of deepening snow, continued cold, and reduced nutritive value of available food, they are more vulnerable to wolf predation than in other seasons. Because more carcasses are available at that time, packs take longer in February and March to utilize carcasses fully than in November and December. Most fresh carcasses are visited until well cleaned (Oosenbrug *et al.*, 1980a). Bison, moose, elk and deer generally do not move far from central wintering ranges; wolves can thus utilize their core hunting areas repeatedly during winter, staying close to

TABLE 1. Flow chart of winter feeding sequence on carcasses of adult moose and bison. Arrows indicate separation of feeding episodes.

MOOSE		BISON	
Rump:	Anus and hip flesh eaten. Belly entered, viscera and blood devoured. Ischia damaged. Femoral greater trochanter damaged. Rumen exposed. Many on one side broken.	Rump:	Tail gone, hip flesh eaten. Belly opened. Ischia damaged. Femoral greater trochanter damaged.
Ribs:		Ribs:	Broken on one side.
Shoulder:	Flesh on one side eaten.	Shoulder:	Flesh opened.
Pelvis:	Cleaned and damaged.	Pelvis:	Cleaned and damaged.
Femur:	Greater trochanter partly removed. Lateral condyle damaged.	Femur:	Greater trochanter partly removed, lateral condyle damaged.
Vertebrae:	Processes broken.	Vertebrae:	Processes broken.
Humerus:	Lateral tuberosity eaten.	Humerus:	Some or all proximal tuberosities removed.
Scapula:	Cleaned, detached, damaged.	Scapula:	One detached, vertebral border damaged.
Skull:	Head defleshed, nasal bones lightly damaged.	Skull:	Nasal bones damaged (Fig. 13). Ear eaten.
Femur:	Distal end damaged.	Spine:	Cleaned, sometimes sectioned (Fig. 8).
Tibia:	Proximal end damaged.	Mandibles:	Sometimes detached. Defleshed.
Legs:	One or both rear legs detached and slightly scattered.	Humerus:	Head gone (Haynes, 1980b: Fig. 4).
Spine:	Separated into two parts.	Femur:	Distal end gouged (Fig. 12).
Mandibles:	Sometimes detached.	Tibia:	Proximal end gouged.
Humerus:	Head gone on one or both (Fig. 11).	Rear limb:	One or both disarticulated from trunk.
Femur:	Patellar trochlea well gouged (Fig. 12).	Tibia:	Crest opened up (as in Fig. 15).
Tibia:	Crest gouged (Fig. 15).	Tibia:	Proximal end gone (Haynes, 1980b: Fig. 9).
Tibia:	Proximal end gone (Haynes, 1980b: Fig. 9).	SCAVENGE DAMAGE	
SCAVENGE DAMAGE			

dependable prey resources and simultaneously increasing the potential for re-encountering older carcasses. While snowfall effectively removes many carcasses from the landscape, wolves are believed to memorize the locations of landmarks such as carcasses in their territories (Peters, 1978). Carcasses of animals which have died from disease, starvation, or other causes typically are not well utilized when found in winter unless consistently re-encountered; these carcasses may, however, be better utilized in the spring, particularly if they are located near denning areas. Occasionally more kills may be made than can be even moderately utilized, especially in severe winters that tax the health of prey animals (Mech and Frenzel, 1971) but such circumstances are most likely exceptional, aside from times of long-term climatic deterioration.

Domestic livestock. Most domestic livestock are routinely easy to kill, and their carcasses are poorly utilized (Young, 1944). However, domestic horses defend themselves as a group, creating a tightly-bunched defensive block that wolves cannot easily penetrate (Carbyn, 1974; L. Carbyn, pers. comm.). This defensive tactic is similar to that used by wild bison bands in Wood Buffalo National Park.

Moose. During the winter, skeletons of adult moose are frequently sectioned by feeding wolves into articulated or isolated parts (Fig. 7). The sequence of this list is not necessarily significant.

(1) Skull, often articulated with mandibles and usually with one or more cervical vertebrae. In some instances the head remains attached to the thoracic cage. Occasionally the spine remains unsectioned.

(2) Lumbar and posterior thoracic vertebrae, articulated, and attached to the sacrum and pelvis. Sometimes the spinal column is further sectioned into an articulated cervical group, the head with a few cervical vertebrae attached, and a thoracic/lumbar group. The pelvis of moose <8 yr old may be detached from the sacrum and lumbar vertebrae.

(3) Scapulae, often detached from the body.

(4) Legs, articulated from proximal end of humeri through hooves, and from proximal end of femora through hooves. One or two legs may be removed from the immediate kill locus.

(5) Isolated segments of rib shafts, generally 15-35 cm long.

(6) Splinters and chips of vertebral processes and ribs.

Bison. When adult bison kills are well utilized by feeding wolves in early winter, the skeletons are often sectioned as follows (not necessarily in this order):

(1) Head, with all cervical and some proximal thoracic vertebrae attached, and some rib heads in articulation. The spinous processes of the thoracic vertebrae are reduced to half their height.

(2) Thoracic and lumbar vertebrae, articulated, attached to the sacrum and pelvis, with some articulated rib fragments (Fig. 8).

(3) Individual legs, one of which may be carried away from the kill site.

(4) Scapulae, both detached and one often far removed.

(5) Scattered segments of ribs, 15-45 cm long.

(6) Bone splinters and chips.

For well utilized late winter kills of bison, the units are:

(1) Head attached to vertebral column, sacrum and pelvis, and articulated with two or three limbs and some rib segments (Figs. 9 and 10);

(2) At least one disarticulated leg, attached to the trunk by hide;

(3) One or both disarticulated scapulae;

(4) Scattered rib segments; and

(5) Bone splinters and chips.

The humeral and femoral heads may be disarticulated from the axial skeleton, but uneaten hide keeps the limbs in nearly anatomical order. A hungry wolf pack will completely separate at least one limb from a carcass.

Limbs. Lower legs of adult bison and moose (from the tibial proximal epiphysis or proximal one-third of the shaft, and from the radius-ulnar proximal epiphysis to the hooves) are rarely stripped of hide during early feedings. Later feedings such as springtime scavenging by bears, scavenging by another wolf pack, or revisitation by the killing pack, may leave the lower legs stripped of hide, but still articulated from the distal end of the tibia or the distal end of the radius to the hooves, the sheaths of which may be partly destroyed by scavengers (Fig. 11). By the end of the

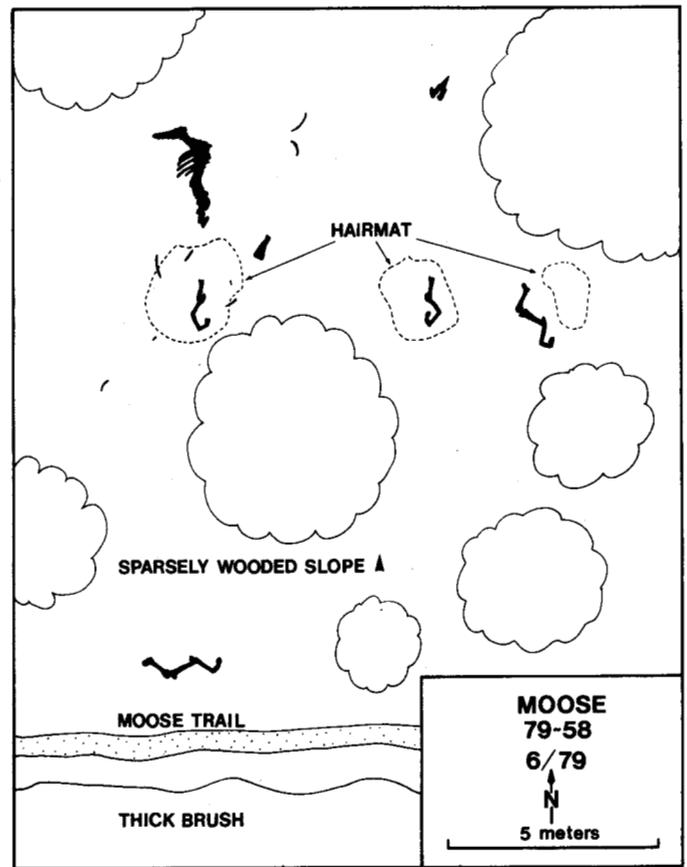


FIG. 7. Map of moose carcass number 79-58, sketched in June, 1979, about three months after date of death, Isle Royale National Park. Note that all legs are present and articulated. The articulated mandibles are at top of map, and the articulated skull, vertebrae, ribs, pelvis and sacrum are at top left.



FIG. 8. Articulated vertebrae, sacrum, pelvis and ribs from the carcass of a fully utilized adult female bison, about two weeks after date of death, December, 1979. The tracks in the snow are from scavenging red foxes (*Vulpes vulpes*).

first summer following death, unless scavenging has been unusually light, the limb bones are becoming separated from each other. Bones lying in warm, moist areas such as



FIG. 9. Carcass of a bull bison, shortly after being killed by a pack of wolves in 1979. Ribs on the right side have been broken off. Photograph: S. Oosenbrug.



FIG. 10. Same animal as in Fig. 9, one month later. Scapulae are detached, and all ribs on both sides are broken. Both forelegs and the left rear leg remain, frozen in packed snow.



FIG. 11. Foreleg of adult female moose killed by wolves on Isle Royale National Park, six months after date of death. Head of humerus has been gnawed off, hide on lower bones has been peeled by scavengers, and the hoof is falling apart.

deciduous woods separate months sooner than elements found in dry, sunny areas, probably due to greater microfaunal activity.

Long bones from fully utilized carcasses of adult bison or moose are rarely fractured, although the entire articu-

lating ends of many are chewed or broken off. Wolves and bears frequently remove the proximal end of the humerus (Fig. 11; Haynes, 1980b: Fig. 4), the greater trochanter and much of the distal end of the femur (Fig. 12), and the proximal end of the tibia (Haynes, 1980b: Fig. 9). It is

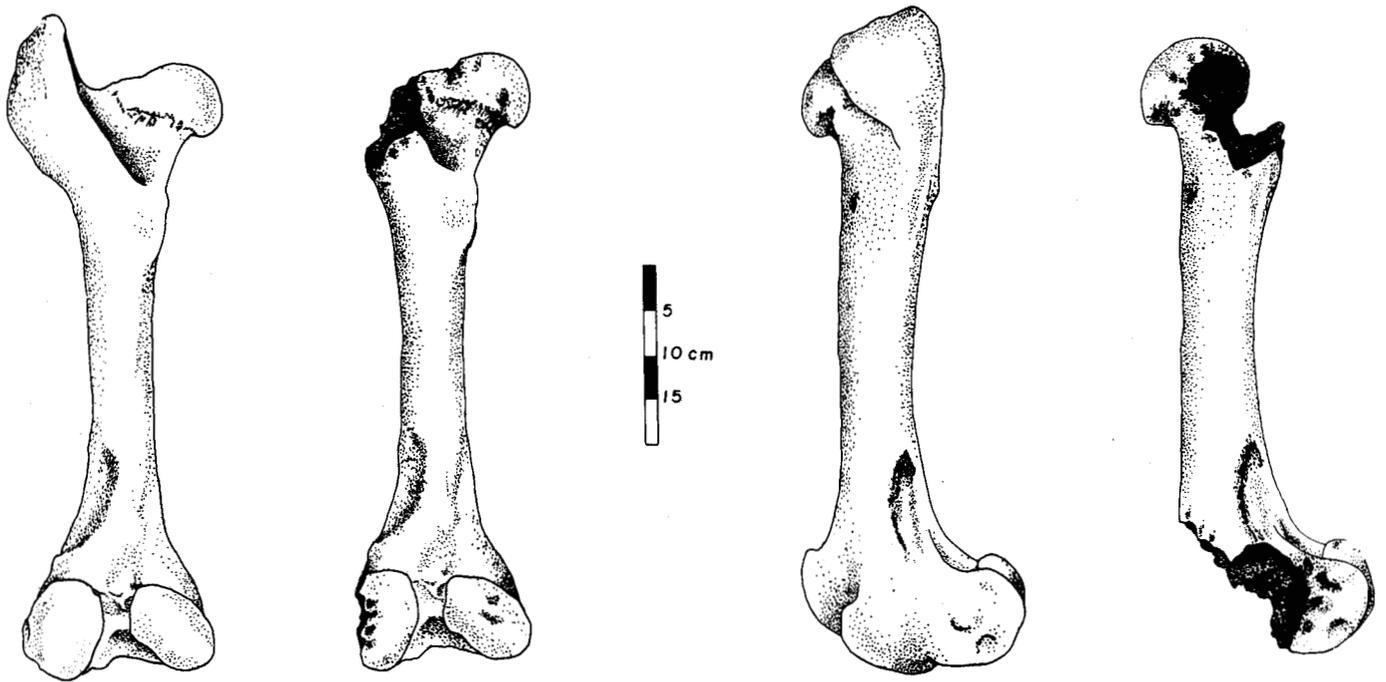


FIG. 12. Comparison of an undamaged bison femur and a gnawed left femur from a fully utilized bison carcass: posterior aspects (left) and lateral aspects (right).

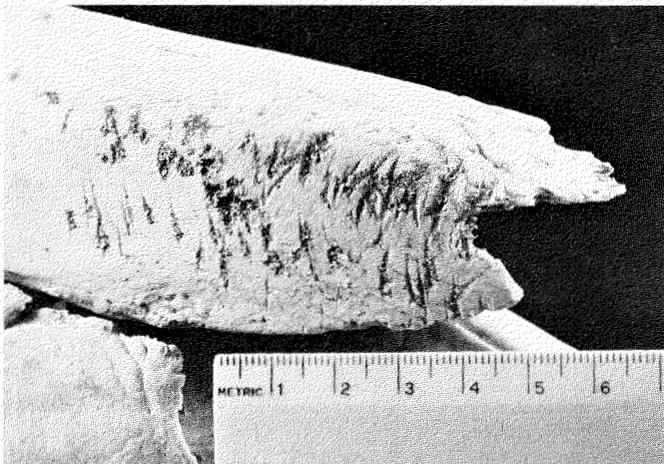


FIG. 13. Damage due to wolf gnawing on bison nasal bone, from a fully utilized carcass. Anterior end is to right.

characteristic of fully utilized kills (Table 2) that one or both humeri are modified by removal of the proximal end into partly or fully open-ended tubes, that greater trochanters of femora are removed, and that some or all ribs are broken off below their articulating ends. The edges of ilia are always gnawed at true kills, and often the nasal bones are gnawed (Fig. 13).

I have attempted to define "stages" of utilization of carcasses of bison and moose, characterized by specific ranges of damage to certain elements (Tables 1 and 2). The tables represent impressionistic summaries, and indicate only major patterns or trends rather than invariable conditions.

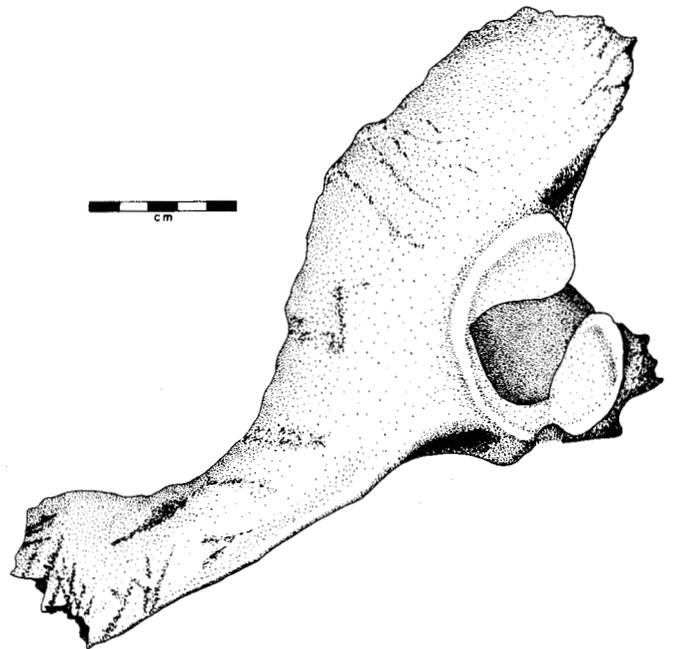


FIG. 14. Remains of a bison left innominate, collected from the fully utilized carcass illustrated in Figs. 9 and 10. Cf. Table 2.

Distribution of Bones at Kill Sites

The first bones detached from the carcass when wolves feed on newly killed animals are the ribs and scapula on the upper side of the body (Table 1, Fig. 9). Scapulae may end up anywhere between a few meters and 100 m from the carcass.

If legs are detached from a moose body, they most often come to rest complete and articulated within 15 m of each

TABLE 2. Damage to bones of adult bison fed on by packs of 10 - 15 wolves at different stages of carcass utilization. Unusual or irregular sequencing may be due to scavenging by non-killing animals, freezing of parts of carcass into snow or ice, removal of parts by caching animals, presence of disease, or other factors. Damage is cumulative from left to right.

ELEMENT	UTILIZATION		
	Light to moderate	Full	Heavy
Femur	Trochanteric stump left, 2 cm high. Greater trochlear rim scored at right angle to long axis, 1 - 2 cm deep. Minor damage to medial condyle. STAGE 1, STAGE 1 - 2	Medial condyle gouged. Surface of lateral condyle gone. Trochlea well opened (5 x 7 cm area). Trochanteric stump gone. Tooth marks undercut head. STAGE 2, STAGE 2 - 3 (STAGE 3 in Fig. 12)	Distal end gone. Head nearly gone. Shaft being broken up. STAGE 4
Tibia	Lateral proximal end grooved or bevelled (Fig. 15). Some furrowing or gouging, too. STAGE 1	Crest opened up or gone. Medullary tissue exposed at lateral proximal end (Fig. 15). Medial edges furrowed. Still articulated to femur. STAGE 2 - 3	Proximal end gone (Haynes, 1980b: Fig. 9). Most fracture edges sharp, with localized edge-rounding. Still articulated to ankle bones. STAGE 4(a). STAGE 4(b) has more edge-rounding. In STAGE 5 the shaft is being broken.
Humerus	Greater tuberosities gone or furrowed. STAGE 1	Tuberosities gone. Tooth scoring on shaft (Haynes, 1980b: Fig. 4). STAGE 2 - 3	Proximal end gone, about $\frac{1}{3}$ of proximal shaft gone. Condyles gnawed in scavenging. STAGE 3 - 4
Pelvis	Edges of ilia and ischia gnawed, cancellous tissue exposed. STAGE 1	Partly defleshed. Iliac and ischia partly one. STAGE 2 - 3 (STAGE 3-4 in Fig. 14)	Broken, only stumps of ilia and ischia left. STAGE 4
Scapula	Cartilage and bone on vertebral border ragged. Still attached to foreleg. STAGE 1	No cartilage left on vertebral border, bone edge splintered and jagged. Detached from humerus. STAGE 2 - 3	Blade crunched and splintered at vertebral end. Spinous process partly gnawed. STAGE 4
Skull	No damage to bones. Horns lightly scratched by teeth. Nasal cartilage and ears gnawed or eaten. STAGE 1	Nasal bones tooth-scratched (Fig. 13). Horns scratched. STAGE 2 - 3	Nasal bones ragged at ends. Anterior premaxillaries may be broken. Horns pulled off cores by scavengers. STAGE 4
Mandibles	Partly defleshed, still articulated. STAGE 1	Defleshed. One hyoid remains. STAGE 2 - 3	Inner surfaces scratched. Disarticulated by scavengers. STAGE 4

other and the trunk (Figs. 7 and 11). Occasionally a femur is disconnected and carried far from the carcass, to be gnawed, cached, or dropped when the pack begins to move in earnest on another hunt. If a femur is successfully disarticulated, the remainder of the leg, from proximal tibia through hoof, may also be carried away from the carcass site, especially by members of small groups of scavenging wolves. Single wolves have been recorded

running several hundred meters through snow over 60 cm deep carrying articulated lower limbs of bison.

Splinters of ribs and vertebrae usually mark a prey animal's death site, which is littered also with body hair and rumen contents. The rest of the still-articulated skeleton may be dragged several meters away, although carcasses of adult bison males are seldom moved. The spinal column of adult moose or female bison is often separated into two



FIG. 15. Proximal end of a moose tibia from a kill in Riding Mountain National Park, Manitoba. The crest has been removed by wolves. Specimen collected by L. Carbyn. Cf. Table 2.

sections, one of which contains the pelvis, and may be dragged or carried a few meters from the head and forepart of the trunk (Fig. 8). Ten or more vertebrae may remain articulated as a unit even after several months of scavenging.

Survival of Bone Elements

When fully utilized carcasses of adult moose and female (or smaller male) bison are finally abandoned by the killing pack, one leg is often missing from the site area. The skull and usually the mandibles remain, as do two lower legs or complete limbs. Phalanges, metapodials and teeth can be considered the elements characteristic of kill sites, even for smaller animals such as calves and yearlings, whose skeletons may be otherwise nearly completely devoured or carried off. Several fragments of rib shafts remain in the original kill and feeding site when all else has been eaten and removed. Fragments of the shafts of long bones may also be found at kill sites of calf or yearling bison and moose.

The marrow in most bones in the study areas survives as a shrunken lump over one spring and summer and part of the fall, if the bones are located in occasionally shaded and moist spots, but greasiness may be gone by the second spring except at epiphyseal ends that were not gnawed open. Scavengers may carry away lower leg elements and try (with little success) to drag skulls away from bison kill sites, since these elements are protected longest by uneaten, unpeeled hide, and remain greasy and fetid. Most scattering occurs after the killing animals have fed and abandoned the remains, and in fact most scattering occurs after soft tissue is gone, several months after the kill date. Toots (1965) made similar observations for skeletal remains in arid environments.

I have surveyed bison calving and feeding grounds as well as traditional migration routes, and found dozens of isolated bones out of a sample of over 2000 elements. The bones most commonly found hundreds of meters from known carcasses or skeletal sites have been vertebrae, scapulae, and metapodials. I have also found partially digested phalanges in wolf scat, and sets of two to five articulated vertebrae, some weathered together as a unit for over 10 years (Table 3). Den and homesite accumulations have not been systematically inventoried, but several prey animals of different ages and sexes are represented by bones at den complexes and rendezvous sites in Wood Buffalo National Park.

After a season or two of scavenge activity, the skulls of most adult bison remain within a few dozen meters of the original carcass site, even when no other bones remain. Moose skulls are defleshed by the first spring following death, unlike bison skulls which retain a thick skin and long hair covering well into the first summer after death. Possibly bison brains decay more slowly than those of moose; bison skulls would therefore retain their appeal to scavengers much longer. Cervical vertebrae articulated to

TABLE 3. Bison elements found over 100 m from other bones¹

Element	Number found	Remarks
Vertebra	14	
Metapodial	10	Usually found within 300 km of skeletal site.
Scapula	10	
Articulated vertebrae	5 groups	Up to 5 articulated.
Rib shaft segment	8	
Humerus	7	
Skull	3	Numerous others found, probably disturbed by humans.
Tibia	4	
Phalanx	5	Two partially digested.
Toothrow	4	Mandibular and maxillary, some without alveolar bone.
Pelvis	2	Fragmented.

¹ These bones were found during travel over more than 200 km of bison calving and feeding grounds and migration trails, over 15 km of dried lake beds, and over 25 km of streams and stream banks. Less than 1% of the total land surface was directly surveyed, but all known areas of heaviest bison use were intensively examined several times.

bison or moose skulls may eventually separate from each other by midsummer. However, in closed-canopy woods bison skulls articulated with cervical and some thoracic vertebrae may remain as a unit for over a year after the animal's death.

In ranges with relatively low summer prey densities, carcasses of prey animals are heavily utilized by many different carnivores including foxes, wolves, bears, mustelids, wolverines, eagles and ravens. Many kill or death sites of caribou, moose, deer, bison, elk, and other ungulates contain no more than one or two bones (see Magoun, 1976, for a study of carcass utilization in northeastern Alaska).

Scavenging bears eat the hide from the lower legs of bison or moose carcasses (M. Meagher, pers. comm.), and gnaw greasy bones, often disarticulating and breaking them (R.O. Peterson, pers. comm.; J. Woolington, pers. comm.). Bears will remove elements from a carcass site, but usually remain at the site feeding on soft tissue, sometimes for days (Magoun, 1976).

I have observed an ermine (*Mustela erminea*) removing a 35-cm-long segment of rib from a fresh frozen carcass of a bison killed by wolves.

Wolverines (*Gulo gulo*) return repeatedly to carcasses to remove bones and cache them elsewhere, in places that would make poor potential fossil locales (and that are nearly impossible for field workers to find). It is not known if cached bones are heavily gnawed, but wolverines are capable of fragmenting long bones from subadult moose (Haglund, 1966).

Table 2 summarizes sequences of bone damage and disarticulation by larger wolf packs feeding on their own kills. Damage other than the kinds described (e.g. heavy gnaw damage to the distal condyles of an adult bison humerus, or to the compact tissue of long bone shafts without accompanying damage to epiphyses) is more likely to have been caused by scavenging animals than by killing animals. Damage or disarticulation of bones out of sequence, or the absence of one or two normal sequential stages, may signify feeding by scavengers rather than by the killers, but may also indicate other processes of disturbance such as trampling by herd animals. The value of the details in Table 2 can be illustrated by the example of a spirally fractured, canid-gnawed bison femur still possessing most or all of its greater trochanter or trochlear rims. The break in such a specimen was caused by an agency other than the animal leaving tooth marks on it, either before or after the bone was gnawed. The bone may have been broken by humans extracting marrow, or, as is common in Wood Buffalo National Park (Haynes, in press b), by trampling or wallowing bison. If the bone was gnawed more than lightly after being fractured, then it must have aged no more than a few months post mortem, probably no more than a single summer. Such a greasy element would be unlikely to fracture as a result of trampling or wallowing by ungulates (Haynes, in press b); assignment of another process of breakage therefore would not be an unreasonable interpretive step.

Some captive bears learn to break long bones by pounding or dropping them onto hard surfaces, in order to get at the marrow (Haynes, 1981). The first successful cases are probably fortuitous, but thereafter deliberate attempts may be made to pound bones on rocks. However, even though captive bears have little else to do besides play with bones, habitual smashing of long bones has not been recorded. I have observed many large bears and other bone-gnawing species (Haynes, 1978, 1980a, b, 1981, in press a), and in my opinion larger bears such as extinct *Arctodus* would have been capable of using their jaws to break bison long bones without producing heavy tooth-scoring damage on compact bone tissue. Yet in spite of a clear potential for such activity, the expectable breakage of large ungulate limb bones has not been demonstrated, at least by modern bear species (Haynes, 1981).

SCATTERING OR ACCUMULATION OF BONES DUE TO PREDATION

In habitats where prey animals are not gregarious, predators must wander over relatively large territories to find potential prey. Species such as moose and deer spread themselves thinly over their ranges, their distribution being dependent on availability of forage and cover (R.L. Peterson, 1955). Preferred areas of the range, such as shorelines and protected natural harbors in Isle Royale National Park (R.O. Peterson, 1977: Figs. 78, 79; R.O. Peterson and Stephens, 1980: Fig. 12), attract higher numbers of moose

than other areas during certain seasons, particularly winter. Wolf packs take advantage of the greater prey densities to kill more often in certain limited parts of the range. Therefore, in spite of the fact that kills from any one season tend to be scattered, since moose themselves habitually scatter, there are a few locales where moose remains from predation almost overlap. When kill sites are mapped (R.O. Peterson, 1977:App. J; Peterson and Scheidler, 1979:Fig. 9; Peterson and Stephens, 1980:Fig. 14), the distribution is clearly non-random and clumped. R.O. Peterson (pers. comm.), on the basis of data accumulated from more than 20 years of study of wolf and moose interactions on Isle Royale, notes that there are a few locales where bones of several years' kills overlap, including bones of up to a dozen individuals killed or dying during a 10-yr period. An arbitrary measurement of 30 x 30 m is here considered to fix the limits of a kill site (actual measurements are in Table 4). It is not uncommon in moose ranges to find the overlapped remains of cow and calf, killed together by wolves (R.O. Peterson, pers. comm.).

In contrast to moose, the bison of Wood Buffalo National Park are an aggregating and clustered resource for wolves. Bison bands range in size from two animals to several hundred cows, yearlings, calves and bulls, with the smaller groups usually comprised of bulls. Many bulls are solitary at times. Band membership is fluid, so sizes of feeding groups vary daily, but groups that contain more than 200 members are not common sights over much of the primary winter range. Because the habitat consists of open meadows interrupted often by trees and willow bush, and because bison tend to travel slowly while feeding, the presence or absence of herds at any one prairie or complex of prairies cannot be reliably predicted from day to day. When wolves encounter bison groups, they may remain in contact with the herd for several days, although they occasionally fall behind after killing an animal and feeding on the carcass (S. Oosenbrug, pers. comm.). Many wolf packs that are traditionally territorial in fixed areas will at times wander away from contacted herds to explore other parts of their territory, thus losing touch with prey for days (S. Oosenbrug, pers. comm; Oosenbrug *et al.*, 1980a, b).

The wolves' urge to travel away from bison results in increased scattering of kills in the short term, as does the packs' primary attack strategy, which is to run at bands and close in on any separated animal (Fig. 16). Bison bunch tightly when cornered or pursued, and can wheel about in close formation to confront their pursuers (Haynes, 1981; S. Oosenbrug, pers. comm.) Because even isolated animals are formidable and mobile in self-defense, several steaming carcasses rarely are found at the same kill site, even when wolves stay close to a single slowly-moving bison band. The only exceptions are when the bison are suffering unusually severe stresses from disease, malnutrition, or winter weather, or, rarer still, when whole herds flounder in crusted snow and are dispatched one at a time by wolves, whose weight the crust supports.

TABLE 4. Range of sizes of various sites, for animals >1 yr old

	Bison		Moose	
	Min.	Max.	Min.	Max.
Confirmed kills	N = 16		N = 7	
Dead 6 - 12 months	3 × 1.3 m	13 × 3 m (2 loci totalled)	3 × 6 m	40 × 50 m
Suspected kills	N = 10		—	
Dead 6-60 months	3 × 1.3 m	30 × 30 m	—	
Drowned	N = 15		—	
Dead >36 months	1 × 2 m	13 × 6 m	—	
Only scavenged*	N = 25		—	
Dead >36 months	3 × 1.3 m	100 × 30 m	—	

*Refers to deaths by disease, poaching, or unknown causes; definitely not predation or mass drowning.



FIG. 16. Bison bull under attack by pack of 11 wolves, one of which is not in the photograph, in Wood Buffalo National Park, 1980. The bull survived unharmed.

Bison kill sites have been mapped for a short time (Oosenbrug *et al.*, 1980a, b), and there are no instances of kill-site overlap, although bones from another animal, undoubtedly brought by scavengers, are sometimes found at skeletal sites of slain adult bison. Sites of accidental or disease-caused deaths, like kill sites, sometimes contain supernumerary bones because scavengers of bison carcasses transport single bones to the sites of other scavengeable elements.

The large-scale spatial distribution of bison kill sites appears clustered, because bison feed and socialize in traditional ranges that do not change character quickly (compare Raup, 1933, to Stelfox, 1977). As with moose, these traditional ranges are where most wolf kills eventually are made. Thus, in spite of the differences in distribution of living prey, scattering of skeletal remains is similar

for both species when killed by wolves; that is, distribution is limited to large, non-randomly located, circumscribed areas, within which carcasses occur with almost no overlap, although a few areas of 1 km in diameter may contain bones of a relatively large number of wolf-killed animals. Remains of bison calves have also been recorded near bones of adult cows, and it is likely that both were killed together by the same wolf pack (S. Oosenbrug, pers. comm.).

Where numerous bison perished together there is a great deal of skeletal overlap. Such sites are found along water courses or the edges of larger lakes, because mass deaths are in most instances a result of drowning during spring breakup of ice. Prevailing wind or water currents concentrate floating carcasses of drowned animals, especially along tree-lined levees (Haynes, 1981).

The dried bottoms or shores of smaller lakes, ponds, or watering holes often contain numerous bones representing several animals (Fig. 17), frequently thoroughly mixed, though most such remains in the bison ranges I have examined do not appear to be either predation-related or penecontemporaneous.

Conceivably, accumulations of bones in bottom sediments of lakes may derive from years of predation by wolves. D. Miller (1975, 1979) describes winter predation of caribou on a frozen lake in Saskatchewan; and Haynes (1981, in press a) discusses winter predation of whitetail deer on frozen lakes in Minnesota. Central kill-site overlap was not observed in these studies, although Miller

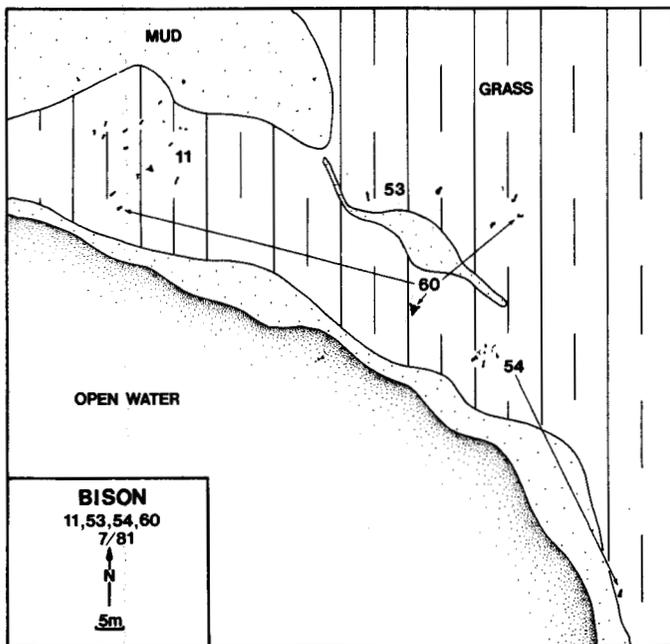


FIG. 17. Map of bones of at least four different bison located on grassy former shores of a drying lake about 0.4 ha in area. Numbers indicate general skeletal loci; irregular specks are limb elements, vertebrae, or skulls. Number 11 was an adult female, number 53 probably an adult male, number 60 a large adult male, and number 54 a subadult (probably female). Numbers 11 and 60 contain skulls.

noted numerous times that two to six carcasses were found near each other in narrows or small bays where wolves had patterned successes attacking caribou; and Haynes recorded two deer kills made within 50 m of each other only two to three days apart.

Bones that settle into the bottom may be bedded or stratified, especially in nearshore areas where bottom-rooted vegetation and organic debris from shore plants contribute to high rates of sediment accumulation. On interior lakes and sloughs that are not disturbed by high energy drainage currents, bones left on the ice by predators tend to float on ice rafts during spring thaw, rather than simply dropping to the bottom. Where the ice is not thick or the water too shallow to float it, some remains may settle gently into the bottom during the thaw, forming discontinuous beds atop earlier skeletal deposits. Shallow ponds are popular with bison and moose, whose trampling disarticulates and mixes elements lying on or within muds or mucks. It seems probable that bones from animals dying in different years would become mixed in the bottom sediments (Haynes, in press b).

DISCUSSION

There are at least two possible uses to be made of the observations here presented, one being of direct concern to archeologists, and the second to paleoecologists.

Animal remains provide a significant proportion of archeological data, but interpretations of modified bones are often based on intuition or superficial familiarity with the literature (e.g., Sutcliffe, 1970; Hill, 1975), rather than on conscientiously weighted lines of evidence. For example, bone modifications may be considered cultural in origin simply because the bones are recovered from prehistoric human sites, when in fact scavengers may have modified bones abandoned intact by humans. In the case of fossil bone assemblages lacking any clear artifactual evidence (e.g. Morlan, 1980), the most important task is to determine what agencies were responsible for any modifications to the bones. The standards for deciding agencies of bone modification have been derived mainly from studies of captive animals (Bonnichsen, 1973; G. Miller, 1969), although a limited body of literature exists on carcass and bone modification by wild carnivores (Sutcliffe, 1970; Hill, 1975; Shipman and Phillips, 1977) and by other natural agencies such as weathering (Behrensmeier, 1978) or trampling (Myers *et al.*, 1980; Haynes, in press b). Many observational reports on the end effects of animal gnawing are not fully documented (e.g. Hill, 1975), argue more than the data warrant (e.g. Binford, 1981), or do not follow up over long enough periods of time to note continuing changes. As a result, archeologists have been provided with catalogues of possibilities for how bones might look when affected by certain processes, but without specific underlying principles that would explain why modifications occurred and when they are to be expected.

The potential ecologic meaning of natural modifications may become apparent when thoroughly detailed observational studies have been carried out. Because the ways in which predators use or dispose of their prey are not haphazard (Carbyn, 1974; Haber, 1977; Kruuk, 1972, 1975; Mech, 1970; Oosenbrug and Carbyn, in press; R.O. Peterson, 1977; Schaller, 1967, 1972), conscientious examination of carcasses, bones, and bone sites will reveal behavioural and ecologic aspects of past predator/prey relationships. For example, the remains of a scavenged carcass can usually be distinguished from those of a true kill (Allen, 1979; Haber, 1977; Mech, 1970; R.O. Peterson, 1977), a distinction possible even for many incomplete collections of fossil bones. The degree of carcass utilization by predators and scavengers reflects important facts about the flow of energy in an ecosystem, such as the effort required by predators to support themselves with local prey (A. Magoun, pers. comm.; Mech and Frenzel, 1971; Pimlott *et al.*, 1969; Peterson and Allen, 1974). Accurate interpretation requires careful study, because factors in the system often interact to affect bone assemblages in complex ways, and different variables may conceal or cancel out each other's effects.

CONCLUSION

The overall aim of the research partially reported here is to examine skeletal modifications resulting from non-cultural agencies such as large carnivores or weathering forces, in order (1) to allow archeologists and paleoecologists to differentiate between culturally created modifications and those that were naturally created; and (2) to provide thorough documentation of some natural processes affecting recent animal bones during their initial phases of entry into the future fossil record. Unknown bone-modifying factors in past environments may be discovered by comparing their end effects with the end effects of recent processes acting on specimens whose taphonomic histories are known, and inferring analogous taphonomic histories for the fossil bones.

The research is not simply an attempt to seek additional empirical data for the use of future analysts working with fossil bone materials. The goal is to document both how bones end up with certain characteristics and why they are modified in certain ways. The basic assumption is that variables within modern ecosystems which affect the hunting success of predators are in many cases the same variables that would have affected hunting successes of past predators. Modern predators' behavior varies according to differences in ecosystemic conditions, such as seasonal factors influencing prey vulnerability. The variations in behavior are materially expressed by kinds or degree of gnawing damage, by carcass utilization in general, and by other related signs that would be expected to appear also on fossil bones. A study of these patterned signs would allow analysts to make interpretive statements about aspects of the past that might not necessarily be observable in the fossil record.

ACKNOWLEDGEMENTS

Field work was carried out with the generous assistance and guidance of L.D. Mech, S. Oosenbrug, R.O. Peterson, L. Carbyn, E. Klinghammer, Parks Canada and members of the Warden Service, and the U.S. Fish and Wildlife Service. Research funds were provided by the United States National Science Foundation (Grant BNS 7901194) and the Smithsonian Institution.

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Editors' note: Haynes, in press a has now been published. The complete citation is: Haynes, G. 1980. Prey bones and predators: potential ecologic information from analysis of bone sites. *Ossa* 7:75-97.