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BONE MODIFICATIONS AND SKELETAL DISTURBANCES BY NATURAL AGENCIES: STUDIES IN NORTH AMERICA

The Catholic University of America PH.D. 1981

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THE CATHOLIC UNIVERSITY OF AMERICA
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BONE MODIFICATIONS AND SKELETAL DISTURBANCES BY NATURAL AGENCIES: STUDIES IN NORTH AMERICA

A DISSERTATION
Submitted to the Faculty of The
Graduate School of Arts and Sciences
Of the Catholic University of America
For the Degree
Doctor of Philosophy

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by
GARY HAYNES

Washington, D.C.
1981

This dissertation was approved by William M. Gardner
William M. Gardner

as Director and by Dennis Stanford and
Dennis Stanford

David T. Clark as readers.
David T. Clark

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ACKNOWLEDGEMENTS

The research partially presented in this dissertation has taken several years to perform and has benefited from a number of financial endowments. During 1976-77 I was supported by a Fellowship from the International Research and Exchanges Board. During 1979-80 I received a Dissertation Grant from the National Science Foundation, and I was also a Pre-Doctoral Fellow in the Smithsonian Institution Department of Anthropology. Many individuals have given me assistance, most of them cheerfully and a few less than cheerfully, but they all deserve my gratitude.

First, the following persons found time to talk to me, show me materials, or otherwise introduce me to some aspects of arctic and subarctic prehistory: Dr. William Laughlin, Bruno Frohlich, and Beverly Holmes, all at the time of the University of Connecticut at Storrs; Dr. Douglas Anderson of Brown University; Dr. Carol Allison, Dr. E. James Dixon, Eugene West, and David Plaskett of the University of Alaska Museum; Dr. William Roger Powers of the University of Alaska; Dr. Henry Collins of the Smithsonian Institution; Dr. William Irving of the University of Toronto; Dr. Richard Morlan of the Archaeological Survey of Canada; and M. Jacques Cinq-Mars of the Archaeological Survey of Canada.

I am pleased to acknowledge my gratitude to Mr. Robert Bechtel of the Catholic University of America; Mr. Bechtel disbursed the NSF funds to me, and suffered through a year of my accounting methods.

Curators, Mammalogists, Keepers, and staff at the National

Zoological Park in Washington, D. C., have consistently given me their support even when they haven't had the foggiest notions about why I am doing what I am doing. I thank the enduring soon-to-be-Dr. Miles Roberts, and also Dr. Daryl Boness, Judith Block, Charley Braxton, Patricia Larkin, Linda Mahn, and Michael Morgan.

The Drs. George Miller, John Guilday, Neal Tappen, Robson Bonnichsen, and George Frison deserve honor for giving me information, encouragement, and for responding to my mail requests. I salute Dr. George Miller for his pioneering efforts in some research which I too ended up doing; I also salute Dr. John Guilday for his gracious advice. Rob Bonnichsen has offered guidance to parts of this research, and has been a congenial advisor.

For collecting materials in the field on my behalf I thank Dr. Erich Klinghammer and Tom Huffman of Wolf Park, Indiana; Ursula Mattsen of Glacier National Park; Jim Davis of the Alaska Department of Fish and Game; Barbara Scott of Simon Fraser University; Jim Woolington of the U.S. Fish and Wildlife Service in the Kenai National Moose Range; Dr. Mary Meagher and Sue Fullerton of the National Park Service in Yellowstone National Park; Robert Larson of the Alaska Department of Fish and Game in Delta Junction; and Robin Magaddino of the National Bison Range.

Dr.James Rooney and Dr. Charles Reid, of ICI Americas and the New Bolton Center School of Veterinary Medicine respectively, attempted to unravel for me some of the mysteries of bone fracturing in living animals. The State of Maryland Department of Agriculture Livestock Sanitation Facility in College Park donated to me fresh livestock carcasses for experimental butchering work; Drs. Saki and Chowdri kindly gave me permission to use autopsied livestock.

For my fieldwork I was dependent on the cooperation of wildlife biologists, who all assisted me above and beyond (and all that). My first and most admiring acknowledgment must be for Dr. L. David Mech of the U.S. Fish and Wildlife Service, one of the globe's busiest and most productive men. He found time to talk to me whenever I asked, he taught me some fundamental things, led me in the right or in better directions, reviewed chapters or manuscripts, arranged field work and trips, and opened his files to me. An admirable counterpart of his in Canada would be Dr. Ludwig Carbyn of the Canadian Wildlife Service, who made the necessary arrangements for me to work in Alberta and the Northwest Territories, and who also provided generous counsel and hospitality.

Dr. Rolf Peterson of Michigan Technological University kindly gave me all the help I could ever have asked for during my work on Isle Royale National Park. With his permission I have used some of his data and unpublished field records. John Brooks, a crew member of Dr. Peterson's, accompanied me for a time on the island, to my profit. Thanks are due to members of the National Park Service, notably District Ranger Chuck Dale and seasonal Rangers Jennifer Youngman and Katy Cannon. Thanks are also due to Head Ranger Stuart Kroll and Park Superintendent John Morehead for permission to do my research.

In regards to my Minnesota fieldwork, I thank Wildlife Technician Jeff Renneberg for help, information, and hospitality. I also thank Rick Field for his imaginative cooperation, and pilot Ken Jouppi of Wings North for his masterful flying.

My work in Wood Buffalo National Park was in many ways the most rewarding of my undertakings (pun not intended). It was also fascinating, enjoyable, and edifying. To Helen Doherty and Sebastian Oosenbrug (then working for the Canadian Wildlife Service in Ft. Smith) I will be everlastingly obliged for free room and ample board, for transportation, and for plenty of good fellowship and counseling. I also got away with an awful lot of unpublished data. Bas and I spent some very pleasant days together in the bush, and a couple that were perhaps a bit less than entirely pleasant, although still edifying, and I am enormously grateful to him. In Edmonton I received assistance from Hal Reynolds, Al Kennedy, and Doug Patriquin of the Canadian Wildlife Service. Doug and Marilyn Anions also gave me their kind hospitality in Ft. Smith; I am especially grateful to them, and I wish I could thank them more adequately.

I warmly thank members of the Warden Service of Parks Canada for generous cooperation and congenial assistance, especially Al Sturko and Al Gibbs (both, respectively, Chief Wardens), Danny Couchie, Ray Whaley, Doug Anions, George Lukiwski, and Duane West, and I thank retired Warden Gerry Lyster. I thank Park Superintendent Dr. Bernie Lieff for permission to do my research in the Park and for continued helpfulness. Most of my flying time was with pilot Mike Bailey of Buffalo Airways, a capable and efficient fellow.

I am especially indebted to Dr. A. K. Behrensmeyer of Yale University for her advice and aid. I also thank Dr. Andrew Hill of TILLMIAP in Nairobi, Dr. Diana Crader of Wesleyan University, Dr. Pat Shipman of Johns Hopkins University, George Krochak and Dr. R. Tedford of the American Museum of Natural History, Dr. Diane Gifford of the University of California at Santa Cruz, Dr. Howard Hutchison of the University of California at Berkeley, Dr. Antony Sutcliffe of the

British Museum (Natural History), Charles MacKinney of the U.S. Department of the Interior, Dr. George Frison of the University of Wyoming (and also of the Smithsonian Institution in 1980), Dr. Durward Allen and Dr. Erich Klinghammer of Purdue University, and Christopher Koch of the University of Toronto, Erindale College for assistance, words of advice, amiable consultation, and so on.

At the Smithsonian Institution, I must thank Drs. Robert Emry, Douglas Ubelaker, Lawrence Angel, Donald Ortner, David Von Endt, and Richard Thorington for aiding me in locating materials, for consultation, and for reviewing parts of the manuscript. In addition, I thank Robert Purdy, Agnes Stix, Phil Angle, Greg Blair, Aleta Hohn, David Yong, Charley Potter, Tommy Fulgham, and Victor Krantz. I am also delighted to thank Mr. Joe Brown, Ms. Janette Saquet, Ms. Mary-Jacque Mann, Ms. Paula Cardwell, and a classic screwball, Ms. Jean Fitzgerald, for all their help.

Finally, I thank William Barse for his sport and solace, I thank Dr. Mel Thurman for making the wheels begin to turn, and I thank Dr. Dennis Stanford of the Smithsonian Institution for unexampled encouragement and cooperation. Thank you, Dennis. My most important thanks go to Ms. Lynn Nyce for her companionship and dependability, and for being a good sustaining comrade. I cannot thank enough my father and my mother for decades of subsidy and affection.

Mistakes and faulty logic in this dissertation were produced by my mortal intellect, and I solely am responsible for any and all such errors. This dissertation is dedicated to Drs. Mildred and Waldo Wedel of the Smithsonian Institution, and to the She-Wolf that I met in 1980.

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Bear Hunt on the Missouri,
by Karl Bodmer.

Courtesy Denver Public Library,
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I. Introduction

The aim of this research was to examine bone and skeletal modifications resulting from non-cultural agencies such as large carnivores and weathering forces, in order to allow archeologists and paleoecologists to differentiate culturally created bone or assemblage modifications from those modifications which were naturally produced. In addition, the research provides uniquely thorough documentation of some natural processes undergone by Recent animal bones during their initial phases of entry into the future fossil record. This kind of information is valuable as an aid in environmental reconstructions, in that certain unknown factors in past environments which were operative to modify bones could be discovered by comparing the end effects of the unknown past processes with the end effects of Recent processes acting on specimens whose taphonomic histories are known, then inferring analogous taphonomic histories for the fossil bones.

The fundamental theoretical orientation in this study is based on the commonplace principle of uniformitarianism, and involves reasoning by analogy: That is, while fossil bone assemblages may misrepresent aspects of extinct animal communities, the nature and extent of biasing factors may be better evaluated by the study of possibly analogous agencies of modification to modern bone assemblages. Since the past cannot be directly observed, the present must serve as a model or example.

Perhaps the most potent empirical generalization which could result from such studies of the present would be a sufficient operating principle upon which to found scientific taphonomic research: Bones that are damaged or otherwise modified by natural forces may bear the distinguishing effects of those forces. This is a principle that must first be demonstrated before being transfigured into a law, and it is the intent of this dissertation to show that many natural causes and effects of bone modification are indeed regular, predictable, patterned and uniformly explicable.

Chapter 2 presents a brief statement of my personal theoretical interests in archeology and a discussion of each of the two research goals, including some examples of other archeological and paleoecological research which is pertinent to a study such as mine. This chapter also sets out my basic program of research and my methods of accomplishing the study.

Chapter 3 is a descriptive discussion of several bone assemblages which contain items that are difficult to interpret or explain unequivocably. Some of these interpretive difficulties are explicitly presented as taphonomic questions. Finally, to show that answers to these questions cannot be effortlessly derived from our present knowledge about natural factors of bone assemblage formation, there is a review of literature that describes natural accumulations of animal carcasses and bones.

Chapter 4 presents my observations of gnawing behavior by captive lions, hyenas, wolves, bears, and rodents; also presented are relatively detailed descriptions of the damage created by these gnawing animals, demonstrating the factors in end results which would allow an analyst to differentiate carnivore family responsible for any particular gnawing damage.

Chapter 5 has two purposes: (1) To introduce the literature on predator-prey relationships and to point out how such studies often refer (even if obliquely) to bone assemblages resulting from predation; and (2) to introduce the field study areas where I conducted research using the literature cited as guides for my research design.

Chapter 6 is an extended discussion of findings from the study area where wolves and deer were involved; Chapter 7 consists of extended discussions of the study areas where wolves and moose, and wolves and bison were observed interacting.

Chapter 8 presents descriptive and comparative data on bone and carcass modifications. The first part of this chapter is concerned with observations in the field study areas, while the second part is concerned with reviewing some results of other field studies on natural carcass decay sequences. The final part of Chapter 8 contains observations made on fossil bones collected in Alaska and the Yukon, and excavated in Colorado, with the intent of pointing out some noticeable (probable) gnaw damage patterns. This chapter provides data on several potential natural agencies of carcass disintegration, and also provides an examination of bone collections which contain much more damage due to gnawing than other paleoecologists have recognized; it is argued that the bones therefore contain much more evidence about the past.

Chapter 9 consists of descriptions of miscellaneous factors in the study areas which complicate the prediction of future fossil assemblages. These descriptions cover such processes as natural burial of bones, natural weathering deterioration of bones, preservation and decay, and similar occurrences.

Chapter 10 consists of discussion of some experimental butchering and bone breakage procedures, a model of bone fracture mechanics, and explicit comparisons of experimental results with observed or expected natural modifications of bones.

The final chapter is a summary of my research contributions. I consider the kinds of findings which I have sought to be indispensable to paleoecological interpretations. In essence, these findings confirm that possible agencies of skeletal disturbance or biasing of bone numbers may be factored out of fossil bone assemblages, by comparing proportions of surviving fossil bones or damage to particular bones with expected survivorship or damage in observed modern carnivore assemblages; if the fit is close, then one can interpret the fossil assemblages as having been affected by inferred species and numbers of carnivores, acting as predators or scavengers, during inferred seasons in the past. The relative ease of predation may potentially be reflected in gnawed fossil bones; it may be possible to distinguish over-scavenged remains from poorly utilized remains (or even single bones or parts of single bones), thus allowing interpretive statements about prey availability or vulnerability. Finally, it may be possible to distinguish natural bone or carcass modifications from cultural modifications, or to separate such different modifications on specimens with complex histories, such as scavenged bones from cultural sites.

II. Research Design and Background

THEORETICAL ORIENTATIONS

I consider it to be an archeologist's primary goal to produce explanations which account for spatial and temporal differences in artifacts, sites, or associations of artifacts and sites. The past human groups of central concern to me were most likely hunters and foragers, who would have sustained themselves (in an archeologically visible way) by utilizing large mammals (see Butzer 1971; C.V. Haynes 1980; Jelínek 1976 for overviews of Pleistocene culture histories in Africa, North America, and Eurasia). The by-products of this archeologically visible energy procurement activity consist in accumulations or assemblages of animal bones which may have been modified during subsistence practices such as carcass dismemberment, extraction of bone marrow, or manufacture of bone tools. However, interpretation of these bone accumulations may often be open to question, in that non-human agencies may have in actuality been responsible for some or all of the perceived modifications.

The ability simply to recognize traces of human behavior is perhaps the most basic necessity before archeological reconstructions or explanations of the cultural past are possible; for that reason, it seems advisable to examine the processes in nature which can create bone modifications that are similar to those modifications created by human behavior.

My theoretical orientations as an archeologist are based on an ecological outlook on the study of human groups (see Steward 1955; Netting 1971; Vayda and Rapaport 1968): Cultures are viewed as social systems which exist within natural environmental systems. Cultural behavior, especially subsistence behavior, can be explained only when it is examined within the framework of the whole ecosystem. This is structural-functionalism, with focal concern being on by-products of subsistence activities, because these by-products are the results of the direct articulation of the artificial (cultural) environment with the natural environment.

There is an isomorphic principle in cultural ecology and biology, which is that in examining the most complex natural or cultural systems, data from certain key or integrative factors validly dominate the descriptions and explanations (Odum 1971; Steward 1955).

Because natural and cultural environments are systems, it is possible to reconstruct and interpret many aspects of the past that are not necessarily materially preserved. For example, animal bones and assemblages from archeologic contexts may be considered to have greater meaning about prehistoric systems than simply revealing what was eaten. A study of animal bones in their contexts might reveal evidence about the relationships of human groups and the natural environment, evidence such as scheduling of meat procurement activity, strategies for recovering products such as marrow and bone grease (besides muscle meat) from slain animals, hunting strategies such as cooperative effort, and so forth.

GOALS OF THE RESEARCH

The first goal of this research is to provide improved guidelines for differentiating animal bones which have been modified by human beings from bones modified by animals, weathering, or other natural agencies. I consider the lack of explicit comparisons of natural and cultural modifications to be the cause of serious interpretive problems in archeology.

A second goal is to explore the nature of ecological information that might be gained from the analysis of animal bones and bone assemblages, in order to make it possible for paleoecologists to distinguish such things, for example, as animal species responsible for gnawing damage on bone specimens, or the type of microenvironments that existed at the time of the bones' original deposition. If it is possible to differentiate bone modifications caused by one type of carnivore or one type of highly localized environment of deposition from those caused by other types, it would then be possible to use even fragmentary materials or selective collections to make more sophisticated reconstructions of past ecosystems.

DISCUSSION OF GOALS

Goal One: Differentiating Cultural Bone Modifications from Natural Modifications.

Animal bones in an archeological site are potential sources of information about the behavior of prehistoric human groups which may have left the bones, about ancient climates and ecosystems, even about the age of the sites themselves (see Read 1971 for a summary discussion of the demonstrated or potential uses of faunal remains in archeologic research). However, bone assemblages need not be direct and clear representations of all circumstances that existed in the past. Because bones are perishable, they probably do not always survive unmodified over time by natural agencies such as scavenging animals, decay organisms, weathering stresses, or geomorphic processes. Soil creep or frost heaving may scratch and polish bones. Bones may be abraded and polished by the action of moving water or winds. Carnivore gnawing might put grooves and nicks on bone surfaces, damage which might obscure or be mistaken for the marks left by human modification, such as butchering cuts. Herd animals may trample sites and break up or scatter bones. Flood waters or foraging carnivores may remove bones from sites. Some bone elements may suffer decay and simply cease to exist over time.

There have been no comprehensive studies published on potential factors of bone or assemblage modification, although some special case investigations have been made available in the literature (see discussion in Chapters to follow). It would therefore seem that many researchers assume they can intuitively distinguish natural from human processes of bone alteration, and in so doing possibly ignore the difficulty by assigning all bone breakage or dispersal at any site to a single, obvious potential cause - most often hypothetical cultural activities. In other cases researchers may rely on limited personal observations, oftentimes considered implicitly to be adequate as a background from which to interpret. Deplorable archeological blunders may result from an over-eager desire to find human behavior in all materials at a site, or from the belief that the meaning of objects in an assemblage is always self-evident.

From time to time a few researchers attempt to improve archeological methods of dealing with altered bones (for example, see Gordon 1976; Shipman and Phillips 1976, 1977; Walker and Long 1978); yet there are flaws in some such efforts, too. For example, Biddick and Tomenchuk (1975), in discussing a system to describe fractured bone specimens, take the position that only fresh bones break in spiral configurations (see Chapter 10 for discussion). The supporting reference is to Tappen's studies of split-line weathering cracks on long bones (see Tappen 1964, 1969), but Tappen's observations cannot account for the presence of spiral fractures, only for the absence of them. Biddick and Tomenchuk simply do not provide positive statements about bone fracturing which can explain the necessity for the highly detailed descriptions that their method involves. In many case judgements which they make in the publication about the degree of bone freshness when broken may not be correct, and certainly are not warranted when there is no explanatory framework provided.

There are many other possible examples of unsubstantiated claims in the literature about bone modifications. For instance, Johnson (1978: figure 2) illustrates a bison humerus from the Llano Estacado and ascribes the damage to Paleo-Indian dismemberment practices. The damage which is apparent in the photograph may be just as likely due to carnivore gnawing (as discussed in Haynes 1978a,b). Fractured bone pieces from Choukoutien Cave in China are classified by Breuil (1938, 1939) (Plate 1) as tools such as gravers, points, scrapers, or trimmed flakes, primarily because of their shapes, although a number exhibit characteristics that Breuil called wear or polish. However, polish and trimming can occur on fractured bones that have been trampled (Brain 1967) or gnawed by carnivores (Haynes 1978a). In fact, P'ei (1938) was much more skeptical about the cultural origins of many of the Choukoutien bone "implements." Black _et al._ (1933) also suggested that some of the bones may not have been modified by man alone. Several bone and antler specimens from cave deposits in Alaska are interpreted by Larsen (1968) as artifactually modified; however, some of the modifications illustrated are often

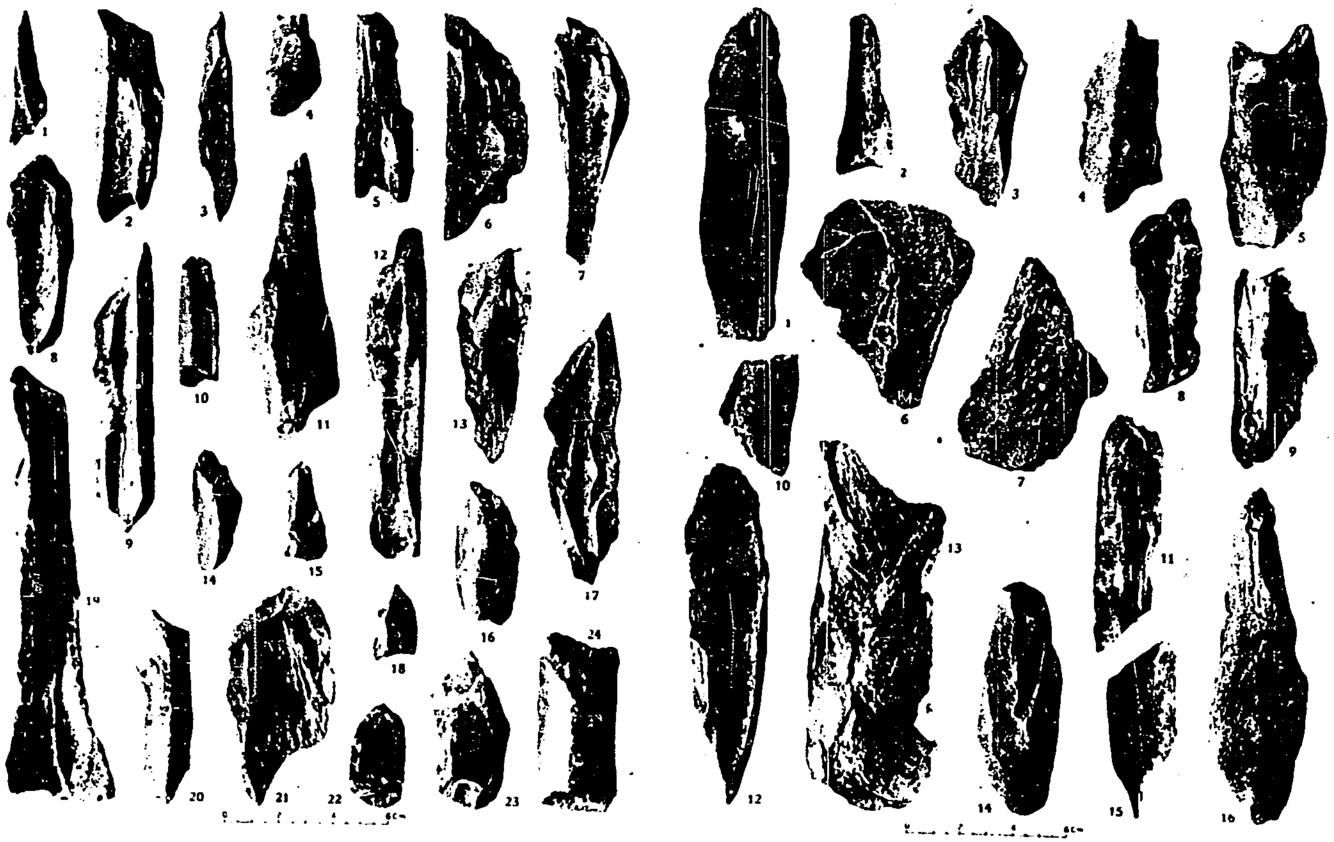


Plate 1. Mammalian bone fragments from Choukoutien (China). Illustration from Breuil (1939).

produced in nature a number of ways, including during carnivore gnawing, a point raised by Larsen himself (1968) (Haynes 1978a, 1980a). Wilson (1974) illustrates two bison tibiae from a prehistoric site in Alberta, and classifies them as tools; the specimens are apparently very similar to bison tibiae which have been gnawed by wild wolves and other carnivores (see Haynes 1978a, 1980a,b). In much of the literature, the presence on bones of polish, striations, and abrasion are judged to be the results of cultural practices alone (see Semenov 1964; Hester 1972; Robinson 1959; Gilbert and Steinfeld 1977 for examples of bone items classified as tools), but water transport, solifluction, trampling, and animal gnawing may also produce polish and striations on bone surfaces (see J. Clark 1970:70).

Occasionally critical re-evaluations of earlier interpretations point out possible errors. For example, Singer (1956) re-examined two so-called chisels of bone recovered from the south African *Australopithecus* site of Hopefield, and he concluded that the bones were more likely to have been shaped by non-human actions, probably carnivore gnawing; he also illustrated recent bone specimens which were gathered from a cave never occupied by humans, and it is apparent that these bones look much like real artifacts such as trimmed points, awls, or cutting implements. Singer and Heltne (1966:263) emphasize that it may be possible to find patterns of bone modifications in any assemblage, but that such statistical uniformity does not *prima facie* prove human involvement with the bones.

There have been very few studies performed synthesizing data that might bear on questions of interpretation of bone damage. Semenov's *Prehistoric Technology* (1964), Hill's unpublished doctoral thesis (1975), Behrensmeyer's published doctoral thesis (1975), Bonnichsen's study of broken bones in Pleistocene collections (1979), and Morlan's related study (1980) are reports that only briefly inventory possible damages due to natural agencies affecting faunal remains. None of these works can be considered comprehensive or definitive, and none claim to be. For example, Semenov (in one page) categorizes the results of natural forces as: general destruction of bone shape and structure by soil processes; destruction of bone surfaces only; partial decay; deformation; surface etching by roots; surface marking by the teeth of carnivores and rodents; and abrasion from rolling in water or sediments. As on stone tools, the presence and nature of localized striations and polish provide the main basis for distinguishing human use of bone items. Unfortunately, Semenov presents no data dealing with natural processes of bone modification. One might infer from such a cursory treatment that human use of bone produces damage that is self-evidently distinct from natural alteration of bone. This is an entirely unwarranted position when there are no supporting data. In contrast to such an intuitive approach, Hill (1975) observed modern bone assemblages in east Africa and discussed the natural factors that damaged, dispersed, concentrated, and modified these bones. In many cases he observed naturally-made modifications that other researchers such as Dart (1957), Robinson (1959), and Kitching (1963) have considered, when seen in possibly archeological materials, to have been made by hominids.

The literature on carnivore gnawing, geomorphic processes, or other processes in nature affecting bone is meager. Because so little information is available to analysts, many published reports do not create strong cases to support interpretive statements; that is, seldom is information presented that would be sufficient to warrant the conclusions offered.

Simply because humans would have produced the alterations to bones from any particular assemblage does not mean that no other agency could have produced them (as argued by Hrdlička 1912). A major error that one might make in interpreting bone objects would be to ignore alternative possibilities and expect the plausibility of cultural origins for the modifications to be positively assertive. A number of possible agencies of bone modification might be involved in the histories of any particular archeologic bone assemblages, and assigning to any of these agencies the responsibility for modification is only an hypothesis. When one possible hypothetical agency finds support in experimental, empirical, or bibliographic research, other hypothetical agencies have not necessarily been invalidated. Likewise, when one hypothetical agency has been disproven, other hypothetical agencies have not been verified, nor have they been further supported in any way.

Many of the published interpretations of bone objects or entire bone assemblages may deserve critical re-analysis; it is not my intention to attack all ill-considered interpretive statements already in the literature, only to point out here that interpretive errors or oversights may exist due to the lack of consideration of alternative possibilities for bone modification. In the following chapters I present data which can be used to develop positive sets of analytic standards by which certain agencies of bone modification may be distinguished under certain conditions.

Goal Two: Deriving Ecologic Information from Bones

Early in the course of my research on carnivore and rodent gnawing of bones I realized that there were some significant regularities in the data. For example, individuals of the same species of bone gnawers invariably damaged particular elements in patterned and identifiable ways. This generalization was first implied by Buckland (1824) and reiterated and expanded by Dawkins (1874:58, 300). I proposed that gnawing damage and bone dispersal from certain sites produced by particular carnivore species were identifiably different from damage and dispersal in sites created by different carnivore species. In addition, gnawing damage by some species in certain seasons varied distinctively from damage done in other seasons. I thought that if I could generalize from these kinds of consistent patterns it would be possible to determine, for example, the presence of certain animal species in extinct ecosystems even when no fossil bones of those species survived, if members of these species left their distinctive gnawing damage on other bones.

Quaternary predators are greatly outnumbered by their prey animals (Krebs 1972:497-498; Odum 1971). It is likely that a very low percentage of animal bones ever survives to become fossils (Darwin 1859; Simpson 1961; Romer 1945:1; Rolfe and Brett 1969:233-234), and therefore it is inevitable that few bones of predators will ever be found, as compared to the number of prey bones. Relative frequencies vary from assemblage to assemblage, of course. The bones of some large carnivores may be quite common at certain Pleistocene collecting localities, such as Rancho La Brea (Marcus 1960; Merriam 1911, Merriam and Stock 1932; Wyman 1926) and some European caves (for example, see Kurtén 1968). But in general predator bones are not abundant. For this reason there would be great importance attached to any additional ecological information about predators (species identification, relative density, ease of predation, etc.) that could be forthcoming from analysis of prey bones. These bits of information when derived for assemblages of fossil bones might add considerably to the persuasiveness of ecologic interpretations and reconstructions.

My planned research was not without potential models. Reports by Behrensmeyer (for example, 1978) on her research in East Africa have shown that the condition of fossil bones may reflect a great deal about their pre-burial or pre-fossilization environments. For example, she found that bones usually suffer weathering deterioration with consistent sequences of surface alterations, even in different micro-environments, although the amount of time that bones spent in each arbitrarily defined stage varied, according to such factors as availability of moisture, amount of shade, and so forth (Behrensmeyer 1978). She proposed that if different bones from a single site display different degrees of weathering, the bone assemblage probably did not originate at one time, but grew by determinable increments. This information would serve to clarify the origins and length of growth period of undifferentiated and unstratified bone beds. When the weathered surfaces on fossil bones were compared to surfaces of modern weathered bones, the length of time the fossil bones were subject to weathering would be estimated.

Behrensmeyer performed her research in arid, semi-arid, and seasonally arid African environments. In North America only George Miller (1975) has systematically observed bone weathering and provided adequate data for setting up staging frameworks, but his work was also in arid environments. The areas of main interest to me are in temperate, subarctic, and arctic latitudes of North America, and there are few data from these regions that are comparable to the data collected by Miller and Behrensmeyer. It was therefore necessary for me to initiate field study of my own in several northern regions, involving examination of bones and skeletons with documented or reliably-estimated dates of death. Practically nothing is known (or at any rate available in the literature) about carnivore dispersal of bones in the north, carnivore and rodent gnawing of bones, bone damage due to repeated freezing and thawing, or related matters.

FIRST THINGS FIRST

Before investigating the natural processes, I first examined a few particular bone assemblages (see Chapter 3) to determine (1) what modifications the bones had undergone, and (2) what were the specifics of past environmental circumstances. These analyses provided me with a synoptic view of potential natural agencies that could conceivably have altered the bones in the assemblages of interest. None of these natural agencies(large carnivores or scavengers, geomorphic forces such as frost-heaving, trampling herd animals) have been yet empirically studied to any great extent, at least as far as fully documenting what their effects on bones could be. For my research an intensive literature review was first undertaken, and the potential modifying influences of some natural forces were evaluated. Since the literature search revealed only a limited number of conclusions about the effects of natural forces, I determined that certain agencies needed to be more fully investigated. I decided to study most intensively the capacities and proclivities of large carnivores to gnaw bones and to modify prey animal skeletons, and the destructive effects of natural weathering in various microenvironments.

First, it seemed necessary to study the ways in which animals gnawed bones to produce breakage or other modifications; this research could be most conveniently carried out using captive carnivores and rodents in a number of institutions which extended their cooperation, namely the National Zoological Park (Washington, D.C.), Carlos Avery Game Farm (Minnesota), and Wolf Park (Indiana).

Second, it also seemed imperative to study the ways in which wild animals damaged bones and dispersed or accumulated prey body parts or bones in undisturbed habitats. This kind of research would be focused on wild predator behavior and ecology, and on the ways in which bone damage or assemblage modification is related to ecosystemic factors, but would also be concerned with observing bone assemblage modifications resulting from herd-animal trampling, rodent gnawing, or densite hoarding behavior.

Third, it was obvious that much more research needed to be performed on geomorphic processes of bone or assemblage modification. This research, which needed to be conducted in the field under natural (that is, undisturbed or un-simulated) conditions, would be concerned with floodwater redistribution of bones, burial in various kinds of substrates, weathering deterioration of bones, the effects of periodic freezing and thawing of bones, and similar as yet poorly-documented processes.

Finally, it was necessary to perform controlled experiments using stone tools on fresh or aged bones, to create documented expected cultural damage, whose attributes could be analytically distinguished from the attributes of carnivore-gnawing damage, frost-heave edge-rounding modifications, or other potential and actual types of bone alteration.

Ideally, the data and information from these studies could ultimately be compared to facts about certain fossil bones and bone assemblages, and interpretations of the prehistoric materials could be re-considered from new perspectives (see, for example, Haynes 1980a).

A FINAL NOTE ON THE RESEARCH

This research was not simply an attempt to seek additional empirical facts which could be made available to future analysts who work with fossil bone materials. The experiences behind these presented facts were attempts to document the "linkage between...by-products and behavior" (Binford 1978:11). I proposed that there were discoverable behavioral or systemic dynamics of predators and environmental states in the past which resulted in a static patterning of the fossil bone record in the present. These dynamics were discoverable because certain formation processes of animal remain deposits would have been "common to both contemporary and past eras" (Binford 1978:12). That is to say, to take one aspect of the proposition, predator species of the past would have behaved in ways that are similar or identical with the behavior of the same or closely related species living in undisturbed parts of the modern world, as far as hunting, feeding, and scavenging activities are concerned (the assumption being that some habitats of the past and present are not qualitatively dissimilar). The variables within the ecosystem which affect modern predator hunting success are in many cases the same variables which would have affected past predator hunting successes. The behavior of modern predators varies according to differences in ecosystemic conditions, such as seasonal factors which affect vulnerability of potential prey animals. The variation of behavior is materially expressed by kinds or degrees of gnawing damage, by carcass utilization in general, and by other related signs. Such signs as these would expectably appear also on fossil bones or in bone assemblages; a study of these patterned signs would therefore allow an analyst to make interpretive statements about aspects of the past that might not necessarily be observable in the record.

The relationship between the dynamics of carcass utilization and the statics of resulting bone deposits are discussed in Chapters 5, 8, 9, and 10. I consider the discussions in these chapters to be theory building, on a middle range level, as such theory building has been envisaged recently (see Binford 1977:6), because I explain not only how bones or bone collections end up looking like they do, but also why they suffer certain modifications. In my opinion, this latter aspect of the data is the part of my research which makes the greater contribution to the sciences of paleoecology. The work of most other taphonomists, archeologists, or ecologists who have recorded carnivore effects on bones (see, for example, Sutcliffe 1970; Hill 1975; Bonnichsen 1973) does not present in-depth discussions about why bones have been modified in certain ways. These works are seldom more than empirical lists of damage done to bones, and to my way of thinking have not adequately used the available data to enlarge the interpretation potential of the fossil record.

III. Assemblages of Interest, Taphonomic Questions, and the Search for Answers in the Literature

INTRODUCTION

There are many possible environments of bone weathering, and many possible effects of animal and human modification to bones. Any one analytic system designed to identify agencies of bone modification must be demonstrably valid when applied to assemblages created under different conditions. No single checklist of attributes could cover all possible combinations of agencies modifying bones or bone assemblages under all circumstances. For that reason, studies of bone modification should be undertaken with particular assemblages in mind, incorporating into these studies basic research about the particular conditions that might have existed in the past and might have affected particular surviving bones. The general principles and insights of paleoecology would thus be applied to the solution of singular problems.

* * *

During the course of this research, which I initiated in 1976, I have examined bone collections from Alaska and the Yukon (as curated in the University of Alaska Museum, the Smithsonian Institution, the American Museum of Natural History, the University of Toronto, and the Archaeological Survey of Canada), and from Colorado and other states (as curated in the Denver Museum of Natural History and the Smithsonian Institution).

The first section presents brief descriptions of some fossil bone assemblages or collections that contain materials whose modifications may be due to factors of human behavior or natural processes.

NORTHERN FOSSIL BONES

Central Alaskan and Old Crow Basin Assemblages: Bones in Alluvium

It is conceded among most North American prehistorians that the route *Homo sapiens* followed into the New World originated in Asia and crossed to Alaska via the Bering Land connection or the Bering Straits (see Wormington 1957; Jennings 1974; Willey 1966). Thus, early sites which pre-date continental United States sites ought logically to be found in Beringia. These sites also ought logically to contain archeologic components somewhat similar to their southern descendents as well as to their Asian antecedents, if the migration or diffusion of traits was not excessively drawn out over time. Unfortunately, there are no such northern North American sites which are clearly genetically related to (and indisputably earlier than) southern sites. The earliest sites or components in the north, if they were in actuality culturally created, contain animal bones and little else, certainly nothing that can be linked directly to Llano culture or even to unquestionable later northern cultures.

For the purposes of this study, there are two kinds of Pleistocene age mammalian bone assemblages of interest from the north; one kind of assemblage is found in cave sediments and appears to be stratified and lying within primary depositional contexts. The maximum published radiocarbon dates for such assemblages are 13,000-16,000 years b.p., which are the oldest dates for any stratigraphic (archeologic) contexts in the north (Wilmeth 1978). The other kind of assemblages occurs in river valleys, along the vertical faces of cut banks, or on river channel bars and beaches. These bones are mostly found redeposited, eroded out of primary depositional contexts by the actions of northern rivers or slumping banks.

Many assemblages of the latter kind were artificially washed from depositional contexts during placer mining operations in the vicinity of Fairbanks, Alaska. Gold miners brought water into their mining area by ditches, thawed and washed away the frozen muck overburden, then thawed the frozen gold-bearing gravels with cold water coursing through pipes driven into the ground.

Many of the animal bones of interest to this research were found as residual deposits left after the frozen Pleistocene age mucks were washed away ("hydraulicked") (see Wilkerson 1932 and Gilbert 1974). Species identified to date include Ursus, Canis, Vulpes, Taxidea, Gulo, Smilodon, Felis, Arctodus, Homotherium, Mammuthus, Equus, Saiga, Camelops, Bison, Rangifer, Alces, Cervus, Ovis, Ovibos, Symbos, Bootherium, Bos, Megalonyx, Castor, Lepus, Lemmus, Microtus, Citellus, Dicrostonyx, and others (Péwé 1975:97; E. Anderson 1977). These frozen silt deposits are common to many valleys in interior Alaska. The deposits may not be internally stratified except on a gross level, and may be overlain or underlain by ice, sands, gravels, peat, and volcanic ash. The fine-grained, highly organic muck may be more than 20 meters thick and extend far up valley hillsides. It usually contains vegetative matter, including branches, logs, mosses, and frozen peat, as well as animal bones. Soft tissue such as skin and viscera may be preserved with the bones (see Péwé 1975: figure 43, figure 44). In some collecting locales a number of fossil bones had been fractured possibly when fresh; there is also a suggested possibility that humans originally caused the bones to accumulate as killsite middens (Porter 1978:2). Some bones show possible cutting damage. There have been claims made that cultural materials were found in association with Late Pleistocene faunal remains in some deposits; finds have included bifacial points and polished bone points (see Rainey 1940). Because the mucks are not clearly stratified at all locales, however, ancient fossil bones may very well have become fortuitously associated with more modern artifacts during natural mixing, which could have occurred from time to time when solifluction or slumping took place following a temporary thaw.

Silts that were not placer-mined along many northern rivers may also contain the bones of Pleistocene mammals (see Bell 1898:373). The best known collecting localities are along the Porcupine and Old Crow rivers of Alaska and the Yukon Territory. In the 1950s O.W. Geist collected on parts of these rivers for the University of Alaska Museum (Geist [1953?], 1962), and recently C.R. Harington (Harington 1970, 1978, among others), W. Irving (1978, among others), J. Mathews (Morlan and Mathews 1978), and R. Morlan (1978, 1979, among others) have been investigating

Pleistocene fossils in the unglaciated basins of the Yukon-Alaska area. Species recovered to date include Homo, Canis, Platygonus, Lepus, Castor, Castoroides, Microtus, Ondatra, Gulo, Panthera, Alopex, Mammut, Mammuthus, Equus, Camelops, Alces, Rangifer, Bison, Lemmus, Dicrostonyx, and Spilogale (Harington 1978:61-62; Irving et al. 1977; Beebe 1978:159). The Old Crow basin bones were originally deposited in a variety of sediments, including glaciolacustrine, channel, floodplain, and eroded fill, during the Late Pleistocene (from Sangamon to Wisconsin times). About 11,000 years ago a glacial lake that had covered the basin was allowed to drain as Laurentide ice retreated. Since then the Old Crow River has meandered through the exposed deposits and washed out many bone specimens (Harington 1978:55). Some bones have been redeposited within reworked sediments, while many others are simply exposed on ground or river bar surfaces. The reworking and transport of many bone specimens has caused recent breakage and abrasion. However, there are many specimens which appear to have been fractured, whittled, flaked, abraded, or otherwise modified when in a fresh state, that is, prior to fossilization or mineralization. A very small number of flaked stone has been found in the area, but none have been found in primary depositional contexts or in direct association with bones. There are several dozen possible bone, antler, and ivory artifacts in the collections; these implements were modified by percussion, cutting, and polishing. There are also hundreds of spirally fractured bone fragments (see Bonnichsen 1979; Morlan 1979, 1980). A human child's mandible and remains of domestic dog are also reported (Irving et al. 1977; Beebe 1978). The abundance of spirally fractured bones led Morlan and Irving to suggest that the Old Crow River was reworking real archeologic deposits of butchered animal remains

(Morlan 1979:141; Irving 1975, 1978b). Some of the possible artifacts are very similar to ethnographically documented materials. A caribou tibia (see Irving and Harington 1973) has been modified into a tooth-edged implement nearly identical with many museum specimens of Athapaskan hide defleshing tools. Some caribou antler implements from Old Crow bear marks similar to whittling or chopping damage. These antler pieces are shaped much like ethnographic examples of wedges or hammers, and are similar to Eurasian Upper Paleolithic antler artifacts (see Shovkoplyas 1965, who describes the site of Mezin in the Ukraine; and Mochanov 1977, who describes the Diuktai Cave site in Siberia). The minimum age of these specimens is 10,000-11,000 years, because this is the latest date on the formation of the sediments from which many of the bones or antlers came (Morlan 1979a). A radiocarbon date of $27{,}000\ ^{+3000}_{-2000}$ years b.p. on the caribou tibia flesher may be in error since it is based on the inorganic fraction, which is more easily contaminated than the organic fraction. Two mammoth long bone objects that resemble flake cores were radiocarbon dated (using the apatite fraction) at $25{,}750\ ^{+1800}_{-1500}$ years b.p. and $29{,}000\ ^{+3000}_{-2000}$ years b.p. Unworked mammoth bone has been dated using the collagen fraction at 22,600±600 years b.p. Maximum ages on these bone materials are difficult to assay because the apatite and collagen fractions of specimens do not give consistent age results (Irving _et al_. 1978:215). Morlan has performed recent stratigraphic investigations of stretches of the Old Crow riverbanks, and has age bracketted sediments which yield spirally fractured bones of large mammals, with dates of over 50,000 years b.p. minimum (carbon date on underlying peat) and 80,000 years b.p. (fission-track estimate on underlying volcanic ash).

The most unusual and potentially significant items found at the Old Crow localities and a few other localities in eastern Beringia are "cores" and "flakes" made on mammoth long bone fragments or ivory fragments (see Bonnichsen 1979; Irving and Harington 1973; Morlan 1980; also see Gvozdover 1953 for descriptions and illustrations of some similar specimens from Upper Paleolithic sites in the U.S.S.R.). These objects may have been deliberately reduced by humans simply to produce flakes for use as cutting, scraping, or chopping implements. If these items are indications of the early existence of a genuinely human technology, the flakes could possibly have served as butchering tools or hide working tools, in the absence or scarcity of local cryptocrystalline, workable stone resources.

Paleoenvironments

Old Crow Area

Parts of the Old Crow area were probably forested 60,000 years ago, and supported forest-dwelling animal species such as lynx and snowshow hare (Morlan 1980, 1979). However, tundra species also are represented at the 60,000 year b.p. time period, as well as species adaptable to both taiga and tundra. The presence of ice-wedge pseudomorphs and sedimentary evidence of cryoturbation would indicate a climate 60,000 years ago that was not dissimilar from today's Yukon climate, if not somewhat colder. This was the time of the early maximum glaciation of the early Wisconsin stage. Morlan (1979) suggests that a mosaic existed of forests, open woods, and treeless tundra, providing an enriched variety and quantity of food and raw material resources.

Gradually in the area forests thinned and disappeared as arctic steppe conditions developed, during the later Wisconsin glacial stages. Well-drained grasslands probably replaced dense conifer woods or boggy tundras.

Schweger and Habgood (1976) suggest that tundra and steppe were mixed with each other in space and possibly replaced each other in time in many northern areas during terminal Pleistocene times. It is possible that tundra-dwellers such as caribou co-existed nearby to grassland-dwellers such as bison or horse or mammoth, or alternatively that each kind of species lived and disappeared separately several times in the Old Crow Flats area.

Central Alaskan Valleys

During the Wisconsin stage of the last glacial period, Mammoth, horse, bison and other species (see Péwé 1975:table 12) may have lived "on the tundra-covered hills and grassy flood plains" of central Alaska (Péwé 1975:101,120). Mathews (1976:74) believes otherwise, that even non-floodplain areas would have supported grasses and other plants requiring good soil drainage; alpine tundra, which undoubtedly existed in Late Pleistocene Central Alaska due to the cold climate, therefore did not extend into lowlying areas (the "tundra-covered hills" of Péwé).

Summers may have been relatively warm and dry (Mathews 1976:75), although mean annual temperatures were possibly 3-4° C. lower than they are today (Péwé 1975:120). Summers would also have been relatively short. "In central Alaska permafrost and the mean annual air temperature may have been colder than today because ice wedges were actively growing then; today they are, for all practical purposes, inactive" (Péwé 1975:120).

After 14,000 years ago much of the large megafaunal biomass began to disappear as shrub/tundra conditions replaced arctic steppe conditions.

The Wisconsin age vertebrate fossils of central Alaska are found in valley bottoms, within "retransported valley-bottom silt...rich in organic material" (Péwé 1975:97). These silts have been gradually moved downslope, and bones within them may also be concentrated "where small tributaries join large creeks" (Péwé 1975:98). The silts are perennially frozen, and were ultimately derived from loess deposited on hills (Péwé 1975:119) during the Wisconsin glaciation. The loess was windblown from "braided scantly vegetated flood plains" (Péwé 1975:119).

Cave Deposits

The second pertinent type of bone assemblage occurs in archeologic deposits excavated from northern caves. These assemblages, which are few in number, often contain unquestionable stone artifacts, although the association of bone, stone, and dated deposits may be uncertain. The sites discussed here are Trail Creek caves in northwestern Alaska, Bluefish caves in the Yukon, and Porcupine River caves in Alaska.

Trail Creek Caves

Two caves out of a number found in a part of the Seward Peninsula yielded broken caribou bones in front or inside of the cavities, and many stone, bone, ivory, antler, and wood artifacts. The stratigraphic conditions within the cave deposits were admittedly "far from good" (Larsen 1968:65), and a sediment stratification sequence was virtually impossible to formulate without many doubts coming to mind. Most of the artifactual assemblage belonged to Eskimo hunters of caribou, no doubt, perhaps dating no older than 2000 years. Some of the later artifact types were found to be intrusive into even older sediments, however, while a few older artifact types were found in upper sediments. The bones of <u>Rangifer</u> occur throughout the deposits; it should be noted that in Beringia <u>Rangifer</u> was an indigent both in Holocene and Pleistocene times. Microcores and other artifact types were found in lower levels of the Trail Creek caves, and their age has been estimated at no younger than 8000 years (Larsen 1968:72).

The earliest possible traces of human activity consisted of a broken bison calcaneus and a broken horse scapula from lower sediments in front of one cave. The horse bone was radiocarbon dated at 15,750±350 years; its presence in association with other bones in front of the cave led Larsen to suggest that it was broken by humans. He did not believe carnivores had dropped it there, since it lacked tooth marks. However, the part of a large scapula which will show tooth marks when carnivores gnaw (see Chapter 8) are the very parts which have been broken off the Trail Creek scapula (see Larsen 1968:figure 42, page 63); that is to say, the blade and the vertebral border of the blade are missing.

The bison calcaneus had been broken in a manner similar to that observed on <u>Bos</u> calcanei from a Danish Mesolithic site. The tuber calcis had been broken off the element; such a break is not common in many bone assemblages, although Larsen observed it on a surprisingly high proportion of bison and horse calcanei from central Alaskan muck-derived assemblages (Larsen 1968:62,63) (A small, camel-like animal's calcaneus had been broken in a similar manner in the assemblage of bones recovered from near Frederick, Oklahoma; these materials are controversial, and some specimens may be cultural in origin [Hay and Cook 1930]). Larsen suggests that the break was part of the butchering process, performed to separate the animal's foot from the rest of the leg without recourse to cutting.

Bluefish Caves

Two caves in the northern Yukon were excavated in 1978, 1979, and 1980 by Cinq-Mars (1978, 1979, 1980 pers. comm.; Irving 1978a; Workman 1980). Cultural material was sparse, and consisted of micro-chips, flakes, a burin spall, and a microblade. Most of the stone artifact inventory is thought to date to more than 12,000 years ago. Pollen and other paleoenvironmental data might indicate a maximum date on the deposits of over 14,000 years (Workman 1980). Bones of animals found at the site include many spirally fractured long bones, some of which also show abundant traces of carnivore gnawing (Cinq-Mars 1979:21). Species identified to date include fish, birds, *Lepus*, *Lemmus*, *Dicrostonyx*, *Microtus*, *Alopex*, *Vulpes*, *Mustela*, a canid, *Equus*, *Rangifer*, possibly *Alces*, possibly *Ovis*, *Bison*, and *Mammuthus* (Cinq-Mars 1979:19). I briefly examined the as yet unreported bone assemblage excavated in the 1979 field season, and saw a wide range of carnivore-inflicted gnaw-damage types. Most specimens appeared damaged similarly to the kennel pattern (see Chapter 4); that is to say, most of the bones had been gnawed by carnivores (large dog sized or slightly larger) possessing a great deal of leisure time, and possibly having a rich external (off-site) source of animal parts or bones. The source may have been a plentitude of ungulate corpses located very nearby, making it thus unnecessary for the carnivores to spend much time hunting or scavenging away from the lair or den; or may have been human keepers or would-be keepers providing body parts or bones to the denning animals. There are possible cut marks on some bones, but in my opinion most damage, including breakage, can be attributed without extravagant argumentation to animal gnawing alone (see Chapter 8 and Chapter 10). Cinq-Mars (1980 pers. comm.) thinks it possible that one cave was a living site (which, in my opinion may have had dogs or domesticated wolves also living there, or which may have been taken over by wolves after humans left the site), and the other cave was the site of an animal jump-kill in use several times. The bones were possibly gnawed by scavengers after humans abandoned them, or the humans' dogs (or wolf-dogs or wolves) gnawed the bones in the bone pile while humans feasted on the fresh meat from the kills.

Porcupine River Caves

Investigations of these caves have not been fully reported yet. Dixon and others have since 1978 investigated a series of cavities which occur in limestone outcroppings along the Porcupine River in Alaska (Dixon 1980 pers. comm.; Workman 1980). Over 50 caves were located, some of which proved to lack stratified deposits. A small number was tested.

Broken and unbroken mammalian bones were found in the sediments of three tested caves; species tentatively identified include Bison, Equus, Ovis, and possibly Alces. The agency which broke the bones of these Pleistocene animals may have been human behavior, or possibly some natural forces. Charcoal and a few unquestionable stone artifacts were found in one cave, but broken and unbroken bones of large mammals were found only in sediments lying below. No stone artifacts were found in any cave in unequivocal association with the bones of large, medium, or small mammals.

These cave assemblages are very meager and very scarce, although their scarcity may be due more to a lack of investigations than to a lack of existence of such materials within northern cave sites. In all cases, most of the large-mammal bones occur in lower levels of cave sediments, and include elements of Late Pleistocene species. The association of stone implements or other unquestionable features with the bones is either nonexistent or disputable. The bones as earliest components seem to underlie all good evidence of stone industries in the northern caves.

BONE ASSEMBLAGES FROM THE HIGH PLAINS

Introductory Note

It can hardly be disputed tha there did exist a geographically extensive archeologic entity that is called Llano or Clovis culture, and that humans which created parts or all of this culture (such as lithic materials) were in existence around 12,000-11,000 years ago (see C.V. Haynes 1964, 1967, 1969, 1970, 1975, 1978, 1980). The existence of a pre-Llano, megafauna-utilizing culture (see Humphrey and Stanford 1979) cannot as yet be accepted without reservations, as expressed, for example, by Stanford (1979b) or by C.V. Haynes (1975, 1980). Therefore it could be of importance to North American archeology to investigate possible genetic relationships or lack of them between Llano and the putative pre-Llano cultures and to analyze the distinctions between pre-Llano and Llano environments, techologies, site systems, and economies, differences which might indicate why there are or are not developmental bonds.

Observations:

Dutton and Selby

The Dutton and Selby sites in eastern Colorado were investigated by D. Stanford of the Smithsonian Institution (Stanford 1979a). These sites contain the sediments of a Late Pleistocene playa (at Selby) and a ponded stream channel (at Dutton) situated in topographic depressions 17 miles apart on the High Plains, between the north and south forks of the Republican River. Both sites contain stratified sediments attesting to probably over 17,000 years of infilling. The basal unit may be Peorian loess, with a soil formed at the top under conditions of water saturation most of the year. Some of the loess may have been redeposited as slope wash. Bones of camel, horse, and bison are found in random scatter within this layer. At the Selby site, a camel metapodial chopper (so-called by Stanford 1979a) was found articulated to a phalanx; this specimen had been broken and possibly cut when fresh, and exhibited possible wear polish and step-fracturing on what could have been the working edge, according to Stanford (1980 pers. comm.). The age of the loess may be greater than 17,000 years and less than 29,000 years (Stanford 1979a).

Mammalian bones are also found in overlying lacustrine sediments, which were laid down at both sites during episodic pond-filling and drying periods. These clays and sands are laminated, and occasionally show minor channel cutting and filling but under conditions of low fluid velocity. The bones are scattered and considered to have been possibly butchered. Several possible bone tools such as chopper types possess polished and rounded edges, step fractures and abrasion on possible working edges, and possible cut and chop marks, which are also present on other bones that are not thought to be tools. Species identified include mammoth, horse, camel, bison, sloth, peccary, deer, antelope, and smaller species. Bones were found concentrated in basin erosional features. Stanford postulates a series of kills were made by humans at the Selby site over a long period of time (Stanford 1979a). The estimated age of the lacustrine sediments is 17,000-12,000 years b.p. (Stanford 1979a, 1980 pers. comm.).

Over the lacustrine levels at Selby is a gleysol formed during a drier period of the pond's existence. This level contains butchered and piled mammoth bones, but there are no stone or bone tools <u>in situ</u>. Several mammoth bones are broken, and one mandible shows a deep cut. Other species found include horse, camel, and bison. At Dutton there is also a similar paleosol formed after the pond was drying. Collagen from mammoth bone taken from this sedimentary unit has been radiocarbon dated at 11,710±150 years b.p. and 7880±150 b.p. This unit at Dutton contained a Clovis point, as well as stone flakes and bone fragments, although preservation was poor. A thick Holocene soil lies atop the paleosol at Dutton, formed on saturated sediments after full glacial retreat.

Stanford (1979a:107) attributes the random scatter of bones to possible carnivore activity and possible depositional disturbance (Stanford 1981 pers. comm.). He considers human behavior to be a type of carnivore activity. Because many instances of human butchering activities create <u>patterned</u> bone arrangements rather than random arrangements, it is possible that 4-legged carnivores may have scattered bones after humans or other carnivore created the site. The fractured long bones appear to have been broken before aging <u>ex vivo</u>. There are impact marks (see Chapter 10) on some specimens, which lack apparent gnawing damage. Few carnivores are represented in the faunal assemblage. There are over 2 dozen bone flakes in the collection.

It is inferred that the sites were located in plains type grasslands, subject occasionally to periods of aridity (Stanford 1979a). The Peorian loess may have been laid down during a time when local temperatures were lower than at later times; temperatures averaged perhaps 2-4°C lower over the year during the deposition of the lacustrine levels. The loess was derived from surface deposits laid down by distant, large silt-laden rivers (Butzer 1971:364), most likely originating from glacial meltwater streams and other enlarged river beds. During later times, when lacustrine deposits were laid down, there may have been a decrease in evaporation <u>without</u> an increase in levels of yearly precipitation, accounting for the creation of lakes and ponds in what would otherwise be considered semiarid areas (Butzer 1971:373-374).

Cooperton

The Cooperton mammoth site in Oklahoma consists of some bones of a young mammoth which are concentrated in an area about 2 meters by 3 meters. Lower leg bones are missing from the assemblage (Anderson 1962, 1975). Radiocarbon dates on bone apatite (the fraction of the bone tissue that may be more easily contaminated than the collagen) are 19,100 ±800, 17,575 ±550, and 20,400 ±450 years. Within the bone concentration area, several rocks and boulders were found, their weights ranging from 400 grams to nearly 9 kilograms. The rest of the deposit containing the bones consists of sands, silts, and clays. The site investigators consider it unlikely that a 9 kilogram boulder could have been washed into the bone mass by the action of water, while at the same time some of the much lighter bones and bone fragments found at the site were not washed away.

Both humeri were fractured at the distal end. Both femora, tibiae, one radius and ulna, the left half of the pelvis, both fibulae, and the upper parts of the humeri were missing from the deposit. One scapula was fragmented, and the one radius at the site was also broken. The fracturing of the bones possibly occurred when the elements were fresh (Bonfield 1975). I have only seen the few photographs of the bones published in reports, but I personally do not think the fracturing was necessarily done when the bones were fresh. This of course is only an opinion.

Mehl (1975:166) attributes fracturing of the ribs and vertebral processes to scavengers. He also proposes that many of the bones at the site were originally "hand placed" (Mehl 1975:168), or stacked up unnaturally.

As an alternative interpretation of the skeletal remains as having been modified by human activity, C.V. Haynes (pers. comm. to D. Stanford, communicated to me 1981) thinks that the boulders and cobbles may have naturally washed into the bone deposit from sediments located on steep slopes almost directly above the site. Scavengers may have removed some elements at the time of the mammoth's death, and some of the remaining bones may have been fractured by natural processes, after which the large rocks tumbled into the bone mass. It is also conceivable that the falling rocks contributed to the fragmentation of some elements.

Lamb Spring

The Lamb Spring site, which is located 1.6 km. from the South Platte River in Colorado, is a partially-infilled topographic depression which in Late Pleistocene times had been a boggy area around a spring vent (or number of vents) and overflow channels. The lowest levels of the site contain silty clays over an aquifer. In the clays are found broken and unbroken mammoth bones, and some scattered elements of horse, camel, bison, and smaller species (Wedel 1965). Some of the bones had been broken and flaked when fresh. Broken or modified camel bones were also found, including a cut and shaved phalanx (Wedel 1965). It is my opinion that the shaving or abrasive smoothing occurred after fossilization, since the exposed cancellous bone is somewhat lighter in color than the rest of the unmodified cortical bone. A 15 kg. boulder was found in the deposits near a broken mammoth bone (Stanford 1980 pers. comm.). This rock is too large and heavy to have been transported into the finer grained sediments by water action; it may have been carried there by people to use for breaking the mammoth bones. A radiocarbon date on collagen from mammoth bone is 13,140 b.p. (Wedel 1965). Since dissolved lignite was also found in the aquifer, this date may be open to question as being possibly too early (Stanford 1981 pers. comm.). There are no hearths, stone tools, or wood charcoal in the lowest levels of the site.

Unit 2 above these levels contains a bison bone bed, radiocarbon dated at 7870±240 years b.p.; these bones are possibly the remains of a Cody Complex killsite. An Eden point fragment was found at the edge of the bone bed, and a "deviant Scottsbluff" was also found, possibly in the same sedimentary unit (Wedel 1965). Archaic cultural materials are found in overlying Units 3 and 4, and Woodland materials are found above them.

Llano Sites

The following sites were studied to gain some ideas of the differences between Llano and the possibly pre-Llano entities: Miami in Texas (Sellards 1938, 1952), Dent in Colorado (Figgins 1933; C.V. Haynes 1966, 1967), Naco in Arizona (Haury 1953; C.V. Haynes 1964), Lehner in in Arizona (Haury et al. 1959; Saunders 1977, 1978,), Union Pacific in Wyoming (Irwin 1970), Domebo in Oklahoma (Leonhardy 1966; Leonhardy and Anderson 1966; Mehl 1966), Blackwater Locality No. 1 in New Mexico (Haynes and Agogino 1966; Hester 1972), Escapule in Arizona (Hemmings and Haynes 1969) (this animal may not have been utilized after it died with two Clovis points in its flesh), Murray Springs in Arizona (Haynes and Hemmings 1968; C.V. Haynes 1979), and Colby in Wyoming (Frison 1978). The Angus finds from Nebraska have not been considered here because there is question about the age of the remains (the species of proboscid is apparently too ancient for Llano) and about the genuineness of the crude Folsom-type point found at the site (Strong 1932).

For all Llano sites (those which contain mammoth bones and stone tools) there are a few obvious trait similarities. All but one site contained some bones of a least one mammoth. Some sites contained elements from several different animals. Bones or teeth of immature animals were present at most sites. All mammoths had apparently died at places where water would have been standing or flowing from time to time, although not perennially in all cases. All sites contained some bone elements which were either still in articulation, lying nearly in anatomical order, or concentrated, suggesting limited post-mortem disturbance to some parts of the mammoth carcass. Yet most sites contained incomplete skeletons, due possibly to cultural or erosional disturbances. Most sites contained debitage or stone tools other than projectile points, although the lithic inventory was quite small for each site except Murray Springs. Radiocarbon dates ranged from 4952±304 to 11,630±400 years b.p. Most dates were in the range of 11,000 to 12,000 years.

Llano versus Pre-Llano

It is possible that prehistoric Llano peoples in the southwest of the present day United States were mammoth killers, and not merely scavengers of mammoth carcasses. That is, these peoples might have been capable of driving, ambushing, stalking, or attacking proboscids, and killing them in pre-arranged places. The killing of large proboscideans is not beyond the capacities of primitive human groups (see, for example, descriptions in Holman 1967; R. Cooper 1914; Sikes 1971; Macphail 1930; Janmart 1952; Hebbert 1925; Lyell 1924). A scavenging human group, on the other hand, would have been able to make little effort to kill unless a prey animal were encountered that was already dying. Llano peoples may have occasionally scavenged, but it appears that they were more likely and more often killing predators. This is suggested because the stone projectile points which were found at some sites may have been lost deep within tissue of the carcasses' rib and spine areas, which are not probable places to stick points if they were lost during butchering rather than insertion during killing. In addition, the carcasses appear to have been utilized before decomposition, wild animal scavenging, or bone disarticulation took place, since the presence of semi- or full articulation at many sites indicates that ligaments, tendons, and other soft tissues still held bones together at the time of site abandonment.

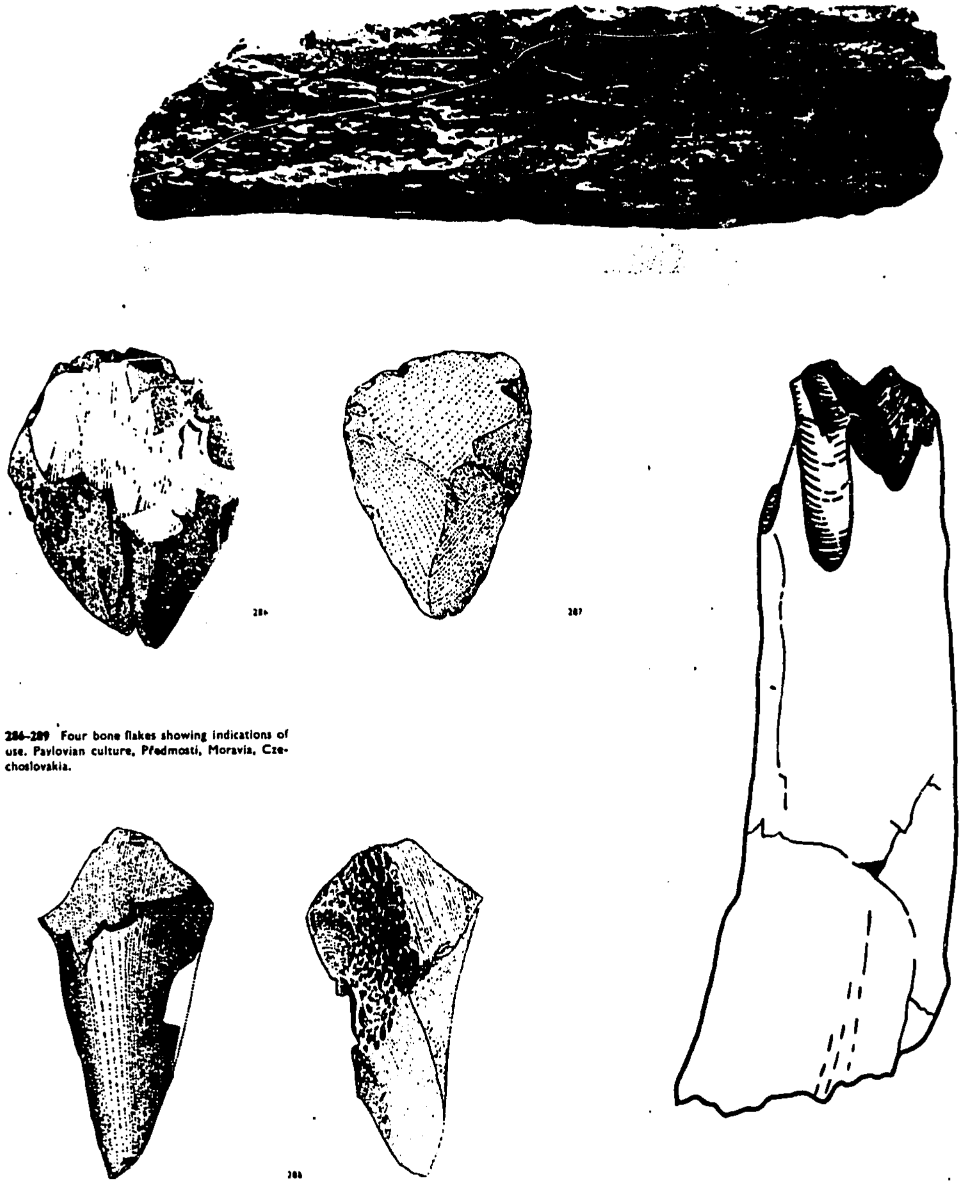
Many of the long bones at pre-Llano sites were broken up when they were fresh (that is, before fossilization). Such breakage occurs on proboscidean long bones at some indisputable Llano sites, but certainly not so extensively or expectably. The only Llano site with abundant (reported) broken bones, the Union Pacific site (Irwin 1970) lacks diagnostic artifacts such as Clovis points. (Cook [1931] reported on broken mammoth and bison bones which may have been cut and abraded by humans when fresh, but these specimens were found on ground surfaces [in blow outs] of the U.S. Southwest, in areas where "Folsom" points had been discovered, and may not be contemporaneous with the points.) Disarticulation of remaining elements at Llano sites is oftentimes very limited; that is, while many joints have been disconnected and many bones have been taken out of anatomical order, nonetheless there are often body parts or associations of body parts remaining at the site. At the Dutton and Selby sites mammoth bones in the lacustrine levels are scattered and isolated, while in the overlying, Clovis-bearing gleysol at Selby there is evidence of bone stacking and sorting (Stanford 1979a:107). There is apparently a more complete sorting through of the mammoth carcass and much fuller utilization of all body parts in most pre-Clovis -age assemblages than is usually seen in Clovis assemblages.

Unfortunately, there are no data available on the rate of decomposition of proboscidean bones, so it is not possible at this time to state how fresh the mammoth bones must have been to have fractured as they did.

Discussion

The flaking or breaking of bones for tool manufacture is postulated or rather well documented for several time periods and in many places throughout the world; for example, from Plio-Pleistocene age in Vallonet Cave (Plate 2, bottom right) (deLumley et al. 1963a, 1963b), from nearly 1 million years b.p. in Olduvai Gorge (Plate 3) (Leakey 1971), from 300,000-400,000 years b.p. in Ambrona and Torralba, Spain (Biberson 1964; Howell 1966; Freeman and Butzer 1966; Biberson and Aguirre 1965), from 4000-5000 years b.p. in Siberia (Okladnikov 1964), from recent or subrecent age in South Africa (Deacon 1976), from unspecified subrecent (neolithic) age in Ceylon (Deraniyagala 1958) (Plate 4, bottom), and from Mousterian "age" in Spain (Freeman 1978) and elsewhere in Europe, especially eastern Europe (Klima 1954, 1963; Absolon and Klima 1977; Jelinek 1976). However, these examples are not ideal analogues for the North American sites or collecting localities, because the New World bone assemblages are not accompanied by other evident and closely associated archeological materials, such as stone debitage, tools, or hearth rocks. All other postulated flaked bone assemblages in the world have been found associated with such unquestioned artifactual items. If the North American materials can be shown to constitute a legitimately defined technological industry (in the sense of Tixier 1974:15: an industry consists of objects of a single type of raw material obtained by the actions of humans on the specified materials), then these assemblages might be completely without precedence.

If the bones are indeed technological items and not accidents of nature they would be evidence of a previously unrecognized hunting-gathering economy operating in habitats that lack modern analogs, and



286-289 Four bone flakes showing indications of use. Pavlovian culture, Předmostí, Moravia, Czechoslovakia.

Plate 2. Bone flakes and possible tools from Paleolithic sites in Europe.

TOP: Part of fractured long bone from Pekarna Cave, Czechoslovakia.

BOTTOM LEFT: Bone flakes from sites in Czechoslovakia.

BOTTOM RIGHT: Fractured and possibly worked bone from Grotte du Lazaret, France.

All illustrations from Jelinek (1976).

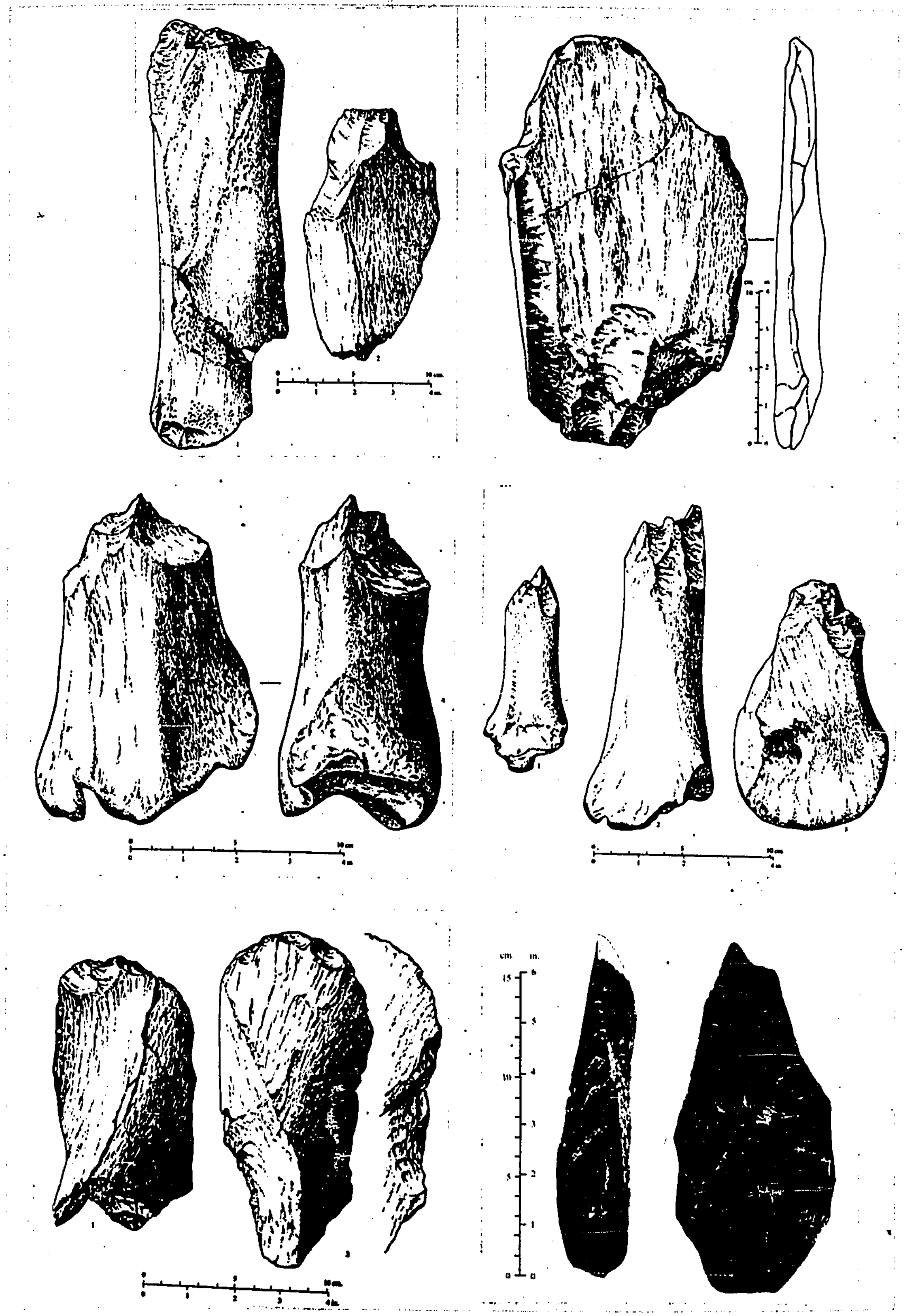
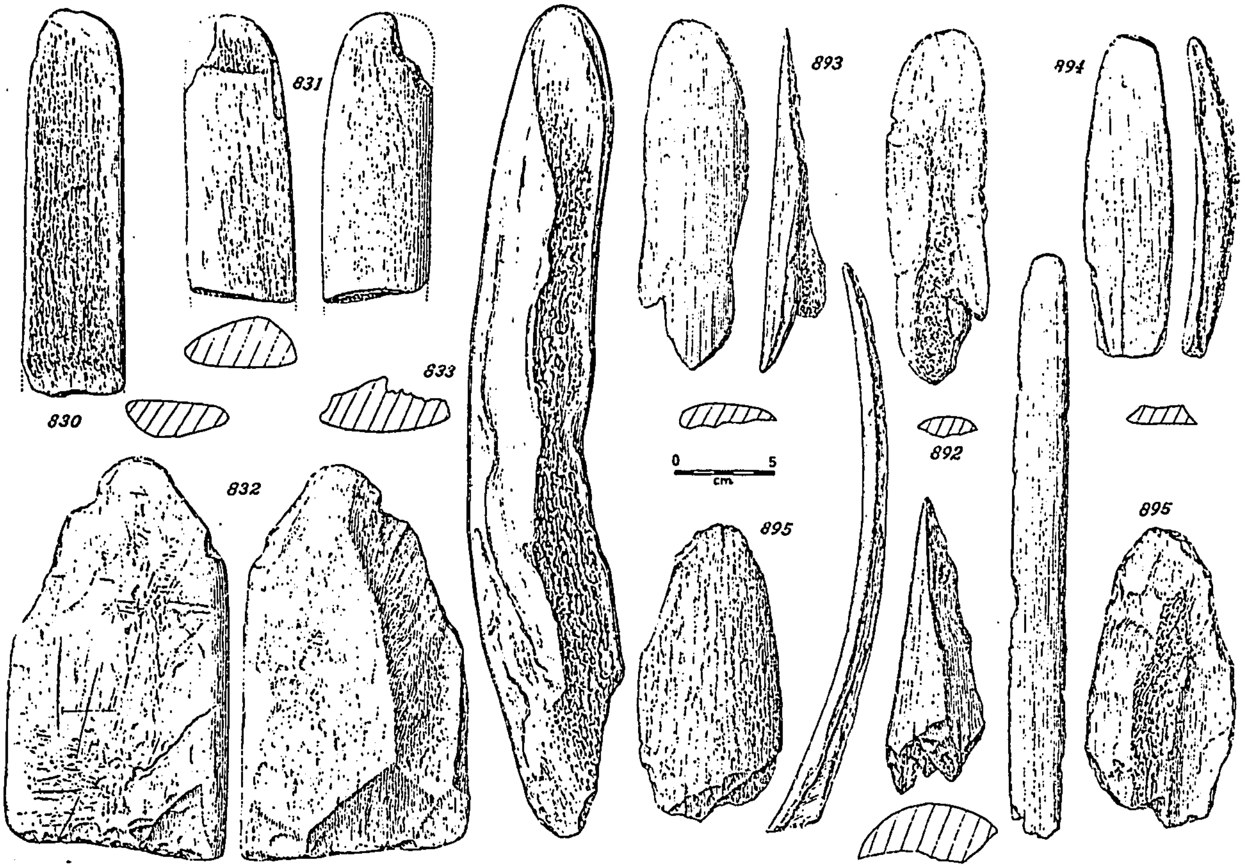


Plate 3. Fractured and flaked bones from Olduvai Gorge, Africa. All illustrations from Leakey (1971).



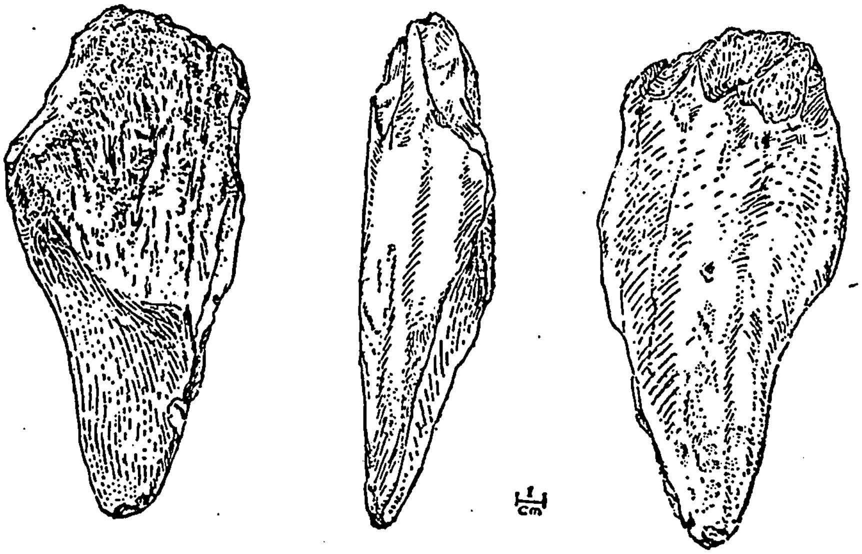


Plate 4. Bone flakes and possible tools.

TOP: Mammalian bones that have been flaked, and bones that have been abraded and smoothed along fracture edges. Specimens from Upper Paleolithic site (Dolni Vestonice). Illustration from Jelinek (1976).

BOTTOM: Elephant bone flake from Neolithic site in Ceylon. Illustration from Deraniyagala (1958).

operating in a manner that also lacks ethnographically described analogs. It is possible that the bearers of this postulated bone technology were the first immigrants into North America out of Asia, and it is possible that they were familiar with advanced techniques of flint-knapping but were occasionally impelled to replace stone with bone as raw material, due to local scarcities of cryptocrystalline rock. Some of the bone items are bifacially flaked and may show traces of platform preparation, as well as a relatively sophisticated mode of flake removal control (using previous flake scars and dorsal ridges to control the shape and direction of new flake removals). Possibly the bone flakers of the Colorado sites and the Yukon were members of a big-game hunting tradition that later floresced as Llano culture in other geographic regions where there were adequate or familiar sources or knappable stone, or possibly the bone flakers were pre-existing populations who were not necessarily predisposed to develop specialized technological and subsistence adaptations such as Clovis-type point manufacture and mammoth killing. Perhaps these earlier peoples used stone much more than bone in their economic activities, but discarded only the bone tools and debris in localities where stone was scarce.

If the dates from the Yukon are correct (that is, if humans were leaving traces of their activity over 50,000 years ago), then it is also conceivable that the bearers of this postulated bone technology were not _Homo sapiens sapiens_. These peoples may have been members of another subspecies of modern humanity not of the fully developed _Homo sapiens sapiens_ line nor of the Neanderthal lineage. No Neanderthal hominines have been discovered east of Uzbek Soviet Socialist Republic or north of south China (Jelinek 1976; Butzer 1971), so there is at yet no indication that Neanderthal or neanderthal-like peoples were moving very far east in Eurasia.

Of course, some prehistorians dismiss the idea of a bone-flaking technology simply because humans have been known to prefer stone tools (or at least they seem to lose or discard them in large numbers) even during extremely early times in prehistory. One might wonder why the bone-flaking technology was so suddenly and utterly abandoned if the bearers of the tradition were ancestral to later peoples, unless the early peoples only considered the technology an exigency reaction to unfamiliar conditions. There are plenty of archeological cases which demonstrate that humans can exist in geographic regions that lack knappable stone, and they survive by acquiring stone from outside the region and using their implements parsimoniously. Humans and stone tools are closely linked in the archeological record for hundreds of thousands of years, and to some archeologists it may hardly be logical to expect human groups to sacrifice the superior efficiency and reliability of stone implements by switching their full technological attention to animal bones.

PROBLEMS OF INTERPRETATION: CHOOSING ANSWERS TO TAPHONOMIC QUESTIONS.

One of the major goals of archeology is to interpret the material remains of past human behavior within the context of historical development and environmental limitations. The sites and assemblages described above have been interpreted by some prehistorians to be manifestations of cultural activities such as animal slaughter, butchering, and processing. However, other prehistorians disagree with these interpretations, and regard the bone materials as having been modified mainly by noncultural agencies, such as geomorphic forces (for example, frost-heave or slope wash) or living forces (carnivore gnawing, trampling by ungulates, or so forth). A number of questions can be asked about the materials, and when systematically replied to may provide enough weight to favor one or the other alternative interpretations.

Taphonomic Questions

Pre-Llano

(1) How did bones of mammoths and other species get into waterhole sediments? Were living animals killed there or did they merely die there? Were bones washed there or carried there by animals?

(2) Why are the bones distributed as they are, with some missing? Is it the result of carnivore or scavenger actions? Is it the result of water action, spring flow, ice-rafting, or trampling dispersal?

(3) Why are some bones damaged as they are, and others not? Is the damage due to trampling, animal feeding, water and/or wind abrasion, marrow extraction, tool manufacture, frost-heave, or sediment loading?

(4) Why were bones buried and preserved as found?

Llano

(1) How did the bones of mammoths get into the water hole sediments, with stone tools and/or projectile points in association? Were the animals driven there and killed? Or did they die there, and were later scavenged by Llano peoples?

(2) Why are some bones missing, while others remain in anatomical order? Is it due to water action? Spring flow disturbance? Human removal? Scavenging by animals? Was post-mortem disturbance minimal? Was each mammoth carcass frozen and thus tended to remain undisturbed (at least

the downside did)? Was freezing quick?

(3) Why are some bones damaged as they are and arranged as they are? Could it be due to marrow extraction? Scavenging by humans or animals? Erosion? Trampling? Weathering? Freeze-thaw cycling? Ice-rafting?

(4) Why are the bones buried as they were? Why were they discovered or exposed? Was burial fast?

(5) Why are some sites different and others similar?

Central Alaskan valley silts

(1) How did bones, carcasses, and mummified carcass parts get into the creek valleys? Are they floodplain accumulations? Lake bottom assemblages? Are they possibly all from winter deaths, accounting for their preservation? They are in different stages of decomposition, so does that mean they are year-round deaths?

(2) Why are some bones disarticulated, and others still frozen in tissue, and others in concentrations? Is water action responsible? Are fresh carcasses being reworked into sediments containing old carcasses? Were predators rare at some times, and plentiful at others, accounting for the differential degrees of carcass utilization seen on different carcasses?

(3) Why are some bones fractured and/or flaked, and others not? Is it due to scavengers? Different taphonomic histories? Human action? Trampling? Ice action? Why are some bones water-worn, others not? Is it due to Frost-heave? Sediment load? Why are some bones gnawed, others not? Is it due to different times being represented, and thus different predator-prey ratios?

(4) Why are some bones buried, jumbled, and preserved?

Cave deposits

(1) How did the bones of horse, bison, caribou, and mammoth get into caves or cave front sediments? Were scavengers denning there? Were humans living there? Or is it due to water action or slope wash?

(2) Why are the bones so distributed, with only body parts represented, and so much disarticulation? Were old carcasses being scavenged? Were animals denning in the caves in summer, and scavenging winter deaths or kills? Is the deposit a midden from human occupation?

(3) Why are some bones damaged as they are, others not? Is it due to carnivores? Humans? Rock-falls Frost-heave? Trampling?

(4) Why are the bones preserved and buried?

Old Crow

(1) How did the bones get into the deep sediments? Are they lake bottom accumulations? Buried middens from human activity?

(2) Why are they all disarticulated? Were they reworked thousands of years ago? Were they midden type deposits from human activity? Is there evidence of scavenger activity?

(3) Why are some bones broken and flaked? Is it due to human activity? Animal activity? Ice actions? Water action? Trampling? Freeze-thaw?

(4) Why were the bones exposed?

Are These Questions Answerable?

Answers to some of these questions could conceivably be found from a review of ecologic literature. The way bones accumulate, the way they are modified, and the ways they are preserved are many and varied.

How did any of the bone assemblages originally come together? In some cases, the bones may have derived from groups of animals that died en masse, while in other cases the bones may have been redeposited by water action long after the original dates of death of the animals. True, undisturbed death assemblages ideally are bone accumulations created and affected only by the conditions that killed animals. There are many natural conditions that could cause bone accumulations; treatment in the literature of any one of these conditions has been superficial and scant. Almost no experimental or observation studies have been performed on catastrophic terrestrial death assemblages, such as those caused by floods, drought, or fire.

Catastrophic Assemblages

Drought conditions may cause animals to concentrate at water sources, where they might die in large numbers (Leuthold and Sale 1973; Shipman 1975; Sinclair 1977). Corfield (1973), describing the pattern of elephant carcass distribution during an especially severe drought in east Africa in 1970, noted that carcasses were concentrated near water courses, where sediments would be most likely to bury and preserve the bones.

Fires have at times wiped out whole herds or large groups of ungulates. Cole (1954) notes a letter written by Ziba Smith Tuttle from Ft. Laramie, Wyoming, dated 30 June, 1850, referring to observations made on a trip between Council Bluffs and Ft. Laramie in May of that year:

> A slope of the prairie burned and it had killed hundreds of buffaloes. We saw as many as 300 lying together with the hair all burned off them while many were roaming around deprived of their eyesight by the fire.

The bones of these unfortunate beasts would most likely have shown no signs of burning.

Snowstorms might also catastrophically destroy large numbers of gregarious animals (see Garretson 1938:70). J. Allen (1877) notes a letter from E.W. Nelson of St. Michael's, Alaska, dated 11 July, 1877, containing information given by two men who came into the Yukon district across the mountains of British Columbia by way of the Mackenzie Basin. These men descended the Peace River and portaged at 118° longitude directly north to Hay River, which they descended to Great Slave Lake in 1871. They were surprised to see "thousands of buffalo skulls" and old game trails that were a half-meter to a whole meter deep, leading east and west, which they encountered on the portage. Local residents (perhaps Indians) told them that large numbers of buffalo had been killed about 50 years before by a heavy and sudden snowfall that dropped over 4 meters of snow. However, as will be discussed in Chapter 9 of this dissertation, it is doubtful that the bones of skulls would have survived 50 years on the ground surface in this area.

Drowning events may be particularly destructive of animal life, especially for herding species. Masson (1889) extracts John McDonnell's journal entry noting the bodies of 400 drowned buffalo passed during the day on a canoe trip along the Red River in 1794. The carcasses "lay on almost every point, huddled together" (McDonnell in Masson 1889:289). In May of 1795, McDonnell observed in one day on the <u>Riviere qui appelle</u> 7360 buffalo which were "drowned and mired along the river and in it." The carcasses in places lay "three to five files deep on shore" (Masson 1889:294). In 1801, Alexander Henry observed "great numbers of dead buffalo...drowned in attempting to cross [the Red River?]" while the ice was weak (Henry in Coues 1897:174). "Entire herds" of drowned buffalo drifted by Henry's trading post that spring, March through April; some of the bodies lodged on the banks or formed thick jams in the current. By mid-April, when most of the ice on the river had thawed or broken up, drowned buffalo were still drifting by (Coues 1897:175).

Ebert (1946) observed nine dead bison frozen in the ice of the Yellowstone River in February, and thought that they had broken through soft ice while crossing a 30.5 meter wide channel. The bodies lay within a circle of about 18 meters diameter. By early March the river had opened a new channel, and the carcasses were still visible but strung out in the river ice and water.

Tempany (1974), S. Cooper (1974), Lyster (1979) describe accumulations of bison carcasses in the aftermath of an enormous flood in Wood Buffalo National Park, in 1974 (see Chapter 5, this dissertation). In Sweetgrass Creek, Tempany observed 241 carcasses of drowned bison floating or lodged in trees within a 3 - 4 km. stretch. The flood occurred 25 April - 5 May; by 1 August, the carcasses were reduced to "bones and clinging white sludge and...[were] extremely putrid" (S. Cooper 1974:2). Lyster (1979) believed that 3000-4000 bison died in the 1974 flood, out of a total of 8000-9000 animals wintering on the affected range. An earlier flood in 1961 also killed an estimated 3000 animals (Novakowski 1961).

Martinka (1969) found 40 elk carcasses frozen in the ice of St. Mary Lake, Glacier National Park, Montana. The carcasses lay in a group forming a rough circle about 20 meters in diameter, and they had probably been floating when solidly frozen; that is, the elk were long dead before their bodies were frozen in the mass. A herd travelling from one part of their winter range to another had most likely broken through weakened ice in February, and the animals had drowned or died of exposure and exhaustion. In the following summer about two dozen carcasses floated to shore, where black bears and eagles fed on much of the carrion.

Fay and Kelly (1980) reported mass walrus mortality in the St. Lawrence Islands during Autumn, 1978; hundreds of animals, mainly females, young, and fetuses, died most likely from traumatization during haulout onto beaches. Many haulouts occurred on beaches where walruses had not been found for 40 or 50 years.

Incremental Assemblages

Some kinds of lake-bottom bone accumulations may result from more than one episode of deaths, such as predator killing over several months (see D. Miller 1975, 1979 for discussion of winter wolf predation of caribou on a frozen lake in Saskatchewan; also see Haynes 1981 in press and Chapter 5, this dissertation for discussion on winter wolf predation of whitetail deer on Minnesota lakes).

Swamps or boggy habitats may be appealing to some animals; Murie (1934) observed on Isle Royale National Park several cases of moose bones and carcasses in bogs and mineral licks, possibly the remains of old or weakened animals unable to extract themselves from mud. Dying elephants, too, have been thought to retire to secluded and wet habitats, there to perish in the water or mud (see Sikes 1971:222; Mathiesson and Porter 1974:55).

Ashe (1808:47) noted that in what is now northwestern Pennsylvania buffalo and other native ungulates habitually used licks, springs, bogs, and ponds, and at times mired themselves in the mud. Early travellers in the North American west often commented on the litter of bones seen around many salt and sulphur springs (see Stoddard 1812:349; Ashe 1808: 188, 291; W. Cooper 1831:158, 164).

Scotter and Simmons (1976) reported on the discovery of a cave in Nahanni National Park, Northwest Territories, which contained the bones of 93 Dall sheep, all found well beyond the daylight zone. The animals probably did not enter at one time as a single group. Small groups or solitary sheep may have intended to shelter temporarily during severe winter weather, but then became lost in the cave's darkness.

It is generally thought that tarpits might trap large numbers of animals, including ungulates and predators. Recent active oil seeps have been observed to contain fresh carcasses of rabbits, birds, and other small animals. The bones of many much larger creatures are abundant at Rancho La Brea, California; these bones most likely derived from ordinary alluvial sediment accumulations, on floodplains or in channel deposits, which were preserved in tar seeps. In other words, the larger animals did not perish in tarpits (Miller and Peck 1979), but instead died on land surfaces or in rivers or wherever, and their bones ended up in tarpits (for earlier opinions on the origins of the deposits, see Matthew 1913; Merriam 1911; Howard 1960; and for a major re-analysis of the origins of the tar assemblages, see Woodard and Marcus 1973). The Pleistocene age asphalt pits at Binagady in the Soviet Union may have been reed-fringed pools whose mud trapped herbivores and carnivores over a long period of time (Vereshchagin 1967a). Redeposition by moving water may have been rare, although a few bones have been polished by sand or water (Vereshchagin 1967:131).

Unique death traps may be found in certain parts of Central Africa. Verschuren (1965) documented the existence of natural toxic gas discharges around pond or earth vents, which are often surrounded by animal carcasses and bones. The remains of rodents, monkeys, birds, reptiles, carnivores, even hippopotamus and elephant have been found at these loci.

For more information on carcass accumulation see Roe (1970:154-203) and McHugh (1972:436-446) who discuss natural agencies which have been known to kill North American bison.

Unusual Assemblages (Catastrophic or Incremental)

Reed _et al_. (1979) observed several instances of mule deer falling down a sheer bank cut, which was the result of highway construction interrupting a migration trail. In one instance four deer fell 15.5 m to their death, while in another instance three fell to their death. The drop was abrupt, with loose turf and soil leading up to the edge of the dropoff. The deer were most likely habitual springtime users of the trail, or springtime followers of an established trail, who did not notice the sheer falloff. No more deaths were reported after the second spring following completion of the cut. While this is not an example of a naturally caused death assemblage, the circumstances do suggest the possibility that some animals are less observant than others, and might perish _en masse_ in certain types of terrain. In a similar vein, an Eskimo told Diamond Jenness (1928:68) that he had seen wolves driving a caribou herd towards a distant cliff, an observation similar to that recorded by Sir John Richardson in the same territory. In neither case was the base of the cliff inspected for the presence of bones.

Natural Trap Cave in Wyoming contains a 20,000 year stratigraphic record of animals which fell to their death into the deep cavity from the grasslands and steppe-tundra above (Gilbert et al. 1978).

The Hot Springs, Nebraska, site (Agenbroad 1978) contains the remains of at least 15 mammoths, and possibly three times that many more, which entered the steep-walled karst sinkhole over 20,000 years ago, and perished there unable to scale the banks and escape. The sink was possibly filled by a spring-fed pool, which may have originally attracted the animals. Isolated teeth from other mammalian species were also found in the sinkhole deposits, but they may have been derived from sediments that washed off adjacent land surfaces during Late Pleistocene times, brfore the sink was filled.

Kills made by humans would of course cause animal bones to accumulate. There are innumerable examples in the literature of mass or incremental animal slaughter sites, dating back into relatively early Pleistocene times (see, for example, Pidoplichko 1953; Howell 1966; Miller and Dort 1978; Frison 1970, 1974; Wheat 1972; Albanese 1977; Davis and Wilson 1978; Reher and Frison 1980).

Selective and Biased Accumulations

Ultimately, the maximum number of bones input into a depositional environment is controlled by the local abundance of animals (hence, of course, abundance of their bones) accumulating in biased or unbiased death assemblages, degree of carnivore destruction or dispersal (that is, dispersal into other and perhaps more destructive environments), proximity of bones to the final depositional environment, and degree of possible dispersal by moving water (Behrensmeyer 1975). Larger or heavier bones are not transported by water as easily or as far as small and light bones. Secondary stream channels may be filled with bones, while faster flowing primary channels are scoured clean; backwaters and slack-water deposits may contain more smaller bones than do channel areas. Behrensmeyer (1975) reasoned that floodplain, delta, and channel deposits would contain diagnostically different bones because the capacity of moving water during the formation of deposits in each of these types of environments varies characteristically, and differential bone sorting occurs.

Carnivores are a major factor in bone input variation because small bones and bones of small animals will be sooner destroyed, hence small creatures or delicate body parts of larger creatures will be under-represented where carnivores are abundant or are especially active.

Carnivore or rodent dens and lairs may commonly contain selected bones of scavenged or killed prey animals. Bearder (1977) discusses densite accumulations of spotted hyenas living in woodland habitats; Brain (1967, 1976a, 1976b) discusses assemblages gathered by porcupines and leopards; Sutcliffe (1970) discusses bones found at spotted hyena densites; Dart (1956) argued vigorously that hyenas do not accumulate bones at dens or anywhere else, but instead eat them all; Haynes (1978a) described some of an assemblage produced by grey foxes and denning rodents in a small Virginia cave; Mills and Mills (1977, 1978) describe bones collected by spotted and striped hyenas at breeding dens; Plug (1978) describes the distinctive bone collecting patterns of six different species of south African vultures. Binford (1981 in press) describes accumulations of bones in northern Alaskan wolf and fox dens and lairs; Haber (1977) lists prey animal bones found at a number of

Alaskan wolf dens as observed in different years; Kuyt (1972) briefly mentions prey animal representation at wolf dens in barren ground (tundra) habitats of Canada.

DISCUSSION

It has been postulated that humans broke some of the animal bones found in late Pleistocene deposits of pre-Llano age, in northern caves, in perennially frozen silts, in the Old Crow Basin sediments, and in the central High Plains; many hunting peoples have been ethnographically documented as utilizing bone marrow by breaking open bones (see, for example, Yellen 1977; Jenness 1928:65-66; Brain 1967; Binford 1978), so that the practice is not merely speculation. Mohl (1972) discusses ways that marrow-splitting techniques might differ when the bones of different prey species are involved, such as reindeer and red deer, the latter of which has bones that are 2/3 thicker than the bones of the former. According to Mohl (1972:12-16) the commonest reindeer-bone splitting technique found in Greenland assemblages of 3000 years age is chopping off of bone ends, followed by removal of marrow from the remaining long bone tubes or cylinders. The usual technique for red deer bones is the splitting of whole shafts lengthwise by striking a series of blows along the element (see Troels-Smith 1960: plate 3, a split metatarsus of a red deer, from an early neolithic site in Denmark). Noe-Nygaard (1977) also distinguished breakage techniques in different site assemblages, although she attributed the differences to cultural development. Other researchers have discussed long bone breakage as a patterned and deliberate activity by humans; see, for example, Sadek-Kooros (1971) on sheep metapodials that she considered broken for tool manufacture; and Lyell (1863) on

Swiss Lake Dwellings and Danish shell mound bones that he thought broken for marrow extraction.

There are no ethnographic examples of humans breaking proboscid bones for tool manufacture, or at any rate there are no unambiguous references to such a practice. There are,however,reasons to believe that such fragmented bones would have been functional items in carcass dismemberment and processing (Stanford _et_ _al_. 1981 in press).

Many bone assemblages contain broken long bones, even those assemblages that are thought by most researchers to be noncultural in origin. Dall (1887:165) described bones from the Alachua clay beds in Florida thus:

> The appearance of the bones suggests that the animals were mired and then torn to pieces by predatory carnivora. Ashes and burnt clay were found under some of the bones at Hallowell's Ranch, but there is no evidence of human agency in this. The fire was probably due to lightning, an everyday occurrence in Florida at the present time. The longitudinal splitting of the long bones sometimes observed may often be the result of the penetration and growth in the hollow of the bone of roots which might afterwards decay and leave no sign.

According to Warren (1852:150,151), the bones of a mastadon receovered from a layer of peat that lay over marl in Orange County, New York, still retained some organic matter and were nearly as elastic and tough as Recent bones. It is conceivable, if the description by Warren is correct and not exaggerated, that these bones, if they were subject to violent natural disturbance such as saltation in swiftly-flowing streams swollen by the addition of melted snow, could have been spirally fractured thousands of years after their original date of deposition.

Similarly, Barbour (1925:108) describes the bones of a mammoth found in a clay in Oak Creek, Nebraska, as being "black, perfect and tough as modern bones, and splinters of them are elastic." Some of the larger bones such as the skull and one humerus had suffered pre-burial breakage and removal of parts, while other elements such as the thinner scapulae had been preserved "without blemish" (Barbour 1925:106).

Vereshchagin (1953:63-64), discussing natural Late Pleistocene accumulations of bones of bison, rhinoceros, horse, proboscideans, and deer found on beaches of the central Volga River Valley, explains the "breaking up and splitting of the ancient bones...by the action of ice, tearing them off frozen ground, and by blows from snags [in the river]" (translation my own) (Plate 5). Vereshchagin (1967b:381) attributes the Russian plain and eastern Siberian bone layers in alluvium and the beach accumulations of bones to catastrophic death episodes in the Late Pleistocene.

Hansen et al. (1978:104) reported on a mammoth find in Marion County, Ohio, at which broken long bones, fragments of long bones, and fragments of vertebrae were collected, some of which had "nonrecent broken edges," due to preburial breakage. The date of death for the animal was probably early postglacial times.

W. Cooper (1831:158) described Big-Bone Lick, Kentucky, as an area of several salt springs and freshwater springs which contained "quantities of bone almost exceeding belief." "The quantity of fossil bones... is truly wonderful." He described damaged elements thus (W. Cooper 1831:164):

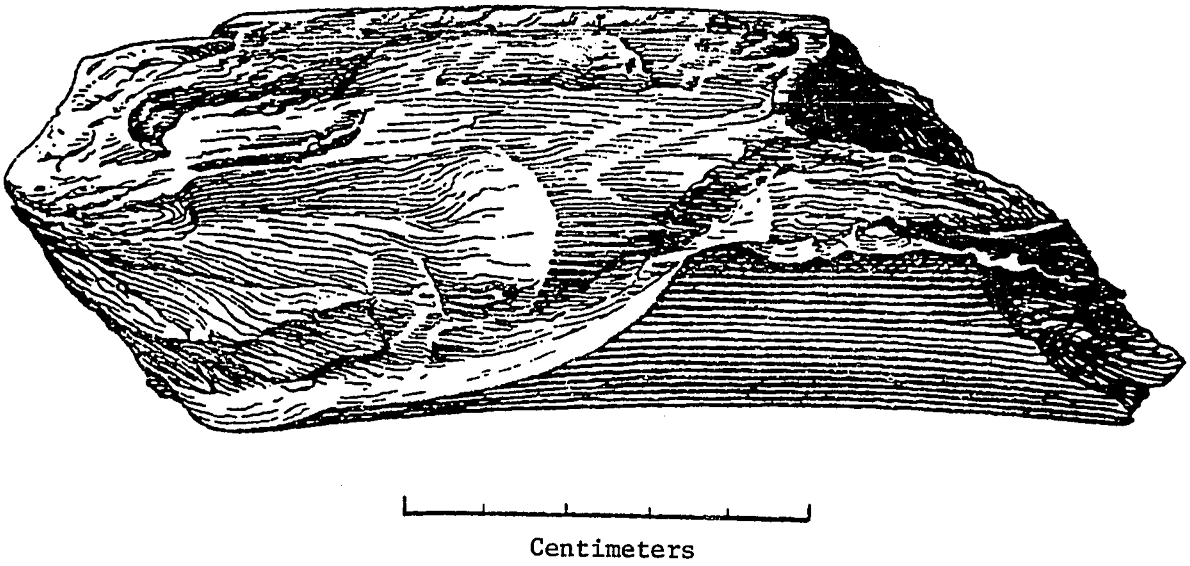


Plate 5. Fragment of tusk of mammoth (Mammuthus sp.) recovered in northeastern Siberia, possibly flaked and broken by the action of river ice. Illustration from Vereshchagin (1977).

> ...numerous fragments, not requiring empirical notice, but like the rest, indicating, by their shattered condition, the violence they were exposed to, before their final deposition at this spot. Some appear to have been a little rubbed, but the broken edges are generally sharp, and the surfaces unscratched.

"Seven humeri [collected in 1830 are] all mutilated, and very imperfect..., [one] consists merely of the condyles, others are no more than the shaft of the bone, with both ends broken off" (W. Cooper 1831: 168).

Briggs (1838) described the type locality of Parelephas jacksoni (the genus designation is now Mammuthus) in Jackson County, Ohio. Broken and unbroken bones at the site were found buried in a lacustrine sand, marl, and clay stratum exposed in the banks of Salt Creek, near the water table. The bone layer contained preserved botanical remains as well. "These bones, from their position, had evidently been subjected to some violence before they were covered with the stratified deposits" (Briggs 1838:97).

Fowke (1928:486) notes that nearly all the mastadon and other bones which he observed at the bone bed of Kimmswick, Missouri, were broken and scattered; he proposed that most bones had been retransported by water to the site.

Merriam (1911:212) remarks on the occurrence of broken and destroyed large herbivore bones found at Rancho La Brea deposits in California; he attributes the breakage to struggling by newly-mired victims of the tarpits and to trampling by ungulates.

Several other possibly noncultural sites of mammoth, mastadon, and other large animals in North America contain broken elements (see Thomas 1952; Goldthwait 1952; Wood 1952; Skeels 1962; Sinclair 1904;

Putnam 1906; Merriam 1906; Ray *et al*. 1967; Pace 1976; O'Brien 1978; however, some of these assemblages could contain evidence of human activity). There is also a small number of reported North American proboscid sites which are interpreted as being culturally affected. Four such sites contain broken bones and partially or wholly disarticulated skeletons of single mastadons -- these are the Manis site in Washington state (Gustafson *et al*. 1979), the Rappuhn site in Michigan (Wittry 1965), an unnamed site in southeastern Michigan (Fisher 1981), and the Willard mastadon site in Ohio (Szabo *et al*. 1978; Falquet and Haneberg 1978). In my mind, questions remain as to whether or not human behavior was responsible for all bone modifications at these sites.

Humans might logically remove certain bones from prey carcasses, especially those elements which support bulky or inconveniently-shaped masses of meat. Humans might also dismember carcasses, remove hide or meat from the isolated disarticulated units, break bones to remove marrow or oily trabecular bone, then abandon bones within task areas or standardized disposal areas. Carnivores might fracture and remove bones during primary feeding or during secondary scavenging. Prey bones might be broken, scattered, or arranged in various ways, depending on the numbers and body sizes of carnivores present. Herd animals might kick bones when moving over carcass sites, thus scattering or fracturing elements. Trampling might bury some bones deep in mud, while others that are unburied might lie on the ground surfaces and deteriorate at a much faster rate. Seasonal temperature fluctuations in cold environments might contribute to bone breakage, since water expands as it freezes, and water that is contained within bone pores or structural spaces might periodically freeze and thaw.

Buried bone fragments in cold environments might be subject to cryoturbation effects as ground sediments react to freezing and thawing processes. Frost-heaving upwards might occur to bones that are buried in the soils of cold areas, and fracture-edges that were once sharp could conceivably be abraded smooth by rubbing against sediment particles. Physical and chemical weathering of unburied or buried bone fragments could also conceivably round once-sharp fracture edges, as of course could the use of these fragments by humans as scraping or cutting tools. Wind- or water-borne sediments could smooth and polish fracture edges, or might scratch bone surfaces. Even earthworms burrowing into unfrozen sediments could move buried objects within the soil matrix (Darwin 1840; Atkinson 1957).

Since all or most of these potential factors of breakage, dispersal, or modification would have been present at each assemblage site discussed above, it might seem to be too difficult a task attempting to distinguish in every case which factors were responsible for which effects, if an interpreter were to use only the available literature. One could decide that all the animal bones were naturally accumulated by carnivores or flood deposition, or that all bones were culturally accumulated. All might have been naturally broken, polished, or scratched; on the other hand, all might have been culturally modified. Perhaps some bones suffered several processes of alteration.

It is of course possible to interpret the bone materials using only the available literature reports (such as Bonnichsen 1973; P'ei 1938; Sutcliffe 1970; Hill 1975; and so forth). However, there are no available systematic descriptions of wild carnivore utilization of prey carcasses, wild carnivore damage to prey bones, trampling damage inflicted by wild ungulates, or edge-rounding produced by water, animal trampling, or weathering, among other processes. Therefore, it appears that archeologists lack a sufficient data base upon which to found interpretations of altered bone materials. Even if an expanded data base were made available, it is possible that no amount of fact gathering will ever entirely eliminate the possibility that interpretations of altered bones will many times still be equivocal, since several different processes of natural or cultural bone modification may create a similar or identical alterations to single bones or whole assemblages. Yet at the present time it appears that much more information about natural bone-modifying agencies is needed before interpretations become more judicious or more than merely personal opinion.

IV. Studies of Bone Gnawing by Captive Animals

My main aim in this part of the research was to observe animals gnawing on fresh bones in order to formulate models of gnawing by particular species. These models would include such information as typical sequences of bone part damage, typical lengths of time required for specific types of damage to be inflicted, length of time the bone is of interest to various species, types of damage inflicted when several animals gnaw, and so forth. If there is consistency and patterning in feeding behavior and resulting damage to bones, then there should be typical sequences of damage to bones or typical forms of damage. There is a great consistency in the data, as became apparent, and there is usually a distinctive consistency which exists for each gnawing animal family and for each bone element that is gnawed. Thus, not only are there very regular attributes associated with carnivore-gnawed bones (attributes which could conceivably be compared to attributes of bones modified by humans in order to differentiate the agencies of modification), but there are also patterned characteristics which can be sources of information about the gnawing animals themselves.

PREVIOUS RESEARCH

A number of researchers concerned with the problems of distinguishing carnivore gnawing damage from modifications due to other agencies such as human activity have fed animal bones to captive carnivores, and then described the resulting damage. Buckland (1822, 1824) was one of the earliest scientists to have published his observations, which were re-popularized a half century later by Dawkins

(1874). Buckland watched a captive spotted hyena feed on cow bones; the fragments left over from the feeding were damaged in ways very similar to the damage on bones found in ancient cave deposits from Britain and continental Europe (Buckland 1822; 1824:38 and Plate 23). Buckland considered this as evidence that hyenas had originally accumulated the fossil bones in many caves.

More of the same kinds of observations were published by P'ei (1932, 1938, 1939), who had worked closely with the Abbé Henri Breuil studying materials from Choukoutien cave deposits associated with remains of Sinanthropus (now termed Homo erectus). P'ei fed bones from a pig and a small ruminant to rats and to a small and a large dog; he then interpreted modifications to bones in several prehistoric Chinese assemblages. Like Buckland, P'ei presented not just an element-specific attribute system: that is, he did not restrict himself to interpreting only those prehistoric pieces similar in all respects to his recently-observed specimens, but instead isolated sets of attributes from possible and observed carnivore gnawing damage in general. Thus, even damage on elements that he had not fed to the dogs, such as rhinoceros long bones, could be interpreted if that damage possessed some of the analytic attributes distinguished during his experiments with the dogs.

Breuil (1938, 1939) made distinctions between bone broken by carnivores and bone broken by man. However, any empirical or experimental data to support his interpretations of Lower Paleolithic bone assemblages were apparently not reported.

Zapfe (1939), writing near the end of an extremely innovative period in German paleontology, also described horse and cow bones gnawed by captive carnivores, and then interpreted fossil bones which showed characteristics similar to those on the recent specimens. But Zapfe's work was published in German, and P'ei's major work was published in French; the first observational studies generally available in English were by George Miller (1969, 1975). In 1973 Bonnichsen, also in English, published an attribute list in a form perhaps more useful than P'ei's. Guilday (1971a) briefly mentions an experiment in which he fed beef bones to his beagle-sized dog, in order to see how canine scavenging might affect mammalian bones and bone part frequencies.

From time to time observations have been published on bone damage done by wild carnivores or other animals. The best known of these studies might be the report by Sutcliffe (1970) on hyena gnawing damage and bone accumulations. There are also brief reports available on bone chewing by hoofed animals (for example, see Brothwell 1976; Sutcliffe 1973 and 1977; Kelsall 1957; Sekulic and Estes 1977). Reports on rodent gnawing are rarer (see P'ei 1938; Haynes 1978a,b). Most discussions of rodent gnawing damage are interpretive, not empirical (see, for example, Breuil 1938, 1939; Harrisson and Lord Medway 1962:337; Bouchod 1974b). These discussions are in effect guesses that rodents created certain modifications, yet these references have become established as reliable guides or analogues for further interpretive analyses of similar damage seen in other bone assemblages.

Two common responses to published observational data on bone gnawing have been a stubborn refusal to alter earlier opinions that human workmanship is always self-evident, or a defense of such earlier opinions as being fair and discriminating. Dart (1964) thought that he and Breuil could fairly distinguish human from animal workmanship of bone, whereas P'ei (who actually observed animals gnawing on bone specimens, and subsequently published his data [1938, 1939]) could not. Yet Koby (1964), writing in the same volume as Dart (1964), could see no certainty in the criteria used conventionally to define agencies of bone breakage.

For paleoecologists who have never done experiments in carnivore gnawing, it is difficult to recognize carnivore damage in many more cases than it is relatively easy to recognize it, because most instances of carnivore gnawing damage have never been illustrated. Carnivore tooth marks, which may not always be present on carnivore-gnawed bones (see Koby 1964: plate 1; Haynes 1981 in press: figure 7), do not always unmistakeably look like tooth marks. Besides, in some cases tooth marks may occur in assemblages that have been culturally produced or modified in the first place, and thus all marks on the bones could be wrongly interpreted as culturally-produced.

METHODS AND MATERIALS

Twenty-three selected species of carnivores, rodents, and primates at the National Zoological Park in Washington, D.C., were fed whole, fresh long bones of cow (*Bos taurus*) that had been commercially slaughtered less than 72 hours before. All bones had been stored in coolers (not freezers), and their moisture content and mechanical properties were probably not significantly altered by aging such a short time *ex vivo* (See Sedlin and Hirsch 1966). These bones varied in size and degree of epiphyseal closure, but the probable age of most cows was around three to four years. Ligaments had been cut to separate joints, and most muscle tissue was trimmed off, but the articular ends and shafts of the bones were never cut or chopped. Most or all periosteum remained on the bones. All bones were examined before being given to the carnivores, so that I could eliminate bones that had been damaged in butchering. Occasionally older bones that had weathered at least two years (and were thoroughly degreased) were fed to some individual carnivores and rodents.

The elements used most often were femora and tibiae; I occasionally used radius-ulna units and humeri. Whenever a whole femur was used, there was usually a sawn-off tibia proximal end articulated to it, without patella, and whenever a whole tibia was used there were usually tarsal bones, an astragalus, and a calcaneus articulated, and usually the sawn-off proximal half of a metatarsal, too.

Bones were fed to animals housed in cages and in indoor or outdoor enclosures which varied in size and construction. Several of the species (cats and hyenas) had regularly received bones in their zoo diet. All animals showing interest in bones were fed at least three different specimens. All bones were recovered by me from cages and enclosures after the animals no longer exhibited interest, except in the case of spotted hyenas, which always exhibit interest in bones or anything else that will fit into their mouths or can be made to fit into their mouths. All bones given to spotted hyenas would probably have been entirely consumed within a few days unless fresher bones were given them. When a number of bones had been given to the hyenas, any one of the bones could be gnawed and eaten at any time, but single bones were seldom gnawed to the exclusion of others.

I spent several hours observing all individual animals gnawing (see Table 4-1), most of which time was spent on Kodiak bears and spotted hyenas. Total hours of observations were divided almost evenly between winter 1977-78 and spring 1979.

Table 4-1

Experimental bone feedings at the National Zoo:

Species	Number of animals with access to bones	Number of bones	Hours of observation
Macaca silenus Lion-tailed macaque	6	1 fresh	0.25 hours
Macaca sylvanus Barbary ape	8	1 fresh	0.25 hours
Ammospermophilus l. leucurus Antelope ground squirrel	2	1 fresh	0.25 hours
Cynomys parvidens Utah prairie dog	6-7	1 fresh 1 dry	0.15 hours
Microtus ochrogaster Prairie vole	1	1 fresh	---
Acomys sp. Spiny mouse	6	1 dry	---
Atherurus africanus Brushtailed porcupine	1	2 fresh 1 dry	1.5 hours
Hystrix cristata Crested porcupine	3	1 fresh 2 dry	0.30 hours
Capromys pilorides Demarest's (Cuban) hutia	2	1 dry	0.30 hours
Canis lupus Grey wolf	2	5 fresh	0.30 hours
Fennecus zerda Fennec fox	6	1 fresh	0.15 hours

Table 4-1
continued

Experimental bone feedings at the National Zoo:

Species	Number of animals with access to bones	Number of bones	Hours of observation
Vulpes macrotis nevandensis Kit fox	2	1 fresh 1 dry	---
Helarctos malayanus Malay sun bear	3	3 fresh	0.25 hours
Tremarctos ornatus Spectacled bear	3	2 fresh	0.50 hours
Ursus arctos European brown bear	2	2 fresh	0.45 hours
Ursus arctos middendorffi Kodiak bear	3	11 fresh	3.25 hours
Ursus americanus Black bear	1	2 fresh	0.25 hours
Ursus maritimus Polar bear	2	2 fresh	---
Martes p. pennanti Fisher	1	1 fresh	---
Crocuta crocuta Spotted hyena	2	15 fresh	1.05 hours
Panthera l. leo	8 cubs	2 fresh	0.25 hours
Atlas lion	1 adult	1 fresh	0.25 hours
Panthera onca Jaguar	2	3 fresh	0.15 hours
Panthera t. tigris Bengal tiger	2	3 fresh	---
TOTAL	74 animals	67 bones	9.85 hours

Besides gathering data from these zoo studies, I have also used comparative data gathered during my field studies of wild wolves. These latter studies are reported more fully in Chapters 6, 7, 8, and 10; in brief, I have been locating in northern North America fresh carcasses of adult bison, moose, and deer, most of which have been killed and fed upon by packs of wolves. These carcasses will be revisited for a number of years so that gnawing damage and bone dispersal can be monitored and documented. Carcasses of bison, elk, deer, antelope, and moose that have died from other causes, such as disease, drowning, or old age, are also being regularly monitored.

Concerning the captive animals, two points must be noted: (1) Some gnawing behavior may be as much a reflection of boredom and object-centered play as of actual species-specific inclinations to feed on bone. Captive animals are probably seldom hungry, and may at times behave eccentrically due to an overabundance of leisure; (2) captive animals may lack the well-developed muscular strength of the jaws that wild counterparts possess (Ewer 1973:34 [footnote]) although captive animals sometimes compensate for weakness by chewing longer on individual bones. However, even wild carnivores will gnaw longer on bones while in home or socializing sites than while in actual killsites or consumption sites peripheral to the killsite. In general, actual damage done by wild carnivores in certain circumstances is very similar to damage done by captive carnivores of the same species, since the capacity for gnawing (that is, the shape and mechanics of jaws and dentition) is very similar.

The major differences between gnawing by captive carnivores and gnawing by wild counterparts are due to (1) differences in motivation (hunger or an urge for exercise), and (2) differences in amount of soft tissue available on the bones. Stripped, disarticulated bones do not present the same gnawing problems as do fleshed and articulated carcasses; yet, upon comparison of specimens gnawed by many wild and captive animals, it is apparent that the main resulting gnawing differences are usually minor. The order in which bone parts are damaged may vary slightly, and certain parts of the bone may not be damaged when there is no muscle tissue covering them, but overall the resulting gnawed specimens are quite similar.

CARNIVORES

Introduction

For this part of the research, the recording of certain aspects of carnivore feeding behavior was of lesser importance than the recording of other aspects. For example, some wild carnivores feed socially, so that many of their prey's skeletal parts would be affected by several sets of teeth. But since most zoo animals were separated from other animals when fed, it was not always possible for me to record the effects of social feeding on bones, unless I circulated specimens among individuals of the same species. Most carnivores in this part of the study displayed no interest in bones that were over one day old, or that had been mouthed by other animals. Therefore, during the experiments with captive animals I was mainly concerned with dental differences between species and individuals, and with how these specific dental and muscular differences affected damage to bones gnawed by single carnivores.

Generalized differences in dentition among families of carnivores are presented below. These brief summaries are based mainly on my observations of several hundred skulls and mandibles in Smithsonian Institution collections (Department of Vertebrate Zoology, Division of Mammals), but references are given for supporting discussions in biological literature.

Canidae (wolves, coyotes, foxes, dogs)

Modern canids typically have long skulls and well-developed, heavy duty carnassial teeth (last upper premolar and first lower molar) that function mainly to shear and slice muscle and skin. Canid molars behind the carnassial teeth on upper and lower jaws have grinding and crushing surfaces that interlock when the mouth is closed (Ewer 1973:36; Romer 1945:375). The canine teeth are large and robust (Figure 1). In wolves there is a well-developed sagittal crest atop the braincase, so that the temporalis muscles are more powerfully directed and attached; these muscles act to close the jaws.

Ursidae (bears)

Bears are characterized by elongate canine teeth, reduced or absent first three premolars, poorly to undeveloped carnassials, and broad, flat, wrinkled, tubercular crowns on molars, reflecting their mixed and mainly herbivorous diet (except in the case of polar bears, which are entirely carnivorous) (Walker 1964). The last or third molar is lacking, but the remaining two are long and carry large grinding surfaces (Romer 1945:375). In polar bears the dentition is somewhat modified; cheek teeth are comparatively higher and sharper (Kurten 1968). Generally in bears sagittal cresting is apparent but not well-developed, and the muscles of jaw closure are developed differently than in canids.

Hyaenidae (hyenas)

Spotted hyenas have probably the most powerful jaws in proportion to body size of any living mammals (Buckland-Wright 1969; Walker 1964:1265). They have large, broad carnassials and relatively blunt but thick canines. Only a tiny molar remains of the upper postcarnassial teeth (Romer 1945). The skulls of spotted hyenas reflect advanced development of masticatory muscles, facilitating seizure and crushing of food, especially bones; and of nuchal muscles, facilitating carrying of heavy prey (Buckland-Wright 1969). All muscles and teeth are huge in relation to the short, round heads, and there are no grinding platforms on cheek teeth.

Felidae (tigers, lions, jaguars, etc.)

Cats are the most specialized carnivores, with comparatively short and high skulls (Romer 1945:371) and few cheek teeth. The canine teeth are extremely large and powerfully proportioned, and premolars are sharp and pointed like carnassials. The carnassials themselves are well-developed into ridged cutting teeth, honed sharp by wear. There are no grinding surfaces on the teeth. There is only a tiny first upper molar behind the upper carnassials. Robust bone architecture and strong cresting reflect powerful development of jaw and neck muscles.

Observations: Gnawing Behaviors

Anyone who owns a dog will probably have seen it gnawing bones while standing up or while resting in a prone position (chest to the ground). There is also a transitional posture, chest to the ground but rear end still standing. Captive and wild wolves gnaw in these upright and prone positions; captive hyenas also display both postures. The transitional position may or may not be displayed, depending probably on individual predispositions. Large cats most often eat while lying chest to the ground (see Becht 1953:512). Bears may sit upright, lie on their chests, rest against walls, or assume a number of other postures while gnawing.

It appears that with canids and hyenas the standing gnawing position is a true, hungry, feeding posture. It may involve holding the bone down with forefeet while using the teeth to pull or slice off tissue.

On the other hand, the prone gnawing position and the transitional, rear-half-standing position seem to be associated with less ravenous and more sustained gnawing, possibly a pastime or leisure activity unto itself.

When bones are fresh, hyenas and wolves eagerly gnawed while standing. After up to an hour or more of this kind of gnawing, the bones may be temporarily abandoned or may be brought into a sheltered den for sustained gnawing by bears, hyenas, wolves, and cats. Bones brought into dens oftentimes are carried out again by wolves, hyenas, and bears, so bone redistribution is an ongoing process with those species. Some bears, such as Kodiak bears and Spectacled bears, moved bones around for days, but other bears such as Black bear and Malay Sun bear tended to ignore bones after eating most of the adhering soft tissue and the softer bone parts.

In general all carnivores use cheek teeth to eat hard parts that have some soft tissue cover, such as cartilage-covered epiphyses, while incisors and canines are used to tug or pull off soft tissue such as muscle or periosteum. I have several times observed captive wolves, bears, and hyenas deftly peeling strips of periosteum from long bone shafts by use of the incisors and a paw holding down the bone.

In many cases large cats such as the Atlas lion for several days show no interest in bones that have been placed in their cages, then very suddenly eat much soft tissue off the bones and create heavy gnawing damage. Such behavior may be a captivity eccentricity, although it seems congruous with popular reports about normal feeding behavior of some large cats who wait for fresh meat to ripen before eating it (see Corbett 1946 on Tigers).

My observations and analyses of specimens gnawed by large cats, wolves, bears, and hyenas have been organized and synthesized to produce descriptions of gnawing sequences for femora and tibiae from animals whose body weight exceeds 250 kg. Scapulae and vertebrae may not suffer damage in closely predictable, patterned sequences, judging by my observations of wild wolf feeding behavior. However, even when there is no predictable sequence of gnawing, the final damage is usually patterned. Humeri are damaged in similar sequence by canids, bears, felids, and hyenas: the tuberosities are eaten off, then the ball-shaped head is gnawed and broken off the shaft. Only occasionally is the distal end gnawed. Gnawing damage on distal condyles usually occurs during secondary scavenging rather than during immediately post-mortem feeding.

Examples of Bone-Gnawing Behaviors

Some observations of gnawing behaviors are presented here; these observations are of particular bone specimens gnawed by individual captive carnivores.

On 17 April, 1979, at 9:00 A.M., I presented one whole, fresh Bos tibia to the female hyena and another to the male hyena. Both specimens had all ankle bones articulated, as well as half the metatarsal, the distal end having been sawn off at mid-shaft..

At first both animals held the bones across their mouths between their cheek teeth, and carried them away from me. Next they both began pulling soft tissue off the shafts, using their incisors while holding the bones down with paws. Both animals remained standing. Next they both began using cheek teeth to grind and audibly crunch distal epiphyses. The incisors and canines were occasionally used at this point to scrape soft tissue off the compact bone.

The female peeled a strip of periosteum off the length of the shaft, using her incisors. At 9:35 A.M. both hyenas were gnawing on proximal ends. Next they began tussling over the specimens, with each animal claiming both as its own. Finally, at 9:50 A.M. each hyena was again gnawing on the distal ends of each tibia. By about 10:00 A.M. both proximal and distal ends were equally gnaw-damaged, with gouging and scoring of cancellous tissue.

I returned three days later to find the entire proximal end of one specimen broken off, leaving jagged edges on the shaft; the other tibia had suffered only some scoring of the proximal articular edges. By 23 April the shafts of both bones were broken.

On 23 April I gave the hyenas two femora. At 10:05 A.M., five minutes after I handed the bones through the bars of the cage, one hyena had gnawed off the greater trochlear rim on one bone, and the other hyena had removed half the greater trochanter on the other bone. The female hyena was gnawing the trochlear rims one at a time at various angles, with loud crunching noises. Most of the time her cheek teeth were drawn across the trochlear rims at right angles (Figure 2). At 10:10 A.M. the male had removed all the greater trochanter on his specimen, and had scooped out the stump. The female meanwhile had removed both trochlear rims and was scooping out the area with her cheek teeth. Both hyenas were gnawing while standing up. In another two minutes the male began to switch from proximal to distal end and back to proximal, while the female switched to a more persistent grinding away of the greater trochanter on her bone. The male began spending more time trying to pull soft tissue off with his incisors, while the female gnawed whole epiphyseal ends. At 10:25 A.M., both animals took their bones into their den.

Bears reacted to bones in various ways, at times indifferently and at other times enthusiastically, although the time of day that I gave them bones was rather consistent. Therefore, the length of time that had passed since they had eaten did not seem to have much to do with their reactions.

On 24 April I gave one whole femur and one tibia/ankle/metatarsal unit to the European brown bear male, an animal over 20 years old. He carried the femur into his den and did not emerge. When the bone was recovered three days later, gnaw damage was minimal.

On 24 April at 11:10 A.M. I gave one tibia unit and one humerus/radius-ulna unit to a female Kodiak bear, who carried the tibia unit into her dry moat, out of view of visitors to the exhibit. She left the bone there and returned to the humerus unit, but walked away from it indifferently. The male Kodiak bear, who had been moving towards the bone, then veered away and retrieved the tibia unit from the deep moat, and also picked up the humerus unit; he carried both units in one forepaw to the wading pond, walked in up to his throat, dunked the bones, then waded out and into his den, still carrying both units in his paws. Both bone units were eventually recovered with slight gnaw-damage.

Bears generally gnawed while sprawled on rump and sides, or while seated against rocks. The bones would be held in or under one or both forepaws, and incisors would be used at first to pull off soft tissue. Grinding of epiphyses with cheek teeth was also seen, but bearing down did not appear to be as hard as it did with hyenas. The female Kodiak bear vigorously gnawed some specimens (Figure 3), using her incisors and cheek teeth, often sustaining hard grinding with her cheek teeth. This particular animal was observed banging a tibia against the rocks until it broke; in actuality she was pulling off soft tissue from the shaft, using her incisors and pushing the bone forcibly away with one or both paws. As the soft tissue tore off or slipped through her teeth, the bone would of course be pushed hard to smack against the rocks she lay on. The bone eventually fractured. In another instance, after she had broken the tibia mentioned above, she carried a tibia to the dry moat, which is a 4 meter deep ditch surrounding the outdoor enclosure, and deliberately (?) dropped the bone down into it, afterwards walking down the steps and retrieving some of the pieces. I recovered most fragments from both fractured specimens. The bear did not repeat these behaviors with any more specimens.

Observations of Gnawing Damage

One underlying proposition is that when captive animals gnaw single, disarticulated bones, they produce nearly the same types of damage as so wild counterparts gnawing articulated prey parts. This proposition has been generalized from observations of 65 femur and tibia units gnawed by captive animals, and from observations of 18 moose skeletons and 50 bison skeletons from carcasses originally fed upon by wild wolves. Thus, I have examined more than 100 tibiae and 100 femora to arrive at these generalizations. It is possible that my sequence models for bears, hyenas, and felids will be in error when compared to the results of wild counterparts' gnawing of whole prey carcasses, because the addition of muscle, ligaments, and tendons to bones somewhat changes the pattern of feeding and bone damage. The differences will not be plentiful or

Figure 1. Right cheek and canine teeth of male Timber Wolf captured in north-central Canada.

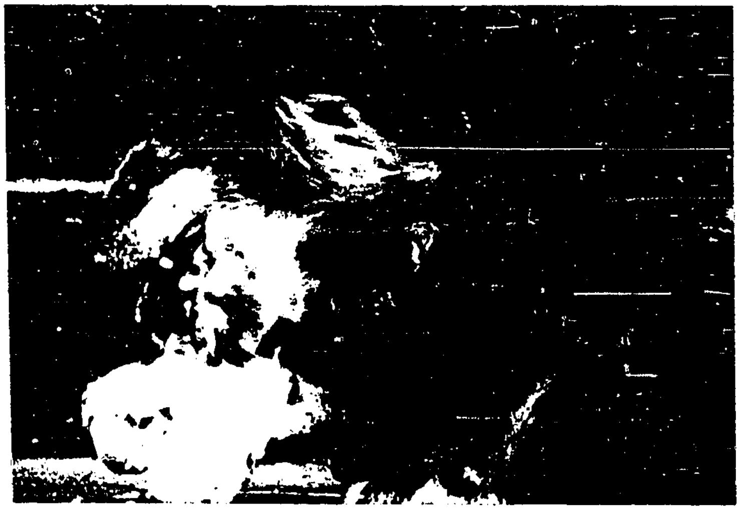


Figure 2. Female Spotted Hyena at the National Zoo gnawing trochlear rim of a Bos femur.

Figure 3. Female Kodiak Bear at the National Zoo gnawing a Bos tibia.

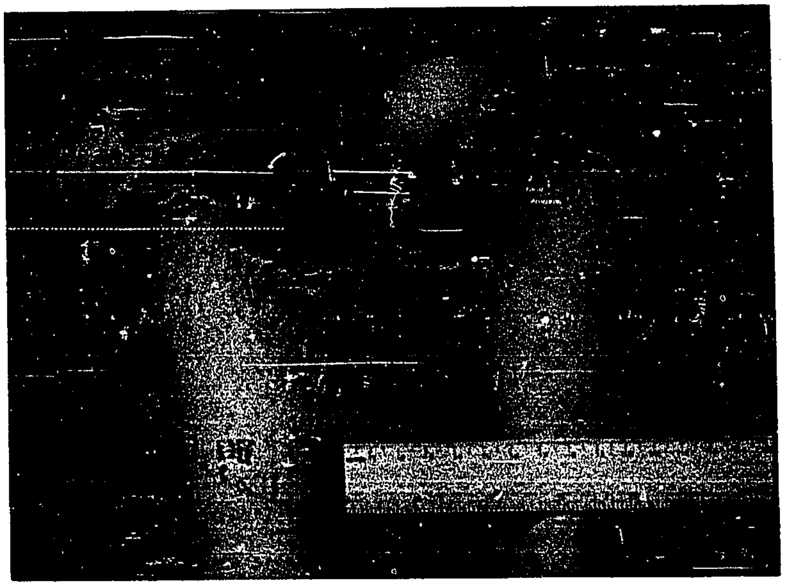


Figure 4. Bison femora gnawed by wild wolves.

critical.

Femur: Hyena Gnawing:

First stage: Upon receiving a fresh Bos bone, a spotted hyena attempts to bite and pull off all soft tissue. Within 10 minutes the greater trochanter has been partially removed, and the stump is scored and faceted. The larger trochlear rim has also been scored by cheek teeth. In this stage scoring generally consists of scrapes and impact depressions on the bone surface, about the size of moderately-worn cusps of cheek teeth, measuring close to 1 cm. x 2 cm. Smaller or larger sizes are also possible, although less common when adult hyenas are involved.

Second stage: This is a stage of sustained gnawing on hard tissue. The greater trochanter has been half removed and the cancellous interior has been scooped out nearly down to the diaphysis of the bone. Both trochlear rims have been removed anteriorly, and the cancellous bone there has been gouged out to a depth over 2 cm.

Third stage: Sometimes the femoral head is nearly gnawed off, and its articular surface may be scraped once or twice by teeth (see Haynes 1980a: figure 5, center specimen). The trochlear area is well-gouged, and only the most distal of the condyles on the posterior side of the bone remains.

Fourth stage: Sometimes the entire proximal epiphysis has been removed, including the greater trochanter and the head. The diaphysis has now started to be pulled apart, fragment by fragment, and these variably-sized shaft pieces may be ignored, bolted down outright, or may be well-chewed by the hyena. Only one distal condyle (usually the medial condyle) may remain. If the femur is at an actual killsite, I would expect it to be abandoned before reaching this stage. However, if it has been carried to a den or has been fed to captive hyenas, it will probably be gnawed again from time to time. This stage may be reached in any time from one day to two weeks, depending on the number of animals gnawing, number of other bones available for gnawing, and number of other activities the gnawing animals have to perform.

Final stage: The bone may be entirely eaten, or it may be abandoned when short segments of the shaft remain; these segments may be 15 cm. long or shorter. Since by the time this stage is reached several days have passed, in warm climates longitudinal splitting of the shaft will have occurred, facilitating final fragmentation of the element. Surviving fragments may have numerous tooth scratches on the surface, as well as many single tooth-cusp impressions. Parts or all of fracture 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 from single teeth, generally cone-shaped and round-bottomed, measuring about 3-5 mm. wide at the widest point, and about 3-5 mm. deep, if adult hyenas are gnawing.

On femora from animals smaller than medium-size adult cows, the entire proximal end may be eaten before the trochlear area is well gouged so that the shaft may be broken up before stage 3 characteristics appear.

Femora damaged in different sequences have been occasionally observed, but in all cases it was possible to distinguish unique circumstances associated with the bones, such as unusually small size, unusual hoarding of bone by one of the hyenas to protect it from the other one, gnawing of dried bone, or gnawing longer than customary on individual bones inside the den because of unwillingness to come out during building construction disturbances outside.

Femur: Wolf Gnawing:

Introductory Note: Most of North America's wolves live (and lived during the Pleistocene) in geographic areas that suffer seasonal subfreezing temperatures and snowfall, and most of Africa's hyenas live in geographic areas that seldom do. However, hyenas of the Pleistocene period in Europe and Africa may have lived in climatic conditions similar to those which today's wolves enjoy. Wolves do their most intensive hunting of many prey species during the winter months (R.O. Peterson 1977; Mech 1970; Oosenbrug and Carbyn in prep.; Carbyn 1974; Haber 1977), whereas hyenas (in areas where game is available year-round) do not show such seasonal differences in kill rates (Kruuk 1972, 1975).

What these facts mean is that timber wolves do most of their killing of adult bison and moose, for example, in wintertime, when uneaten or partially eaten carcasses and body parts freeze solidly or may be covered with snow. Uneaten meat and hide, if frozen, are extremely difficult to eat and require long periods of mouthing and gnawing to soften enough to bite off. Wolves generally do return to frozen carcasses before and after the spring thaw, although the scale of carcass exploitation is not intensive. But the important point to be made in this discussion of damage sequencing is that once the bison or moose carcass begins to freeze, it will seldom be moved out of its position by wolves. Thus, bones on one side of the dead prey, the side resting on the ground, may not be gnawed as much as bones lying on the side that is up and easily accessible. However, wolves enter the prey animal's body cavity through the rump, belly, and neck after eating meat from these areas, so that even humeri and femora packed into hard snow, partially-digested gut content of the prey, and frozen hide may be well-gnawed. Paired long bones may not be symmetrically damaged. Normal sequencing of bone damage through gnawing may be altered by inaccessibility of certain bone parts.

Observations: First stage: The first parts of the femora to show damage from wolf gnawing are the greater trochanter, trochlear rims, and lateral condyle. Wolves feeding on disarticulated femora may not damage the lateral condyle at all. The larger trochlear rim is damaged early, but oftentimes very lightly, not as much as is the greater trochanter. Damage in all cases is the result of carnassial penetration of the outer bone surface, exposing trabecular bone (see Haynes 1980a; figures 6 and 7). The stump of the greater trochanter rarely consists of a 5 mm. high rim of compact bone encircling cancellous bone (Figure 4, right specimen). The larger 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 single and isolated tooth punctures through outer compact bone into cancellous tissue, or sets of single tooth punctures that run together.

Second stage: Within one day, if a single wolf is gnawing on a single bone, the greater trochanter has been mostly removed, and cancellous bone at its base is scooped and gouged (Figure 4, left specimen). Individual tooth furrows may be visible. The larger trochlear rim has been gouged out. In the case of wolves feeding on articulated carcasses, the medial condyle is damaged but not as much as is the lateral condyle. Damage consists of removal of outer compact bone and exposure of cancellous tissue in patches about 1 cm. diameter, near or on the articular surface. The cancellous tissue may have tooth furrows or impressions in it. The neck of the femur below the head is also tooth scored and furrowed. A pack of 10 wild wolves will often reach this stage on one femur of an adult bison carcass by three days of feeding; the other femur may be relatively or entirely undamaged, or may be in a stage 1 - stage 2 transition.

Third stage: The lateral condyle has been almost completely destroyed, and the entire distal end, including the epiphysis attached to 2-3 cm. of the shaft, is nearly separated from the main part of the shaft. The femoral head is eventually severed from the rest of the bone, but often is not eaten. At times this removal may precede removal of the distal end. In actual killsites, at this point, the rear leg has of course been disarticulated from the pelvis. This stage may never be reached for winter kills, and may never occur after the thaw if the carcasses are not heavily scavenged by wolves.

Final stage: The shaft survives as a hollow cylinder and there are shallow tooth scratches on it at right angles or diagonal to the long axis, for the most part. The scratches may be up to 3 cm. long or longer, and may be 1 mm. deep by 1 mm. wide, or up to 2-3 mm. wide. These scratches are most abundant near the ends of the diaphysis. Broken edges of the shaft may have been somewhat polished in a few places, possibly due to repeated chewing and licking or abrasion on ground surfaces. The femoral head and one or part of one of the distal condyles may also survive. Impressions from individual teeth in trabecular bone are about as wide and deep as those left by hyenas, but are not as round-bottomed.

Femur: Bear Gnawing:

Most bears will not sustain hard gnawing on bones after soft tissue has dried or been removed, although there are wide individual and species differences in gnawing behavior.

First stage: Most of the greater trochanter is gnawed off between cheek teeth, and the larger trochlear rim is also ground between cheek teeth, with the jaws aligned parallel to the rims. Damage from bear gnawing is distinct from damage caused by canids or hyenas, in that bears' broader cheek teeth 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.

Second stage: The stump of the greater trochanter is faceted or flattened, and the exposed cancellous bone may be gouged into fewer than five pits that are 6 mm. deep and 10-20 mm. long, about the size of single cheek teeth for brown and black 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. There may be no tooth scratches on the bone shaft surfaces. The occasional tooth marks on compact bone appear as short and wide sets of parallel scrapes, each seldom wider than 1½ mm. or longer than 9 mm., or as roughly circular pits no deeper than 0.5 mm. The lateral condyle may have been partially ground off by cheek teeth. The medial condyle may also be slightly damaged in a similar manner.

Femur: Large Cat Gnawing:

African lions, Bengal tigers, and jaguars will not often sustain gnawing on aging bone, although captive cubs and adults may mouth bones and gnaw briefly from time to time. The trochlear rims are scraped off between carnassial and other cheek teeth, leaving a few relatively deep, identifiable grooves from individual tooth cusps running perpendicular to the larger trochlear rim. The grooves, if clearly produced, will usually be larger than grooves created by hyena or wolf teeth, and may be fewer in number, probably because large cats have fewer and larger cheek teeth than other carnivores of similar body size.

The neck of the femoral head is partially bitten through, usually on the lateral side (Figure 5, left specimen). The greater trochanter will have been bitten off, leaving an irregular outline shape on the edges of the stump (Figure 5, right and left specimens). Lion cubs may actually gouge out only some of the trochanter, leaving a discontinuous 3-7 mm. high rim of compact bone around the internal cancellous bone; lion cubs in fact produce gnawing damage very similar to stage 1 or 2 damage created by wolves (see Haynes 1980a: figure 5, left specimen). There may be scratches on the compact bone of the diaphysis, most of these marks nearly perpendicular to the bone's long axis, and all very shallow but rather sharply incised.

Because large cats are relatively nervous and picky feeders, especially in captivity, the nature of their bone damaging may differ more widely than bone damaging done by other carnivore families. The trochlear rims may not be gnawed at all by jaguars or other cats, especially if there is not very much soft tissue adhering. The outline of the greater trochanter may be irregularly gnawed into deep round pits, and there may be no tooth scratches on the diaphysis. The basic identifying characteristic of large cat gnawing is the rough and irregular marking left by biting on and through cancellous bone of the epipyses. These marks are wide, deep, and countable, and are inflicted by the large cheek teeth.

Tibia: Hyena Gnawing:

First Stage: It is my impression, judging from observations on wild wolf gnawing damage to whole bison and moose carcasses, that large carnivores will probably produce damage to the proximal end of the tibia first, if it is articulated to the femur when attacked. However, when the femur/tibia articulation is separated, carnivores begin gnawing on the distal part of the tibia and articulated ankle bones. The sheath of tough tissue surrounding the tarsal bones is crushed and ground between cheek teeth, and is tugged with incisors while the bone is held firmly under one paw. The incisors and the canine teeth are actually applied to cartilage during hard grinding and crunching of the calcaneus and distal end of the tibia.

The bones are occasionally picked up crossways in the jaws and carried about in what appears to be excitement or nervousness at the proximity of other feeding animals. This carrying and the frequent attempts to peel periosteum using incisors leave numerous tiny scratches on the bone shaft, most of them perpendicular to the long axis.

After gnawing distal ends for a half hour or so, when all soft tissue that can be pulled off has been removed, hyenas will switch their attention to proximal ends, which lack muscle and the flabby sheath of soft tissue that the distal ends have. In a few minutes the lateral and medial edges of the proximal articular end have been damaged by some shallow gouging. At this point either the distal or proximal end has the same attraction for gnawing; that is, any more tissue that can be swallowed has to be gained by hard gnawing from now on, and either end of the bone has no advantage over the other.

Second Stage: Continued damage to the tibia may occur in killsites during feeding, but often the continuation of damage is due to sustained densite or leisure site gnawing. The proximal anterior crest is gouged out, and tooth furrows are visible in the exposed cancellous bone. By the end of this stage, the entire proximal end has been removed, and the shaft has jagged fracture edges which for the most part are not rounded. Toothmarks on the shaft are shallow scratches more the result of periosteum peeling and carrying of the bone in the mouth than of deliberate gnaw grinding. The calcaneus may show incisions or scoring which go around the shaft near the tuber calcis.

Third Stage: The shaft is pulled apart, each fragment measuring possibly 5 cm. long or longer, and possibly terminating as might a stone flake, with a so-called feather termination (see Crabtree 1972). The broken edges of the shaft may show gnaw rounding and heavy tooth marking of compact bone surfaces, sometimes leading to exfoliation of very thin bone layers in patches crushed between teeth. There is a great deal of shaft scoring perpendicular to the long axis. The tarsal bones have been nearly disarticulated, but they are not tooth-marked

Fourth Stage: Shaft fragments may be gnawed one at a time as they are broken off, but the shaft itself is usually the center of attention. Thus, fragments of compact bone may be pulled off but not gnawed, and so they will show little or no tooth marking. Up to half a dozen ungnawed pieces may be present.

Final Stage: Less than one-third of the shaft remains, its edges well rounded and its surfaces very tooth marked. The extreme distal end often survives practically unmarked by teeth.

Tibia: Wolf Gnawing:

Even on well-utilized carcasses, such as moose or bison killed by wolves and fed on by more than one pack for up to three months after the original kill date, whole lower legs may remain articulated from the femoral head or proximal end through the hooves. However, oftentimes the femur/tibia/patella articulation is fully disjoined, and the entire proximal end of the tibia may be gnawed off. This occurs most often on arthritic joints or on joints from smaller animals, such as subadults and females.

First stage: The lateral and medial edges of the proximal articular end are acraped and shallowly scored by cheek teeth. The lateral edge is more often damaged first or solely. This stage of damage on the tibia accompanies stage 1 damage on the femur.

Second stage: Most of the damage in this stage, accompanying stage 2 damage to the articulated femur, is simply stage 1 damage a slight bit advanced. The cranial (anterior) proximal crest of the tibia may be gnawed and scored, or partially removed. Exposed cancellous bone inside the element may show a little tooth furrowing (see Haynes 1980a: figure 8).

Third stage: The tibia is disarticulated from the femur. The proximal crest has been entirely removed on the cranial side of the bone, and distinct furrows and tooth impressions are noticeable in cancellous bone. A small number of tooth scratches may be present on the shaft perpendicular to the long axis.

Final stage: The entire proximal end has been removed, and there are polished irregular edges on the shaft, with scratches, scrapes, and pitting abundant near the edges but also on the rest of the shaft (see

Haynes 1980a: figure 9). The tarsal bones may still be in articulation with the nearly undamaged distal end.

Occasionally the bone shafts will be broken up by the killing pack of wolves after proximal end of tibiae have been removed. Scavenging bears and scavenging wolves may break back the shaft to get at the marrow which remains inside the tibia or while gnawing the greasy compact bone, even months after the original killdate (see Haynes 1980a: figure 9, left specimen).

Tibia: Bear Gnawing:

I have seen few examples of the results of bear gnawing on articulated femur/tibia/patella units, and it appears that black or brown bears will not often severely damage bones of large adult herbivores unless wolves have first gnawed off epiphyses.

First stage: The lateral and medial edges of the proximal articular end are the first parts of the tibia to show damage from bear gnawing, although in my studies on captive animals the articulated calcaneus and tarsal bones were actually attacked first.

The damage 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 an occasional tooth cusp impression in the proximal end of the bone, consisting of single, nearly flat-bottomed holes entering cancellous bone. There may also be sets of parallel furrows on the crest, resulting from the filing away of bones by separate tubercles on the cheek teeth. The cheek teeth may produce a few short scratches on the shaft. These scratches appear similar to rodent gnaw marks, as short, parallel, shallow, and straight scoring.

Final stage: When tibiae are abandoned by bears, the tarsals, calcaneus, astragalus, and metapodials are usually still articulated. In the wild a hungry scavenging bear may completely disarticulate and separate long bones. At this time, stage 1 damage is a bit more advanced on the proximal end, but there may be no tooth marks on the shaft. Occasionally one or a very few shallow pits are produced on the shaft by cusps of cheek teeth (see Femur: Bear Gnawing for description).

Tibia: Large Cat Gnawing:

The main damage I have seen from large cat gnawing on the tibiae has been moderately deep and isolated scoring of parts of the proximal articular edges on lateral and medial sides. The cranial proximal end (or crest) is also occasionally furrowed perpendicular to the bone's long axis, probably during consumption of muscle and tissue around the patella. In some cases the proximal end of the tibia crest may be broken off, and part of the crest may be pulled away from the shaft as a large spall or flake (see Miller 1969 for illustration).

Bone Destruction by Captive Wolves

I have also observed feeding behaviors among members of several captive wolf packs and family groups. There are two captive packs in Forest Lake, Minnesota, maintained for studies supervised by L.D. Mech of the U.S. Department of the Interior.

For the three years prior to my first visit in 1979 these two packs had been fed whole or ½ a whitetail deer carcass about once a week, during times of the year when road kills were available. The packs each included 8-10 animals, not counting pups. During May, 1979, I observed both packs feeding on deer carcasses or carcass remains (Figure 6), and I did two conscientious walkovers of 100% of one pack's ½ acre enclosure. I collected from the surface of the ground all teeth, toothrows, mandibles, and crania; I also collected or counted all vertebrae, calcanei, astragali, phalanges, and ribs. A selective sample was collected of long bones in various stages of gnawing damage or breakage. Surface visibility of the enclosure ranged from excellent to poor, with deer hair, dried wolf scat, dead grass, and fallen leaves covering about 30% of the ground.

Some areas of poorest visibility were examined twice, once before cover was disturbed and once after the cover was swept away. The areas of least visibility were farthest from the main feeding areas; only three mandibular toothrows were found after ground cover was cleared away from 40% of this area. I would conclude that I may have failed to collect no more than eight toothrows from the entire enclosure (compared to a total of 38 collected).

The minimum number of deer represented by mandibular toothrows was 27, of which 16 are younger than 1.5-2.0 years. Cranial toothrows represented 22 deer, of which 14 are younger than 1.5-2.0 years. There are only 10 rib fragments recovered from the ground surface, possibly representing no more than one deer. Eight vertebrae represent two to eight deer. Ten calcanei were found, representing no fewer than five and no more than ten deer; 13 astragali were found, representing 7-13 deer; and 13 phalanges were found, representing 4-13 deer.

Because this pack is so limited in the area it can feed and move about in (and assuming their communal and individual feeding behaviors are not too eccentric when compared to wild counterparts, an assumption based on simple mechanics and anatomy as well as on predictable and consistent social characteristics of wolves [see Mech 1970; Klinghammer

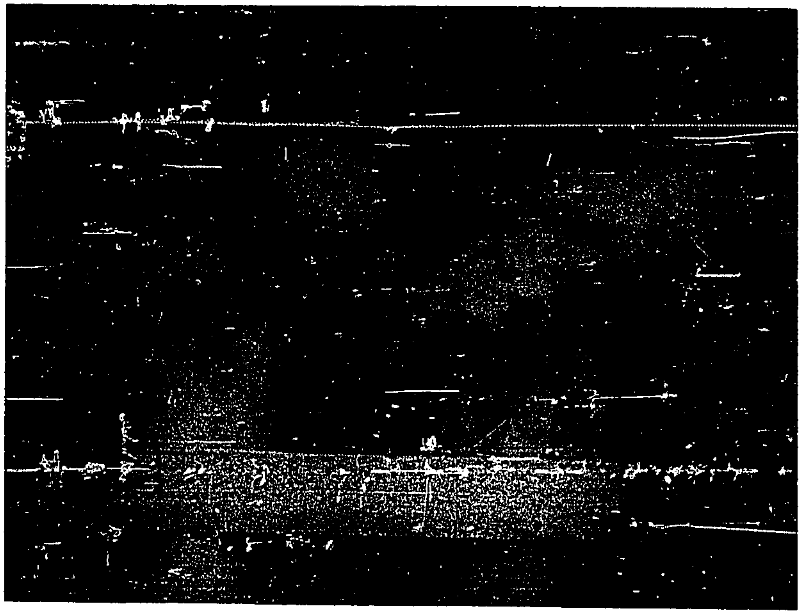


Figure 5. Bos femora gnawed by captive lions.

Figure 6. Pack of captive Timber Wolves in Minnesota eating a Whitetail Deer carcass.

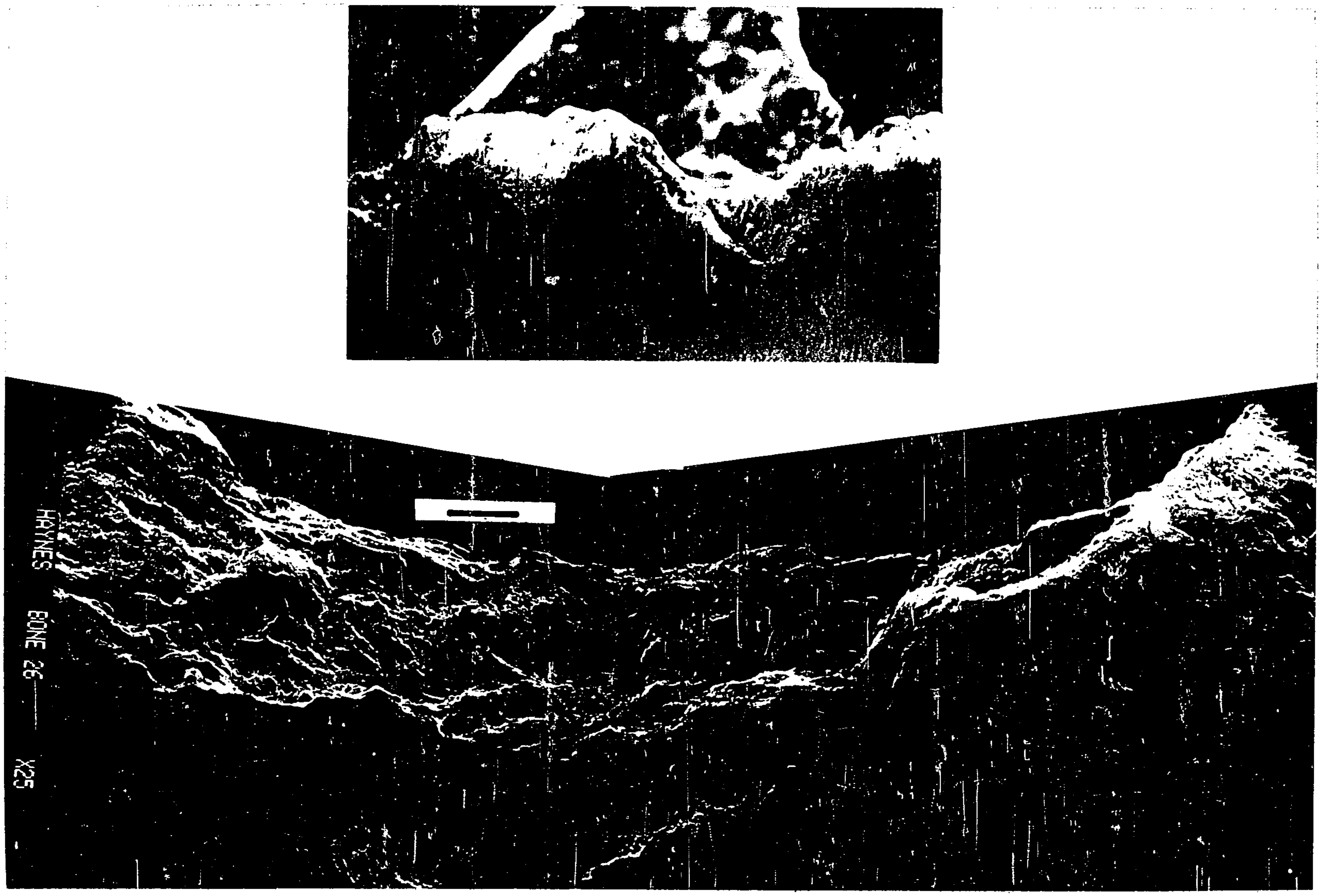


Figure 7. Gnawed Bone. TOP: Actual size photograph of a wolf-gnawed *Bos* tibia, proximal end of shaft.
BOTTOM: SEM photograph of part of the remaining edge. Scale bar= 500 microns.

1979]), it is possible to see that the colony is producing bone destruction and gnawing damage typical of homesites, killsites, and consumption sites, but not spread out or distributed in discrete units. See Chapter 6 for a discussion of site types.

In the assemblages which I collected from the captive pack, there were bones possessing damage identical to that found in wild wolf killsites (see Chapters 7 and 8) mixed with bones damaged by sustained gnawing, which latter type is common in captive animal assemblages (Haynes 1978a and unpublished data). I am predicting that this latter damage (edge rounding, longitudinal _and_ spiral fracturing [see Chapter 10], more tooth marking) is similar to that which will be found at dens and rendezvous sites.

Note the rarity of phalanges, which are characteristic of killsites in the wild (69% occurrence in sample--see Chapter 6). Deer representation by phalanges, if one accepts one phalange per deer as a reasonable estimate, would range from 15% to 49% (there are four to 13 deer represented by phalanges) of the mandibular representation (or maximum Minimum Number of Individuals, which is 27). If one accepts one phalange per leg as a more reasonable figure for representation, then the phalanges in the assemblage represent only 11%-15% of the deer present, as indicated by mandibular toothrows. Seven of the 13 collected phalanges were partially digested. White bone scat in the enclosure attested to the ability of wolves to digest some bones and bone pieces completely.

Because the ground was a fine sandy silt, and tends to become muddy when snow melts in spring, there is another significant factor to consider besides wolf digestion that possibly bears on poor representation by phalanges, the factor of burial. I could not adequately assess the significance of this factor, but I have concluded a few things that might minimize its potential significance. I watched a pack almost completely eat a small yearling deer carcass in less than 24 hours and I could find no vertebrae from the carcass the next day when I walked over the enclosure, nor could I find more than three phalanges, which were still greasy and articulated to a metatarsal. This bone unit would probably be further gnawed and destroyed. It is probable that neither vertebrae nor phalanges were trampled into the ground but were completely eaten. I was over 30 meters away from wolves feeding on the deer carcass, but I could plainly hear loud crunching of bones as the wolves ate.

This evidence, plus the evidence of partial digestion of seven of 13 phalanges from the collected assemblage; and the evidence of wolf capabilities of completely digesting bone, is sufficient to explain the poor representation of deer by elements smaller than calcanei. Of course, some elements undoubtedly are buried by trampling, and some bones may be cached by wolves in shallow holes, although I observed only hide in cache pits. It is not probable that scavenging birds or rodents remove smaller bones, because the wolves range over nearly all the half-acre pen many times during the day and night.

Perhaps it can be inferred that if one does not find phalanges from deer at killsites, the chances of ever finding them at other types of sites are extremely low, because of potential wolf destruction. This is speculating in terms of an idealized paleontological investigation of an entire wolf territory, with the understanding that every bone, even those rare scattered body parts from consumption sites or rendezvous and den sites, will be found.

Other Captive Wolf Studies

Another group of captive wolf packs and families that I have observed feeding is found at Battleground, Indiana, in a nonprofit institution called Wolf Park. Dr. E. Klinghammer of Purdue University runs the facility as a public-oriented research zoo, initially founded to take care of rejected or problem pet wolves. During this study, the park contained a pack of 12 wolves who lived in a one acre enclosure, three wolves in a 3/4 acre pen, and two pairs in two other 3/4 acre enclosures. The wolves are fed sectioned livestock carcasses, and after a few days uneaten bones are cleaned from pens. Some of these specimens were gathered from time to time by park personnel and added to my reference collections.

In many cases, when long bones were fed to the wolves, both proximal and distal epiphyses would be gnawed off, producing open-ended diaphyses cylinders. Almost all recovered bones and fragments were well-marked by teeth imprints, scratches, furrows, or crushed tissue. Many long bones of _Equus_ and _Bos_ had been broken up into spiral and other fracture configurations. In the case of tibiae, fracturing begins at the proximal end, following gnawing off of the proximal epiphysis. Femora are usually fractured from either end, following removal of the epiphyses; humeri are most often fractured from the proximal end first. In most cases, the fracture edges are mixtures of rounded and sharp surfaces. Bone fragments are levered off during sustained gnaw action, and these fracture edges are at first sharp, until abraded by rubbing with paws, rubbing on the ground, continued licking, or grinding between teeth (Figure 7).

I have termed the kind of damage observed in this assemblage to be a "kennel" pattern, indicative of sedentary, sustained gnawing by animals who do not hunt often or for the greater part of their food.

RODENTS

Species Descriptions

Several species of rodents were observed gnawing on antler or bone at the National Zoölogical Park. Most species were not native to North America, but there are some that were similar to New World species: Hystrix cristata (African porcupine), Atherurus africanus (brush-tailed porcupine), and Capromys pilorides (Cuban hutia), in characteristics of their skull, body sizes, and dentitions are similar to several North American species, respectively Castor canadensis (beaver) or Erethizon dorsatum (American porcupine), Marmota monax (woodchuck), and Ondatra zibethicus(muskrat).

Discussion

(1) Rodents typically begin at once to gnaw bone placed in their enclosure; the bone may be either dried and sun-bleached or still fresh with tissue adhering. As has been observed in the wild, rodents gnaw a bit, leave to perform other business, then later return, sometimes (but certainly not always) to resume gnawing near the same incisor grooves or on the same end of the bone. However, not all rodents in captivity, and probably in the wild, too, gnaw bone.

Much rodent gnawing is on processes or protuberances where good leverage can be gained for the jaw to bear down on the bone surface. Most tooth marks result from scraping the upper incisors along the bone, but the lower incisors occasionally leave similar marks. There is much gnawing on the shaft and on flattened areas which have little curvature.

(2) When animal skulls are left to dry, invariably the orbital edges, nasal bones, and cranial ridges and crests are faceted by rodent

gnawing. This pattern occurs on large and small skulls, but the rodent species seem to vary with skull size. Some denning rodents will remove portable bone specimens to the den (cf. Dart on African porcupines 1958), there to gnaw on at their leisure, just as observed often at the zoo. American porcupines (Erethizon dorsatum), do not hoard bone (Mech 1977 pers. comm.) at least in some northern parts of their range.

African crested porcupines (Hystrix cristata), hoard bone in the den, and this bone may get set aside and superseded by bone hoarded each day, but all bone is generally returned to and gnawed at any time.

(3) The width to tooth marks from carnivore and rodent gnawing varies with the part of the bone gnawed, as well as with the material gnawed and length of time the material is gnawed (Figure 8). When gnawing wood, African porcupines leave wide grooves, but when gnawing bone the grooves are narrower, although the length of incisor grooves appears to be similar (although always extremely variable) on hard and soft materials. The groove lentth may depend only on mechanics of the jaw or shape of the material surface being gnawed, while the depth and width may depend on hardness of the material. The width is determined by the amount of incisor cutting edge which actually scores the surface. Groove width may be widened by continued gnawing in the same place (as in Figure 8, bottom right). I have made a few unsuccessful attempts to identify genus of rodent from tooth grooves alone; identification may be possible, but at this time I very much doubt it.

(4) Many rodents such as the Antelope ground squirrel (Ammospermophilus l. leucurus) and the African and Brush-tailed porcupines are fond of the fat and meat on bones, but many captive rodents will not gnaw the bone itself if there is any meat on it, and do not gnaw green

bone at all even after the tissue is removed, although many of these same animals do gnaw aged, dried bone in their enclosures.

In other words, to generalize from these observations and others, many (perhaps most) rodents only gnaw compact bone when it is dried, not when it is relatively softer and fresh.

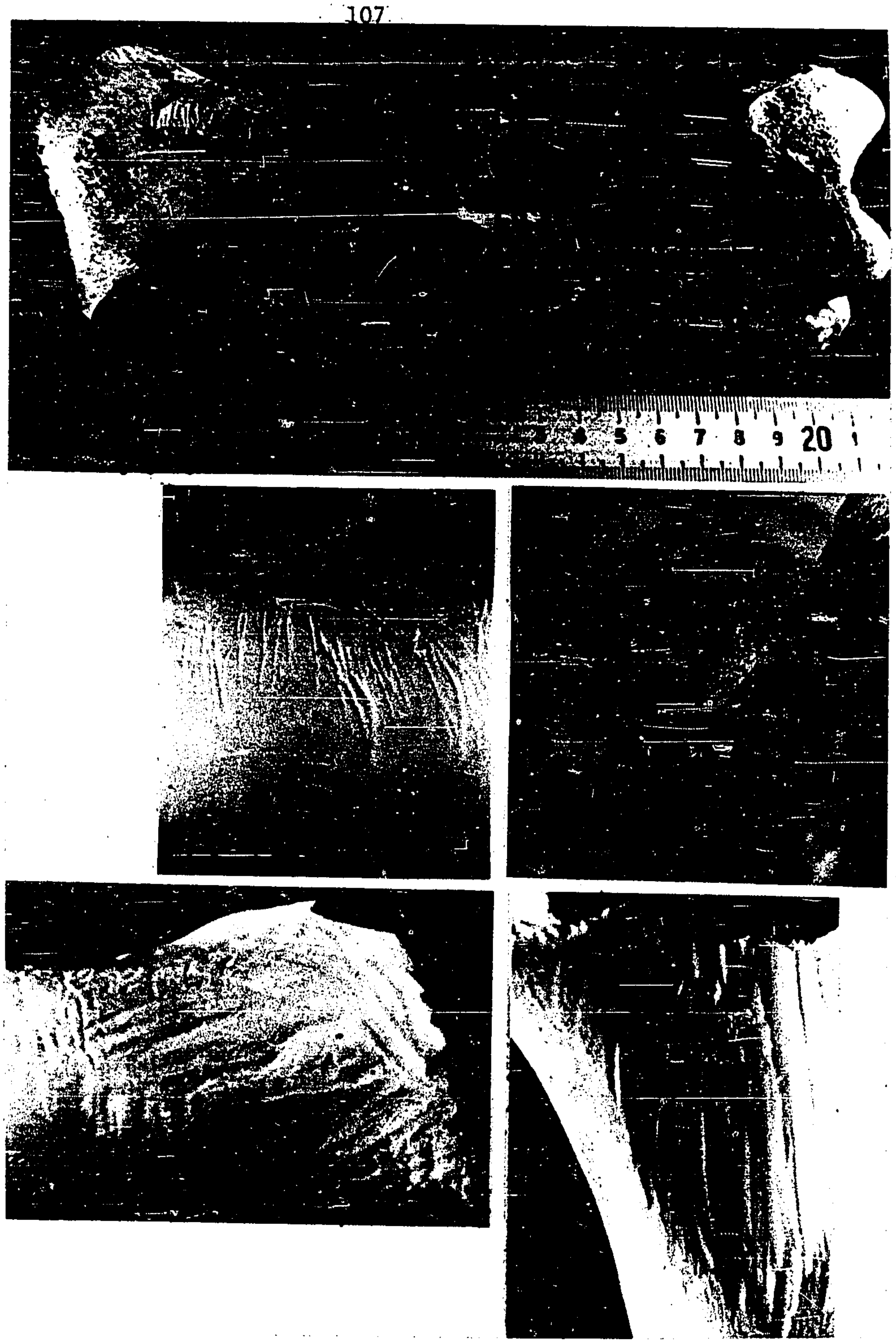


Figure 8. Rodent gnaw marks on *Bos* long bones.
TOP: Damage by Brushtailed porcupine.
CENTER LEFT: Close-up of part of top specimen.
CENTER RIGHT: Damage by Cuban Hutia.
BOTTOM LEFT: Damage by Crested porcupine.
BOTTOM RIGHT: Damage by Crested porcupine.

V. Introduction to Studies of Bone Gnawing and Carcass Utilization by Wild Animals

In Chapter 4 it was proposed that gnawing animals create bone damage that can be differentiated from damage created by human activity. In this chapter the proposition is examined further by observing wild animal utilization of prey carcasses.

In addition to the goal of defining explicit attributes which distinguish natural bone damage from cultural damage, I also intended to investigate the possibility of discovering facts about the ecosystem, as the facts may be decipherable in prey bone assemblages.

BONES CONSIDERED AS EVIDENCE ABOUT ECOSYSTEMS: PREDATOR-PREY SYSTEMS AND MODERN STUDIES

The behavior and ecology of hunting animals are subjects of widespread interest to game managers and research biologists. Because the ways in which hunting animals use or dispose of their prey are not haphazard (see Schaller 1967, 1972; Kruuk 1972, 1975; Mech 1970; Haber 1977; Carbyn 1974; R.O. Peterson 1977; Oosenbrug and Carbyn 1980) it may be possible to determine many behavioral and ecologic aspects of past predator prey relationships by a conscientious examination of bones, bone sites, or carcasses in the field. Many field biologists believe that the bones of a scavenged carcass can be distinguished from those of a true kill (see R.O. Peterson 1977; Mech 1966; D. Allen 1979; Haber 1977), and that the degree of carcass utilization reflects some very important facts about the ecosystem (Pimlott _et al_. 1969;

Mech and Frenzel 1971; Magoun 1979 pers. comm.). These facts, of course, must be sorted out by careful study, because certain factors in the system often interdigitate to affect bone assemblages in complex ways, or the effects of some variables may damp out the possible effects of other variables.

Results of my own field work (Haynes 1978a,b, 1980a,b, 1981 in press) confirm that large North American predators such as timber wolves (Canis lupus), when subject to minimal disturbance by man, will utilize prey carcasses in uniform, patterned, and predictable ways according to a number of qualifying factors that for the most part affect or are affected by ease of the hunt (Carbyn 1974; R.O. Peterson 1977; Mech 1970; Haynes 1981 in press). These separate factors would include such things as season (in the north late winter killing of prey is usually easier, as prey animals are feeling the rigors of the cold season); severity of the winter (even the healthiest prey animals are more vulnerable in harsher winters); age structure of the local prey population (the very young and the very old are usually the most vulnerable members of the herd, but if few or no such animals are available predators may change strategies of hunting and killing, and of carcass utilization); or simply the general availability of any prey within the predators' hunting area (in areas where packs have traditionally preyed on whitetail deer but where deer are rapidly declining, wolves may prey more and more on moose or other alternative prey, and carcasses will be utilized differently than deer carcasses found in the same areas [Mech 1979 pers. comm.]). When killing is relatively easy, prey carcasses are not utilized as fully as when hunting is difficult (Pimlott et al. 1969; Mech and Frenzel 1971).

When a high proportion of the prey herd is very vulnerable, the carcasses produced by hunting wolves would be lightly utilized (that is, a relatively large amount of meat may not be consumed); when winters are unusually severe, a greater proportion of the prey animals thought least vulnerable may be killed by wolves (R.O. Petersen 1977), and the carcasses would not necessarily be fully consumed. The _most_ vulnerable prey animals, during unusually severe winters, would probably be dying without predation. Their carcasses would be little utilized, if at all (see D. Allen 1979; R.L. Peterson 1955), since even well-fed wolves, when they get hungry, may be more inclined to hunt and kill living prey animals than to seek out frozen carrion for the bulk of their food. Frozen carcasses _are_ visited and scavenged by hunting wolves and other animals, but are not usually fed upon or disturbed to the extent that are freshly-killed carcasses.

There are most likely optimal size ranges for wolf packs which prey selectively on each particular prey species: bison seem to be most efficiently hunted, killed, and utilized by packs containing no fewer than 8-10 nor more than 15 wolves, moose by packs of no less than six to eight nor more than 12 animals, and so on (see Mech 1970; Oosenbrug and Carbyn 1980 in prep.; R.O.Peterson 1977; Carbyn 1980 pers. comm.). Packs of different sizes exist, of course, especially in areas where alternative prey species may be available or where there is human influence (such as fur trapping or hunting). Smaller or larger than optimal size packs might be expected to utilize prey carcasses in ways somewhat differently than do "normal" size packs. There are surely some comprehensible reasons for particular pack sizes to vary, but the gnawed bones of a carcass may have no unambiguous clues to offer.

Some carcasses may be poorly utilized not because they are scavenged, as opposed to being true kills, but because the feeding wolves may have been disturbed, usually by humans. And some carcasses may have been utilized by several species of carnivores, such as bears, wolverines, foxes, and mustelids, besides wolves. Thus, the skeletal material will not be directly decipherable using ordinary wolf-killsite reference materials. Fortunately, most of the time it is possible to distinguish the bone damage and carcass dispersal done by various species, in the absence of tracks or visual documentation, by examination of gnawing damage to bone elements (see Chapter 4); similarly, Buskirk and Gipson (1979) discuss characteristic points of attack and wounds resulting from wolf and bear predation on moose, sheep, or caribou.

It can be seen that the data to be gained about ecosystems from a study of bone sites is not entirely straightforward or self-evident, but such a study is clearly of value. Much more work in simple observation is necessary, as well as much more work in interpretation and theory.

This chapter presents background information derived from the available literature on some aspects of predator-prey studies which are of potential usefulness to paleoecologists. The following discussion is concerned with prior research about large predators, and provides a few select references to data on the ways that prey bones might be affected by different environmental conditions and different behavior patterns of predators; the purpose of this discussion is to show that prey bones, in such characteristics as spatial distribution or degree of gnawing damage suffered, might reflect significant ecologic relationships within animal communities.

Very few studies have been made which adequately document carnivore utilization of prey carcasses. Magoun (1976) made such a study in northeastern Alaska, and found that carcasses of sheep, caribou, moose, or bear were fed on by scavenging bears or wolves for generally less than a week before most or all meat was consumed. The average time was about three days, although moose carcasses "lasted 7-13 days" (Magoun 1976:90). By the end of those times, bones were either cleaned, consumed, or entirely missing from the sites.

She found that most parts of summer carcasses would be utilized by scavenging animals, even skin, hooves, and bones. In her study area a great many underutilized carcasses of wolf-killed caribou were eventually fully utilized after live caribou moved out of the area in summer.

She presents a few observations on patterned disarticulation or dispersal of bones by differing species of scavenging carnivores (such as grizzly bear, timber wolf, or red fox). Foxes enter the prey body through the rump and anal flesh, but do not disarticulate bones. Wolves will clean tissue from the skull, vertebral column, and rib cage, and leave most of the bones intact and articulated. Wolves will also break many ribs, and disjoin limbs from trunks. Bears, on the other hand, will disarticulate skulls, separate vertebral columns into several pieces, and disjoin most of the rib cage of caribou or sheep carcasses.

Magoun observed two wolves scavenging the carcass of a caribou, and the sequence of disarticulation was as follows:

(1) Tail eaten.

(2) Two ribs eaten.

(3) Ribcage fed upon.

(4) Hindquarters disjointed. Ribs eaten and broken off.

(5) Brisket eaten: sternum and ribs broken.

Time elapsed for this sequence was two days. Within three days the remaining cleaned bones had been dragged away from the site.

G. Schaller (1967, 1972, 1975) has contributed importantly to biological studies of predators in the wild. He has observed and recorded much information of potential interest to paleoecologists, including the types of bone damage inflicted on prey carcasses by feeding tigers (Schaller 1967:300), signs of lion killing versus scavenging on prey carcasses (Schaller 1972:27,28), sizes of territorial areas utilized by certain numbers of lions as related to prey densities (Schaller 1972), dispersal and movement of prey carcasses or carcass parts by feeding lions (Schaller 1972:267), sequences of carcass utilization by lions (i.e., feeding) (Schaller 1972:268-270),average daily food intake for Serengeti lions (Schaller 1972:277), diet and feeding sequence for cheetahs (Schaller 1972:319-320), and distribution, density, diet, and feeding habits of wild dogs (Schaller 1972). Rudnai [1977?] also offered many valuable observations of African lion range sizes, hunting habits, prey selectivity, kill location preferences, feeding sequences on carcasses, and bone damage resulting from lion feeding.

Kruuk (1975, 1972) described spotted hyena scavenging activities and carcass utilization sequences, differences in carcass utilization resulting from differences in hyena densities in different areas, and other related facts of possible value to paleoecologists. Mills (1978) compared scavenging and hunting behavior of spotted hyenas in open country and bush country of east Africa. Myers (1977) observed the competitive nature of cheetah hunting and killing and hyena scavenging and carcass robbing. It is possible that certain predator species may co-exist in the same range (see Schaller 1972 and Estes 1967 on the predator-rich east African habitats), while other predator species (such as cheetah and hyena) may <u>not</u> co-exist well. Thus, one might expect to find many bone assemblages which contain both lion and hyena bones, or prey bones damaged by either hyena and lions, but few assemblages which contain both hyena and cheetah bones or bones damaged by both predator species.

Bears and wolves may share much of their range with each other (Mech 1970, Magoun 1976, see Pulliainen 1965 for conflicting opinions, Couturier 1954, Bromlei 1973), so their own bones or the damage they respectively inflict on prey bones may be found together in single assemblages.

Behavioral and ecologic studies of timber wolves and prey (see below) and of bears and potential prey (for example, Behrend and Sage 1974) are becoming more commonplace in the biological literature. Many such studies contain observations on the dynamics of predator-prey systems which can be used as analogues for reconstructing past animal communities. Herrer (1978) compared black and brown bear behavior patterns and evolutionary ecology; he postulated that brown bears may have evolved to exploit the seasonal productivity of non-forested, periglacial environments, where wolf numbers would also be expected to be high. Brown bears probably developed habits of carcass scavenging due to an abundance of carrion food sources in open habitats. Some of these carcasses may have resulted from wolf kills.

It is possible that wolves and coyotes do not share their central territories (see Berg and Chesness 1978:242), at least in habitats that are being newly colonized.

The wolf interacts with bears found on its range, sometimes violently. Couturier (1954) considered the European brown bears' most dangerous enemy to be the wolf, which may attack in packs and bring down adult bears. In the Soviet Far East, tigers may be the principle enemy of brown bears and the indigenous Himalayan black bear, attacking them more often in their lairs than in the open (Bromlei 1973:111-112). Wolves may also kill bear cubs that are separated from their mothers. Bromlei (1973:126) mentions the usual method of attack by brown bears, which is crushing the victim's skull with the teeth, a method which might produce distinctive and recognizable bone damage in assemblages. Bromlei (1973) also discusses patterns in bear scavenging behaviors and scheduling, as does Magoun (1976). These kinds of information could be valuable in interpretive studies of fossil bones, because one could use such data to determine, for example, the possible season of prey animal's death and the possible availability (or density or vulnerability) of prey animal populations, as suggested by degree of bear-gnawing damage to bones. Bear would expectably gnaw or damage bones most often in spring or fall.

Mech (1970) surveyed the known data about the behavior and ecology of Timber (or Grey) wolves; he estimated that only where predator-prey ratios are below about 24,000 pounds of prey per single wolf, wolf predation is probably the major controlling mortality factor for prey populations (Mech 1970:277). Mech also concluded that wolves "concentrate on species of big game that are easiest to hunt and kill, [and] they also rely more on the individuals that are most easily caught" (Mech 1970:176) (emphasis in original). Mech summarized available information regarding wolves and their various co-existing prey species and competing or non-competing non-prey species throughout the world.

International studies of wolf behavior and ecology are not commonplace. Kozlov (1964) very briefly described known or suspected wolf behavior in the Soviet Union. Novikov (1956) described the carnivores of the USSR; Stroganov (1969) discussed carnivores of Siberia; Pulliainan (1965) discussed his studies of wolves in Finland, where prey is mostly domesticated animals (such as, for example, sheep, reindeer, dogs). There are many other research publications which deal with wolves and other large carnivores of the world, but rarely do these works include explicit descriptions of bone damage or feeding sequences, correlations of prey vulnerability and carcass utilization, or other information of direct concern to taphonomists.

Some of the most valuable data available to paleoecologists can be derived from recent English-language studies of wolf-prey ecosystems. Studies of wolf and whitetail deer (for example, Joslin 1967; Pimlott et al. 1969; Mech and Frenzel 1971; Mech and Karns 1977; Mech 1977a) often contain data on carcass utilization as it may relate to winter severity or prey availability, prey selection by wolves, bone damage done by wolves, kill rates and territory sizes for packs, and the nature of various types of sites created by wolves. These subjects would be of use to paleoecologists as possible analogues to apply to fossil ecosystems which show evidence of having contained wolves and deer (see Haynes 1981 in press).

Studies of wolf-caribou interactions contain similar bits of potentially valuable information (see Kuyt 1972; F. Miller and Broughton 1974; D. Miller 1975 and 1979; and Haber 1977) on the relationships between prey vulnerability, winter severity, predation rates, prey selection and carcass utilization, and seasonal differences in these variables. Haber (1977) observed that with scavenged carcasses the skeletons were abandoned intact and mostly articulated; fresh kills, on the other hand, were usually well dismembered, and bones were scattered over an area 6-10 meters in diameter (see Haber 1977:371-372). Haber also listed the species and number of individuals of prey represented by bones found at wolf homesites (Haber 1977:717-718).

Wolf and elk interactions have been studied by L. Carbyn, whose research is currently being prepared for publication (see Carbyn 1974, 1980; Carbyn _et_ _al_. 1978). From these studies, Carbyn has shown that densities of available prey species in wolves' hunting territories need not positively correlate with percentage of those prey species in a wolf's annual diet; that is to say, a wolf's diet may be 40% mule deer, in habitats where mule deer are only 1/6th as abundant as other species such as bighorn sheep or elk (Carbyn 1974). Thus, in these habitats one might expect to find many more wolf-gnawed mule deer bones than wolf-gnawed elk bones, indicating not a preponderance of mule deer in the biomass but a selectivity by predators for or against certain potential prey species.

Wolf-moose interaction studies are also a potentially rich source of ecological analogues (see Mech 1966; Buskirk and Gipson 1978; R.O. Peterson 1977; Peterson and Scheidler 1979). Mech (1966) recognized the differences between scavenged moose carcasses and fresh kills. Buskirk and Gipson (1978) recognized the differences in results of prey attacks by grizzly bears and wolves, including some possibilities of greatly differing bone damage types. R. O. Peterson (1977) was concerned with prey productivity and availability, and vulnerability towards predation as a result of winter severity. He also devised an empirical system for judging the age of bones found on the ground, using as a guide known and kill-dated mapped moose remains found during earlier research. He showed that carcass utilization may vary with wolf pack size, size of prey killed, and ease of hunting (R.O. Peterson 1977:62; Peterson and Scheidler 1979:13). He argued that environmental influences on ungulate prey populations may affect their vulnerability towards predation more than it affects their numbers. Wolves, being selective, respond to these changes by killing a greater proportion of the more vulnerable individuals (R.O. Peterson 1977:185), even though other individuals may be more numerous locally.

Studies of wolf-bison ecosystems are by far the least common in the literature of wolf behavior and ecology (see Van Camp 1979; Oosenbrug _et al_. 1980; Oosenbrug and Carbyn 1980). The major concern of these recent research projects has been with the possible effects of wolf predation on bison herd size and health, but these studies have also produced much information of value concerning wolf pack territory sizes, predation rates, carcass utilization and food habits and the relation of these variables to weather conditions and prey selection. In Van Camp (1979:21) black bears were observed feeding on bison carcasses and following bison bands during the calving season, although no attacks or kills were recorded. In Oosenbrug _et al_. (1980) it is postulated that wolves hunt, kill, feed, and travel very differently during different times of the year, and also when preying habitually on different species of ungulates.

A FRAMEWORK FOR COMPARATIVE ANALYSIS

Because certain facts associated with certain aspects of ecosystems are herein expected to be revealed by examination of prey bones modified by predators, the types of data necessary to reveal correlations and relationships among ecologic variables will be rather specialized and peculiar. For example, it is necessary to know the sequences of feeding by predators on prey bodies and bones under different conditions (scavenging of already-dead animals versus feeding on freshly-made kills; feeding after easy hunting versus feeding after difficult hunting). It is necessary to know the usual size of predator hunting groups, and how the size varies from prey species to prey species; and it is necessary to know the usual territorial hunting area (or most travelled hunting area) and how that varies with seasonal differences in prey behavior.

When many factors of ecosystemic dynamics are known, it will be possible to compare them to other variables such as typical degree of prey bone damage, relative proportions of damaged bones compared to undamaged prey bones, and degree of prey bone dispersal from carcass sites. These variables of bone damage are concretely definable and to be found upon examination of actual assemblages, and they should correlate in patterned ways with season, climate, and other environmental variables not otherwise preserved in fossil deposits.

The following variables are considered significant for this kind of research:

(1) Prey species.

(2) Prey age (body size) and condition.

(3) Density and Distribution of prey groups (herds).

(4) Density and Distribution of predators at time of kill.

(5) Season and seasonal variations in variables 3 and 4 (weather conditions, etc.).

(6) Site type (homesite, killsite, scavenge site, etc.).

(7) Climate.

(8) Numbers of predators feeding at fresh kills and later.

NEW DATA ON WOLVES AND PREY: INTRODUCTION TO THE CASE STUDIES

Because the wolf is at last well-studied in North America, it is possible to begin correlating traits of bone assemblages produced by wolves with the observed ecological dynamics of particular wolf and prey communities. There is more to making these correlations than simply studying all pertinent wildlife research reports and then manufacturing model after model. In making studies of modern communities, it has been necessary for paleoecologists to supplement known zoological data with new data they have collected while working closely with field biologists in the study of living animals. (Much of the time, this new information actually has to do with recently _dead_ animals.) A. K. Behrensmeyer, for example, has reported on contemporary bone assemblages in east Africa as they represent or misrepresent contemporary animal communities. For this research she collected her own data and relied on data collected by a zoologist, D. Western (Behrensmeyer _et al_. 1979; Behrensmeyer and Dechant Boaz 1980). She has also reported on bones as sedimentary particles undergoing natural processes of burial and transport (Behrensmeyer 1975; Gifford and Behrensmeyer 1977). She has even shown that recent bones record local weather and environmental conditions (Behrensmeyer 1978). Other researchers have examined the manners in which bones undergo disarticulation, fluvial transport, and burial (Schafer 1962, 1972; Toots 1965; Hill 1979; Voorhies 1969), but the number of empirical and experimental research programs remains low, so in effect each report breaks new ground.

The next chapters describe my research in vertebrate taphonomy and experimental paleoecology. Field work was performed in a number of wilderness areas of North America, with the cooperation of the U.S. Fish and Wildlife Service, the National Park Service, the Canadian Wildlife Service, and Parks Canada. The main research involved observations of skeletons of large animals killed by timber wolves or other natural agencies; the skeletons are subjected to scavenging, gnawing damage by carnivores and rodents, and also to various agents of dispersal. The fundamental theoretical position is based on the principle of uniformitarianism: that is, while fossil bone assemblages may be biased, the nature and extent of the biases may be evaluated by studying possibly analogous modern agencies of attrition. It is essential in studies of this sort that there be comparability in behavior and anatomy of possibly analogous past and Recent gnawing animals. The first research task consisted in assuring that the operating principle, which is that bones damaged or otherwise modified by natural forces bear the distinguishing effects of those forces, was a sound and potent empirical generalization.

Propositions Being Tested Empirically

The degree of damage done by large carnivores to prey skeletons and bones differs according to

(a) spatial context - an assemblage in a primary killsite and feeding site shows differences from an assemblage in a secondary comsumption and gnawing site. Homesite assemblages are also distinct.

(b) temporal context - for many carnivores, there is seasonal variation in degree of carcass utilization, and the variation is patterned. Hunting may be easier in the winter, so winter-prey carcasses may be lightly utilized; in summers young prey animals may be available, and may be more easily hunted than adults, so that the carcasses of very young prey animals are utilized less than in succeeding seasons. The size of the feeding group may vary seasonally, and activity levels may also vary.

(c) motivational context - a hungry carnivore eats more, of course,but the cause of its hunger may be difficulty of the hunt, low density of prey in the catchment area, elevated metabolic levels, or other related ecologic factors.

Hypotheses accounting for these generalizations refer to biological and behavioral data, and I have relied on wildlife investigators, zoologists, and animal behaviorists as sources of explanatory statements.

I have attempted to formulate sequences of carcass utilization by wild wolves, and I have correlated some behavior traits of wolves with different attributes of bone assemblages from different types of sites. Finally I have devised hypothetical sets of behavior traits conceivably associated with ecologic circumstances not identical to those observed during the field work, and I have postulated attributes of bone assemblages that could result.

Observations are limited to predatory and feeding behaviors of timber wolves in North America where whitetail deer, bison, or moose are the main prey species; however, the concepts advanced should have general applicability to any ecosystem where there are carnivores and prey of fairly similar habits. The conclusions and propositions from this research are intended to apply to vertebrate assemblages dating to the late Pleistocene or early Recent periods, especially those assemblages that have not been winnowed, retransported, or seriously disturbed. Many fossil deposits _have_ been disturbed between the time of their original formation and the time that they are discovered, and in those cases the usefulness of some of my conclusions will be low. But while the following discussions admittedly apply to ideal situations of near perfect preservation and stratification, they might also be useful as baseline data for other situations. Analytical procedures followed for larger prey animals in North America (for example, moose [_Alces alces_] and bison [_Bison bison_]) require somewhat different presentation than for deer, and so are discussed separately.

Summary of Materials and Methods

Field work was performed in Superior National Forest of northeastern Minnesota where timber wolves prey on whitetail deer and moose, and where fishers, foxes, and bears may scavenge carcasses (see Haynes 1981 in press); on 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 free-roaming bison and occasionally on moose, and where a number of other apecies such as bears and foxes may scavenge carcasses. In these three locales, the winter activities and movements of wild wolves are monitored regularly from the air, and fresh kills or revisited carcasses are examined from the ground after wolves complete feeding (see Figure 9). Skeletal material has also been collected from Glacier National Park, Montana (mule deer, sheep, and cattle fed upon by wolves, grizzly bears, and coyotes); the National Bison Range, Montana (elk, bison, and antelope scavenged by coyotes); Carlos Avery Game Farm, Minnesota (deer and moose fed upon by captive wolves); Wolf Park, Indiana (horses, cattle, and deer fed upon by captive wolves); the Kenai National Moose Range, Alaska (moose fed upon by wolves and bears); Yellowstone National Park, Wyoming (elk and bison scavenged by coyotes); and several other parks and preserves in North America. By the end of 1980, a total of 170 days had been spent in the main field locales, investigating over 90 carcass sites of bison, moose, and deer that were killed by wild wolves, or died due to other known natural agencies at known times. Included in the sample are the remains of:

(1) At least 30 bison that drowned in a single, dated flood, their skeletons having been naturally deposited in a relatively small area (Wood Buffalo National Park);

(2) 22 bison killed by known numbers of wolves on known dates (Wood Buffalo National Park);

(3) Seven bison that died naturally at known times and were scavenged by wolf packs (Wood Buffalo National Park);

(4) Six bison that were poached by humans, and partly utilized by wolves (Wood Buffalo National Park);

(5) Several dozen bison slaughtered at known dates for disease control, many of whose bones were scavenged by wolves and other animals after disposal (Wood Buffalo National Park);

(6) <u>15</u> moose, 10 of which were killed by known numbers of wolves on known dates (Isle Royale National Park);

(7) <u>15</u> deer killed by known or estimated numbers of wolves on known dates (Superior National Forest).

The study sample also includes many other, less well-documented remains of moose, deer, elk, pronghorn antelope, and bison. Complete records of over 800 other animal remains (wolf-kills or other natural deaths) have also been studied. Most carcasses and skeletons used in this study have not been modified by human activity in any way, except when wildlife researchers or I have collected bones or bone fragments. All skeletal sites have been re-inspected more than once over the year following death, and will be re-inspected several more times over the next two decades to monitor bone and body part modifications due to natural agencies.

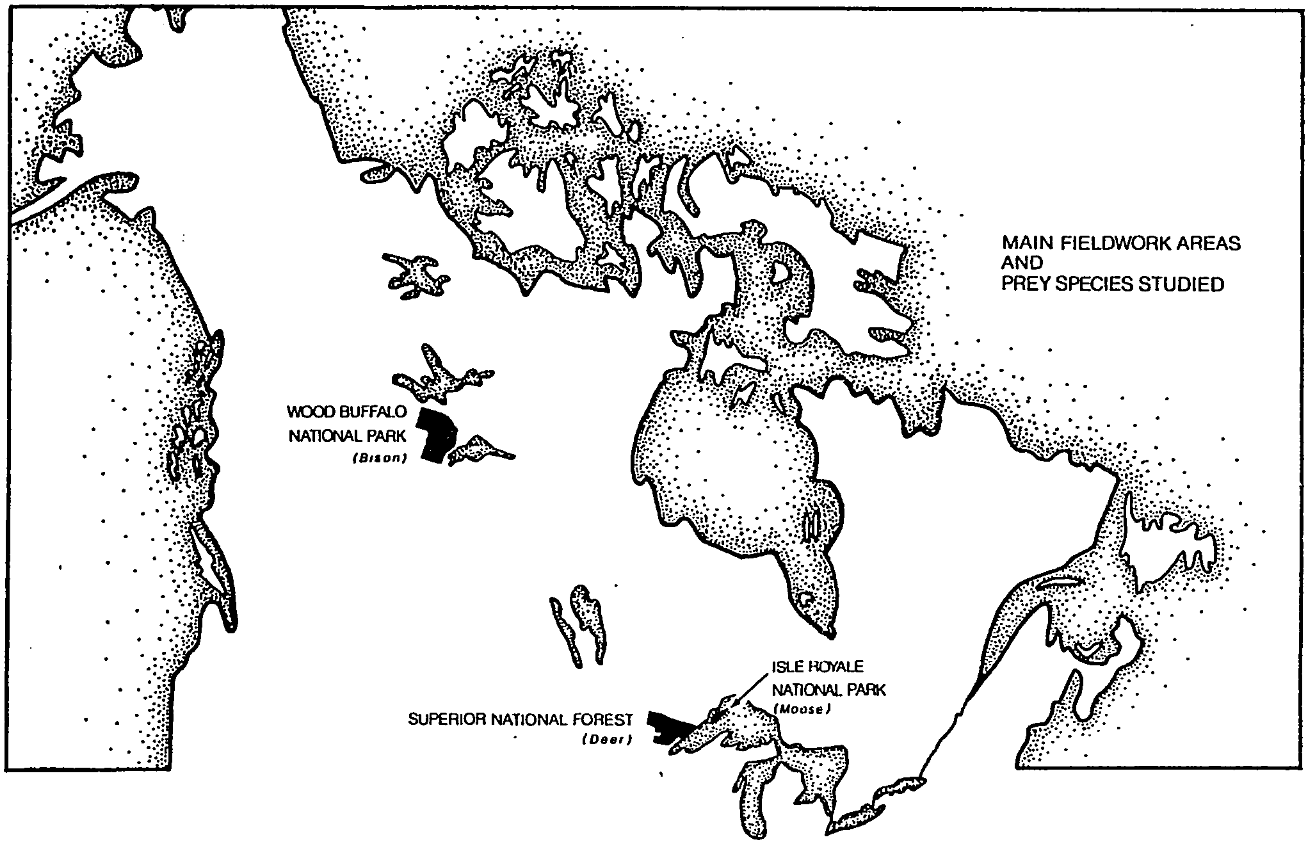


Figure 9. Map of major fieldwork areas.

VI. Field Study of Bone Damage and Carcass Utilization by Wild Wolves: Case Study I. Superior National Forest Descriptive Data

METHODS AND MATERIALS

Intensive biological studies of timber wolves and whitetail deer have been carried out in northeastern Minnesota for over a decade (Mech and Frenzel 1971) with the support of state and federal agencies. Current research is under the leadership of Dr. L.David Mech of the U.S. Fish and Wildlife Service. Since 1968 over 180 wild wolves have been live-trapped by biologists, fitted with collars containing radio-transmitters, and then freed to be regularly monitored from small, fixed-wing aircraft by means of radio receivers in the aircraft. Weights of healthy adult wolves have ranged from 25 to 42 kilograms (Mech 1977b: table 5). Many of these wolves associate with other wolves in territorial packs (Mech 1972, 1973, 1974), so that a remarkably high number of them have been under observation. A number of deer have likewise been monitored, and deer signs and deer have been observed systematically since 1972. Background information on the area and the animals is available in Stenlund (1955), Mech and Frenzel (1971), and Mech (1972, 1973, 1977a, 1977b).

The data used here were collected primarily by wildlife biologists working at the Kawishiwi Field Lab near Ely, Minnesota, during the fall and winter months of 1976-79; in 1979 I collected additional data while working at the Field Lab. The predatory and social behavior of wolves and the activity and distribution of deer vary substantially throughout the year, and only during the winter

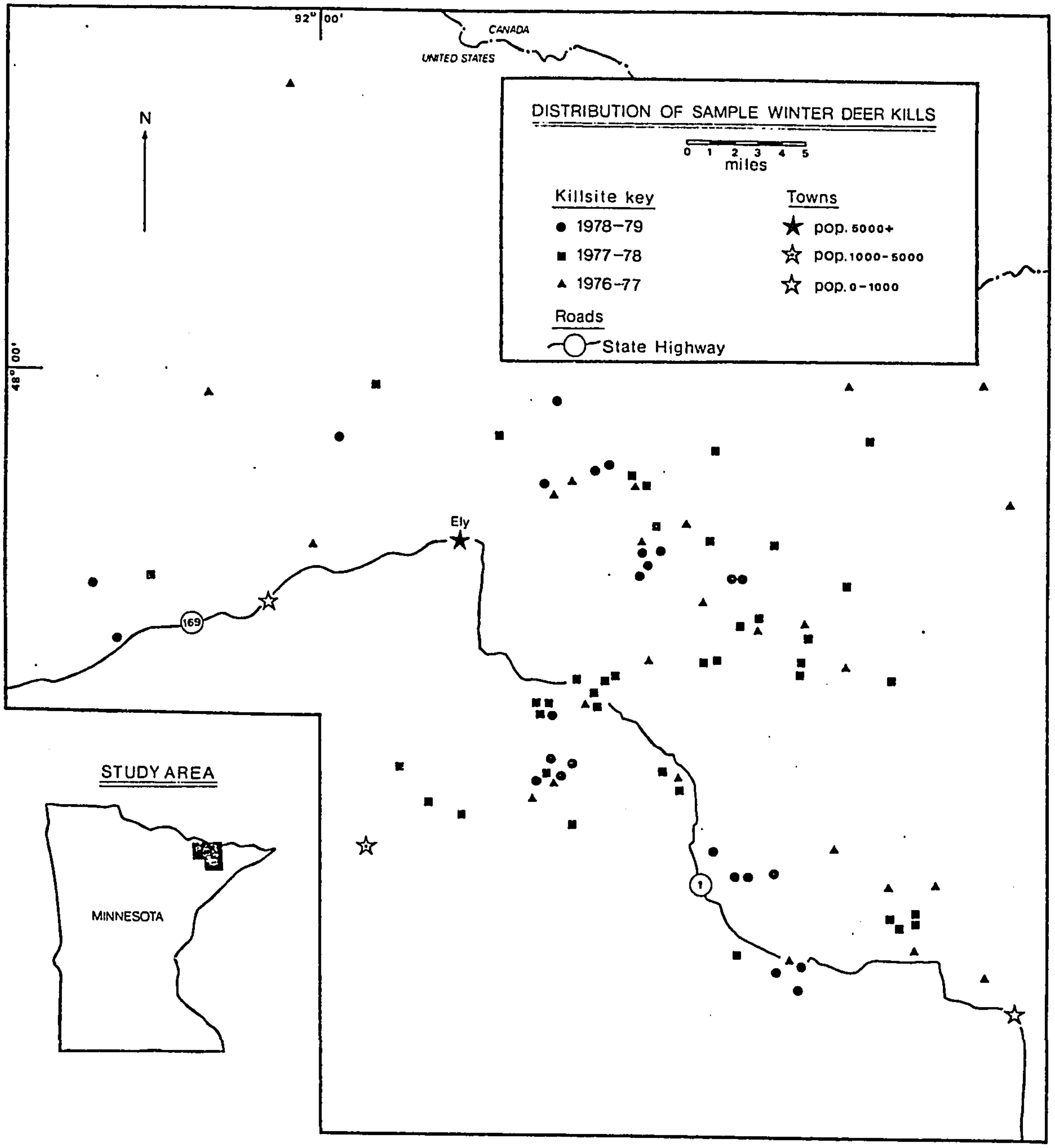


Figure 10. Map of deer carcasses in study area in northeastern Minnesota.

months are the necessary kinds of information on kills available. Most wolves prey on beaver in the summer, but subsist mostly on deer in winter (Mech 1977a). No large scavengers other than wolves are active in the area in winter, so winter kills are not disturbed except by foxes (*Vulpes vulpes*), fishers (*Martes pennanti*), and ravens (*Corvus corax*).

The current (1980) average density of deer in the study area (Figure 10) is about 0.6 per square kilometer (Floyd *et al*.1979), but was higher when most of the kills in the sample were examined. The density of deer in the area has varied from the recent figure to about 2.3 per square kilometer (Mech and Karns 1977). Each wolf in the study area killed on the average one deer every 15 days in winter (Mech 1977a). Deer numbers in the study area have generally been declining (Mech and Karns 1977) since the late 1960's, when maturing local vegetation reached seral stages less favorable as deer habitat, and a series of severe winters began. Wolf numbers have not declined in a direct relationship to the decline in deer numbers. Apparently wolves can resist numerical decline much more so than do deer and other prey, and may even respond to very localized and temporarily higher prey vulnerability by an increase in numbers (Mech 1977b). Wolves may also seek alternate prey, or may sleep more and travel less to save energy, or may expand their hunting territory or trespass neighboring pack territories (Mech 1977a:76).

For the purposes of this study, pertinent effects of the deer decline have been:

(1) Carcass utilization by wolves is higher. That is to say, much more of a deer is consumed now than before (Mech 1978 pers. comm.; Mech and Frenzel 1971:21-30).

(2) Wolf pack sizes have dropped, and amount of prey available and killed has dropped (Mech 1977b). There are fewer bone assemblages from kills per unit geographic area than there were before 1968, when the deer population first dropped seriously.

SAMPLE

Whitetail deer that had been killed by wolves in the intensive-study area (see Mech and Karns 1977:4) (Figure 10) were recorded on mortality data file forms by Mech and associates. I selected 94 kills as my sample, out of 700 on file, using the following criteria:

(1) carcass considered to be from unquestioned wolf-kill,
(2) kill occured between fall 1976 and late winter 1979,
(3) kill dated to within five days,
(4) kill located to within one mile on 1:250,000 scale map,
(5) number of hooves present at carcass noted,
(6) presence or absence of teeth (usually mandibular) noted.

In many cases the number of wolves feeding was also documented or estimated, and a general estimated percentage of kill consumed by wolves was made by the field observer (usually Wildlife Technician Jeff Renneberg).

However, completeness of data collected for the 94 kills varies, especially when different observers were involved. Therefore, many of the calculations used here do not consider all 94 kills. Of the sample, 26 kills were included from 1978-79 (out of a total of 30 recorded deer mortalities), 39 were included from 1977-78 (out of at least 60 deer mortalities and possibly a few more with incomplete identifications), and 29 were included from 1976-77 (out of a total of 45 recorded mortalities).

Figure 10 illustrates the distribution of 88 killsites for the three years. Not shown are five scattered kills from 1979, located about 40 miles west and northwest of Ely, and one kill from 1979 located about 40 miles south of Ely. Maps in Mech and Karns (1977: figures 5-7) show distributions of known kills in the area from 1965-75.

There are hundreds of small lakes in the study area, although none are drawn on Figure 10, and over half the 94 kills in the sample were located on the snow and ice of these lakes.

The territorial ranges of monitored wolves may have influenced the mapped distribution of kills, since unmonitored wolves were also making kills in the area. But because 43% (n=40) of the 94 kills were made by unmonitored wolves, yet were discovered by field researchers, it is possible that mapped distribution of kills approximates the true distribution of all carcass remains throughout the study area. Many smaller deer and fawns may have been entirely consumed, thus they would be underrepresented, but other serious biases may not exist.

DATA

Factors Related to Percentage of Carcass Remaining at Killsites

How much of a deer is eaten or carried away and how much remains at the site of a kill depends on three mutually interacting factors:

(1) The time that wolves spend feeding on the carcass negatively correlates with the amount of carcass remaining, if factors 2 and 3 are considered.

(2) Number of wolves feeding on the carcass positively

correlates with how much is eaten in any given time, as well as with how much is carried off to be gnawed or consumed, if factor 3 is considered.

(3) Motivation and hunger of the feeding wolves can affect factors 1 and 2, by causing a lengthening or compressing of the number of days a carcass satisfies the pack, or by causing a change in the degree of carcass utilization in given units of time.

My empirical controls over these variables were simple. For factor 1 (age of kill affecting use made of it by wolves), I sought evidence of the abandonment of killsites by feeding wolves. Although wolves may never permanently "abandon" a killsite, they do of course leave sites to make other kills. Wolves will defecate most ingested food from 8-56 hours after feeding (Floyd _et_ _al_. 1978:529), and they will therefore probably feed on kills at least every day or two, unless they leave the particular kill to make a new one. For some kills observed in this sample, if there were no wolf tracks less than 24-48 hours old, the kill was considered abandoned. If a monitored pack were observed elsewhere seeking or feeding on another kill or were observed more than one mile from the original kill, then the original kill was considered abandoned. A number of killsites was found to contain only the rumen of the deer, a part apparently almost inedible to wolves (or considered inedible by wolves), and also a patch of hide commonly 10-20 cm. square but rarely larger, and small bone fragments and splinters. Such an assemblage would not provide an adequate meal for an adult wolf, and was therefore considered an abandoned assemblage.

During the course of their territorial wanderings wolves re-encounter killsites and may devour the pieces of hide or bones and fleshy parts which may remain there. But kills of increasing age usually get covered with snow, freeze and dry out, and eventually become uninviting. Many re-encounters with older kills occur probably by chance rather than by design, especially those which occur years after the kill was originally made.

As for factor 2 (number of wolves feeding on carcasses as this factor affects utilization), the number of wolf tracks at killsites was evaluated, as well as the number of wolf bedding and gnawing sites where consumption and resting occurred. The radio-telemetry tracking system allowed visual documentation of exact numbers of wolves feeding on most kills.

Factor 3 (wolf motivation and relative hunger) is less ideally controlled. Even within geographic areas of resource privation, wolf hunger could vary substantially from individual to individual in the pack, because dominant animals are typically better fed than other pack members (Mech 1977:62). Large scale comparative studies may be necessary, allowing very specific comparisons between and among pack members in areas of high and low predator densities.

Direct Observations of Wolves

Before proceeding with the analysis of data, it might be instructive to present some examples of aerial tracking notes.

(1) 1979, 31 January: A pack of two wolves was observed at a very fresh deer kill, 50% of which was eaten (as estimated during low-level passes in the airplane).

Twenty-five hours later, on 1 February, the same two wolves were observed at the same spot, and the kill was estimated as 99% gone. Only parts of hide, the rumen, frozen blood, some bone fragments, and possibly two extreme lower limbs remained (J. Renneberg 1979 pers. comm.). In less than two days the two wolves had almost completely eaten a carcass. The deer was probably subadult.

(2) 1979, January: Three wolves were observed at a kill that was 90% eaten; the rumen remained, as well as two or three lower legs, some hide, vertebrae, pelvis, and scapulae. Forty-eight hours later the same three wolves were recorded at another kill that was 90% eaten, located about 8 km. from the first site. In one and a half days three wolves had almost completely utilized the second carcass.

(3) 1979, 8 February: A lone wolf was observed at a kill that was 80% gone, and this wolf had been plotted the same place the day before. About 20 hours later the wolf was once more recorded at the same place, and again 28 hours after that (10 February) was spotted at the same site. Twenty-four hours later this loner was elsewhere. This one wolf spent at least three days at a single kill, and fully utilized the carcass.

(4) 1979, 8 February: A lone wolf was observed at a 90% eaten kill, whereas about 24 hours earlier this wolf was recorded 9.7 km. away. This wolf was probably eating a very small deer or a fawn, or was scavenging a carcass killed by other wolves or by other causes, since a single wolf would probably not be able to eat 90% of an average sized adult deer in such a short time (Mech 1977a).

(5) 1979, 12-14 February: A lone wolf was observed for three days within 275 meters of the same spot, although a kill could not be seen from the air. On 11 February this wolf had been several kilometers

away.

(6) 1979, 7 February: A lone wolf was observed at a kill on a lake. The carcass appeared to be about 80% utilized; that is, possibly all four lower legs remained, as well as the head and some vertebrae, some ribs, the pelvis, possibly one or both scapulae, some hide, and the rumen. Twenty-four hours later, when the kill was examined on the ground, these parts were still remaining at the site, with the exception of one lower leg and one scapula. A single wolf scat at the site contained three small fragments of upper leg bones. Both of the recovered rear legs had breaks at midshafts of the femora, but were otherwise undamaged down to the hooves. The lone wolf had utilized about 10% of the already well-eaten carcass in a day.

Synthesized Data on Winter Feeding by Wolves

Deer in the study area are generally killed by packs after a pursuit that may end up on frozen lakes, usually less than 30 meters from any one shoreline. In this study packs contained up to nine wolves, but mean size was about four. Wolf numbers were sometimes estimated from tracks at killsites, so it is possible that a number of packs were larger than recorded. This is because wolves prefer to travel in tracks already made in the snow. The clarity of tracks and the number of resting imprints at the end of some tracks were occasionally observed, to strengthen estimates of wolf numbers.

Feeding behavior begins before the deer is actually dead; in fact, it may well be that the urge to pull off a piece of the prey is what kills the deer - it is simply pulled apart (Klinghammer 1979 pers. comm.).

I have directly observed 10 carcasses in the wild, and I have received complete collections from five others and partial collections from 35 more; these carcasses ranged from fully utilized to very poorly utilized. It is from observations on these materials that the following discussion is derived.

The deer's paunch is penetrated very early, and most organs and blood are immediately consumed. If more than two wolves are feeding, meat from the deer's rump and upper rear legs are next consumed, during which process the proximal ends of femora and the pelvic bones often suffer gnawing damage (tooth scoring of compact and cancellous bone occasionally, and breakage of long bones). Ribs and vertebrae, one scapula, and the entire pelvis are soon exposed and partially gnawed, as hide and muscle is consumed from these elements. The throat may be opened up and the tongue partly eaten. The angle of one or both mandibles may be slightly gnawed or chewed off. One scapula is disarticulated and the lateral tuberosities of the humerus are damaged or gnawed off. One entire forelimb may then be disarticulated from the rest of the body, as is a rear limb (still assuming that a medium-size pack is feeding). The femur may be disarticulated at the acetabulum, or may suffer a midshaft spiral break. Deer carcasses can be rolled and twisted by even a single feeding wolf, so the carcass need not remain lying on one side. If more than three wolves are feeding, one or two legs may be removed from the killsite within two hours.

Single wolves may carry off disarticulated lower limbs, individual bone elements, or units of articulated bones to gnaw on privately although they have not yet eaten their fill of red meat. Individual wolves may gnaw pieces of a carcass up to 30 meters from the main killsite, but usually nearer. If each wolf has eaten at least

1.5 to 2.5 kg. of deer (but probably much more - 4.5 to 6 or 7 kg. is likelier [Mech 1979 pers. comm.]), it may rest or sleep near the kill, to return and feed perhaps 3-8 hours later if any part of the carcass remains. At that time parts of the skull and the ribs are eaten. The head as a unit may also be removed from the killsite and be consumed elsewhere (but nearby). By about one half day after feeding has begun, meat scats may occur at the killsite, runny or semisolid or containing densely compacted deer hair with chips and splinters of undigested bones inside (Floyd et al.1978). Some of the bone fragments are identifiable, including articular ends of ribs or teeth segments.

Rear legs not carried away from the killsite or fully consumed there may be gnawed down to the tarsal bones, which remain articulated to the ungnawed metatarsal; forelegs may be eaten to the articular distal end of the humerus. Hide and ligaments may keep the elements from ankle and wrist down to the hooves in articulation.

Sites of solitary gnawing and consumption by wolves may contain lower legs in gnawed or eaten conditions similar to those seen at killsites, or possibly more damaged (see Ream and Smith 1980:3 for brief descriptions of a single wolf's transported bones or food caches). These sites are difficult to find even when tracking wolves in fresh snow, since elements may be picked up and gnawed many times in several different places before being finally abandoned or consumed. Conceivably these sites could contain the same elements that characterize killsites, especially when larger packs feed. In an effort to eat peacefully, members of larger packs may more often escape the crowded killsite with a dismembered piece of the carcass than would members of small packs. However, due to the solitary and scattered nature of consumption sites and the tendency of wolves to eat ravenously, there would never be more than a single bone or fragments of single bones or single small articulated bone units at secondary sites; more likely, these sites would be only stained places in the snow with some deer hair and possibly a few bone chips around.

Ribs and vertebrae, after initial cleaning by wolves at the killsite, may be thoroughly cleaned by foxes, fishers, and ravens, but suffer little or no additional breakage and gnawing damage.

Wolves and foxes sometimes carry the rumen a short distance, a few meters if at all, possibly to lick blood from it, but it regularly occurs at killsites even after all the hide is devoured and most lower legs have been eaten.

Skulls and mandibles are either carried off or consumed at the killsite. Crania are broken into for brains, and only toothrows may survive; mandibles show damage at the angles (from early feeding through the throat to get at the tongue) and lower borders, which are often removed. Generally at least two legs have been disarticulated and eaten or carried away to be consumed before the head is damaged, assuming pack size to be about three to five wolves.

A proposed sequence of consumption, based on numbers of feeding wolves, has been synthesized from data on the 94 sample kills as follows:

1 wolf: Three days to utilize all but rumen, about one square foot of hide (sometimes up to a square meter may be unconsumed), perhaps two lower legs from midfemur through hoof.

2-4 wolves: One to two days to utilize all but rumen, some hide, all but one or two lower legs.

By the end of day one, meat and hair scat from wolves, foxes and ravens appear at the site.

5-7 wolves: if hungry, under 36 hours to utilize all but rumen, some hide, one or two lower legs (tarsals to hoof or carpals to hoof).

By day 2, if a pack of three wolves has been feeding, all legs are cleaned of soft tissue down to the metapodials, and two legs may no longer be at the killsite. Ribs, vertebrae, and fragments of pelvic bones, as well as mandibles (minus angles and perhaps lower borders) may survive. The cranial teeth, with a little attached bone (palate or maxillae), and nasal portions of the skull may also remain.

After the killsite has been abandoned occasional scavenging may occur. At this time only rumen, hide, and one or two lower legs remain at the site; mandibular or maxillary toothrows or parts of rows sometimes remain, as do pieces of ribs, parts of scapulae and pelvis. Sometimes only bone chips remain; even pieces of frozen hide have been scavenged.

Figure 11 illustrates the number of wolves in packs included in this sample by year as graphed against the mean number of days required by those packs to reach 85% utilization of a carcass, which would be the point at which at least two legs have been removed or eaten, and scat containing ribs and teeth might be found.

It must be pointed out that the "number of days a pack feeds on a kill" was oftentimes estimated by field personnel, as based on times of recorded sightings of packs near or no longer near carcasses, age of tracks around kills, or other indirect evidence. The greatest potential cause of error in the calculations of mean numbers of days (in Figure 11) would be the fact that deer mortality data files contain only observed or estimated dates for when kills were made, and dates for when killsites

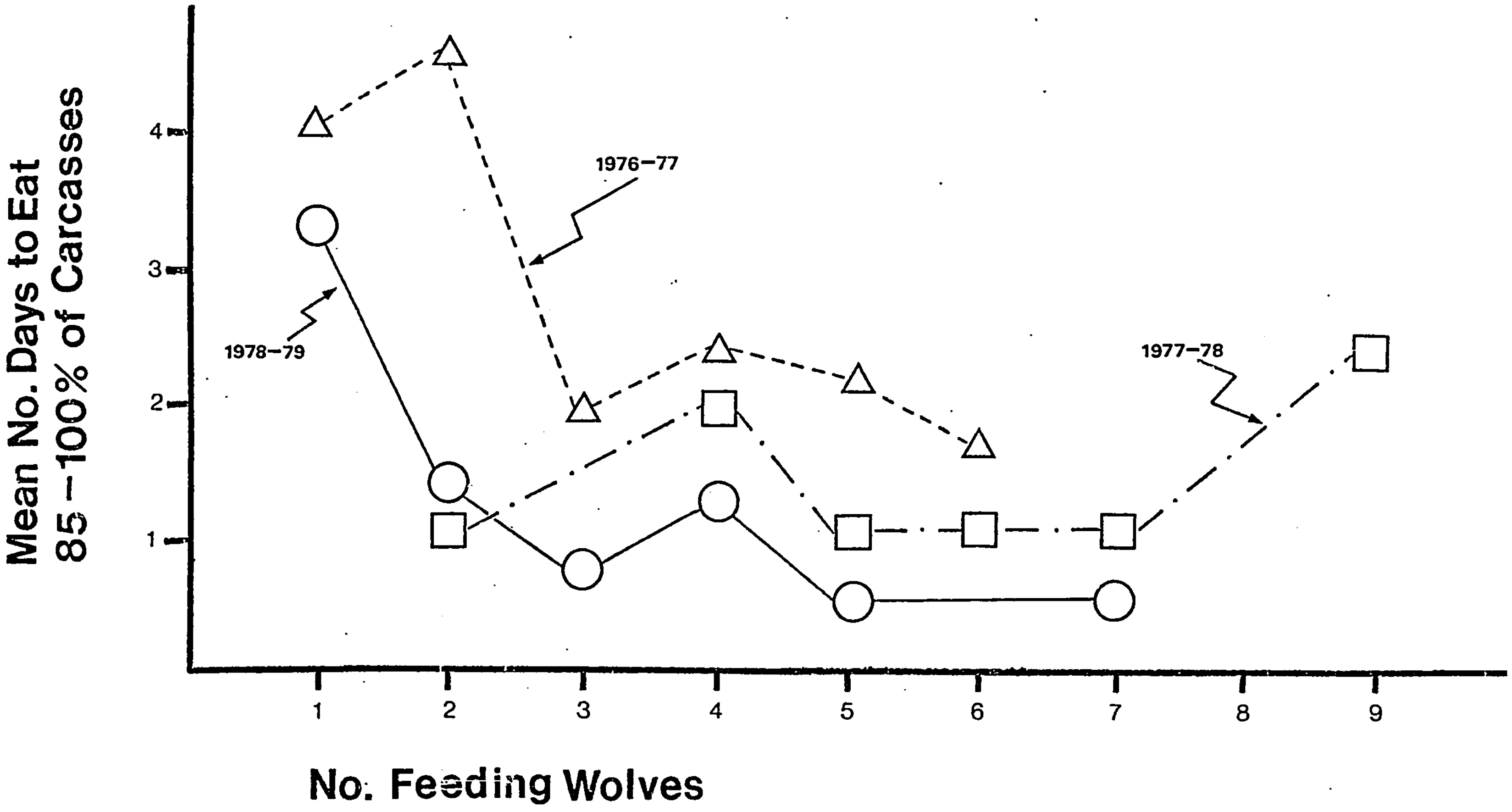


Figure 11. Graph of mean number of days wolves took each year to eat 85-100% of Whitetail Deer carcasses.

were visited by a biologist, which might have been the same day that wolves abandoned the site or days later. Therefore, the number of days wolves feed on kills, as I have interpolated the information from data files, is from time to time an inflated estimate.

During both 1976-77 and 1977-78, kills made by a nine member pack were investigated after two to five days, averaging over three days, a rather long feeding duration for such a large pack. The figures for this large pack do not fit the curve suggested by the points graphed on Figure 11. It is possible that observer scheduling of visits to kills was affected by unrelated and unrecorded factors such as bad weather, but it is also possible that the large pack actually did spend more time at kills, which may have been large adult deer. All kills used in this sample and made by the large pack were very well utilized; in all cases where more time of feeding is involved, the degree of utilization is higher.

ANALYSIS OF DATA

Deer Representation by Selected Elements at Killsites

Field biologists rarely recorded the presence or absence at killsites of most bone elements, because there was little interest in such data. In the sample of 94 kills there are complete inventories for only 12 assemblages, nine of which I investigated in the field during several days of aerial and ground reconnaissance in February, 1979. For each of the other kills in the sample there are annotations on presence and number of hooves (which information has been interpolated to find number of lower legs), and presence or absence of incisors or other teeth (herein interpolated to indicate mandible and mandible fragments or cranial toothrows). Figure 12 summarizes available or interpolated data on presence or absence of teeth, phalanges, pelvis, and vertebrae/ribs units. Also included in the table is the number of killsites that contained only bone fragments. In all cases on the table, the designation n refers to the total number of killsites with adequate records to indicate presence or absence of the selected elements or units.

The percentage for phalanges would probably hold true for metapodials as well, since no hooves or phalanges were ever observed without a metapodial still attached.

Judging from the kills and assemblages I have personally examined (n=15) and from the data available on the better annotated kills in the sample, it appears that lower legs are by far the most common surviving bony parts at deer killsites when carcass utilization is high. These parts of the deer are least desirable to wolves (leaving the rumen out of consideration), because they contain little meat and are relatively hard to chew, although wolves certainly are capable of eating them. I conclude that if wolves eat lower legs they are unusually hungry, possibly because pack size has surpassed an optimal upper limit for the prey on hand or the prey that is preferred.

But there is more than the fact of hunger or lack of it reflected in bone assemblages such as those under analysis. Variation in the survival of certain bones at each killsite is related to other variables which would not be immediately apparent to a paleoecologist who has not had the opportunity to observe his fossils being deposited.

At this point a paleoecologist might consider that the number of lower legs at a site constitutes a valid and direct index of wolf hunger,

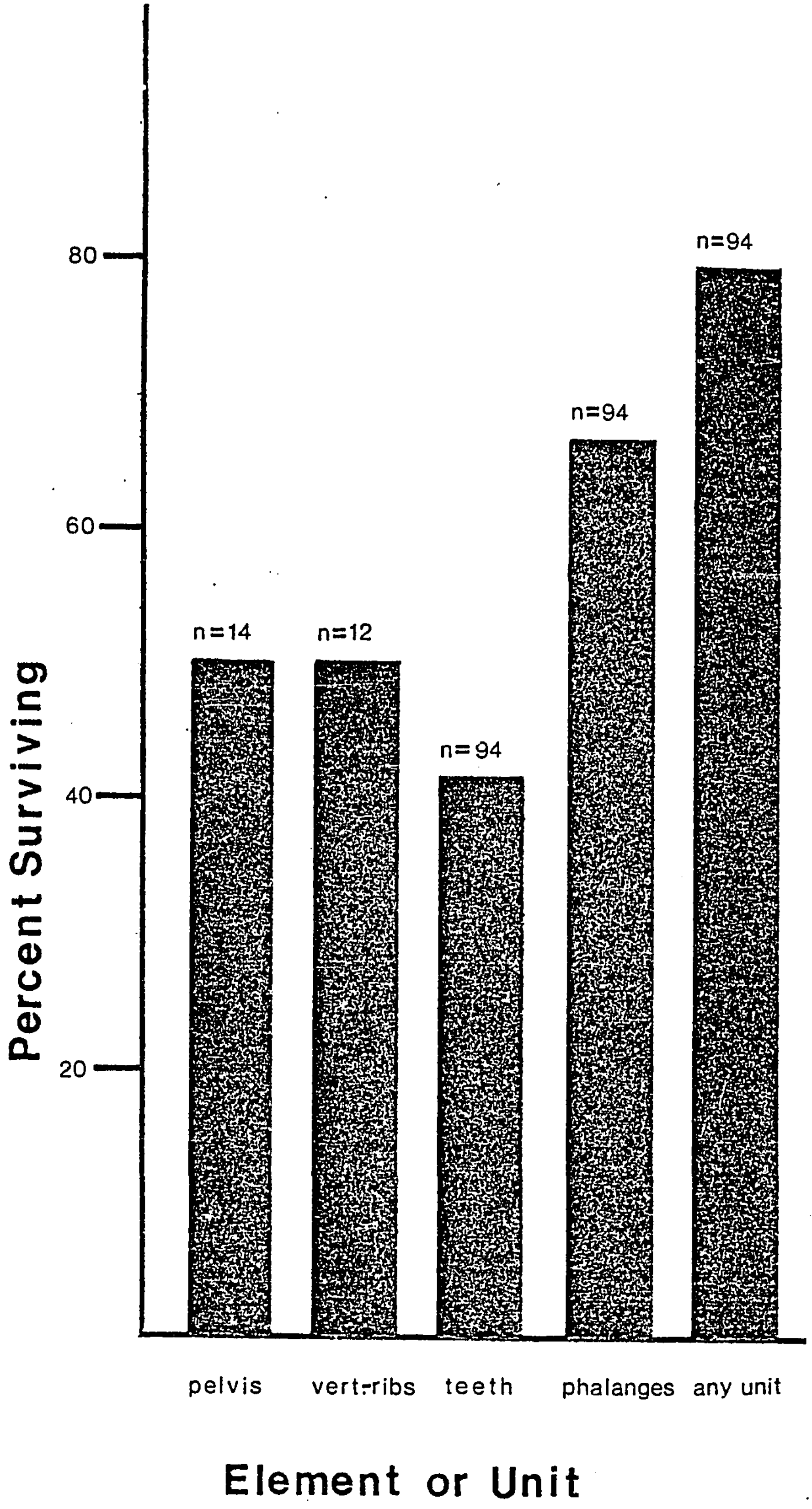


Figure 12. Graph of actual bones or bone units remaining at killsites compared to potential numbers of bones or units.

if he realized that lower legs are least desirable to wolves. But two other factors would in effect be undiscoverable to the bone analyst: number of wolves in the feeding group and number of days the carcass was fed upon.

To illustrate time trends in carcass utilization the paleoecologist might graph the number of lower legs eaten at killsites against the number of cases per year (or per epoch or age or whatever) (Figure 13).

The graphs of my three year sample would show that utilization of sampled carcasses was very high for 1976-77 cases, while for 1977-78 cases carcass utilization dropped considerably, only to rise again the final year, 1978-79. These trends require some examination.

The year before the first kills of my sample were recorded (that is, from 1975-76), the numbers of wolves in the study area rose unaccountably. Mech (1977b:566) suggests this may be due to an unobserved slight rise in the number of deer in the area. I would speculate that if the higher wolf numbers survived into 1976-77 and I sampled their kills, they were being poorly sustained by deer, since most carcasses were being fully utilized. The next year, 1977-78, carcass utilization was down although the mean size of packs has not significantly changed from the year before (Table 6-1). If there are no sampling errors involved, one possible explanation for the change might be a rise in the number of vulnerable prey. An increase in deer numbers could push up the proportion of vulnerable prey available (specifically by increasing the number of fawns), but a severe winter could also achieve the same result, as well as a number of other factors, such as the passage into old age of a high proportion of the deer population, if

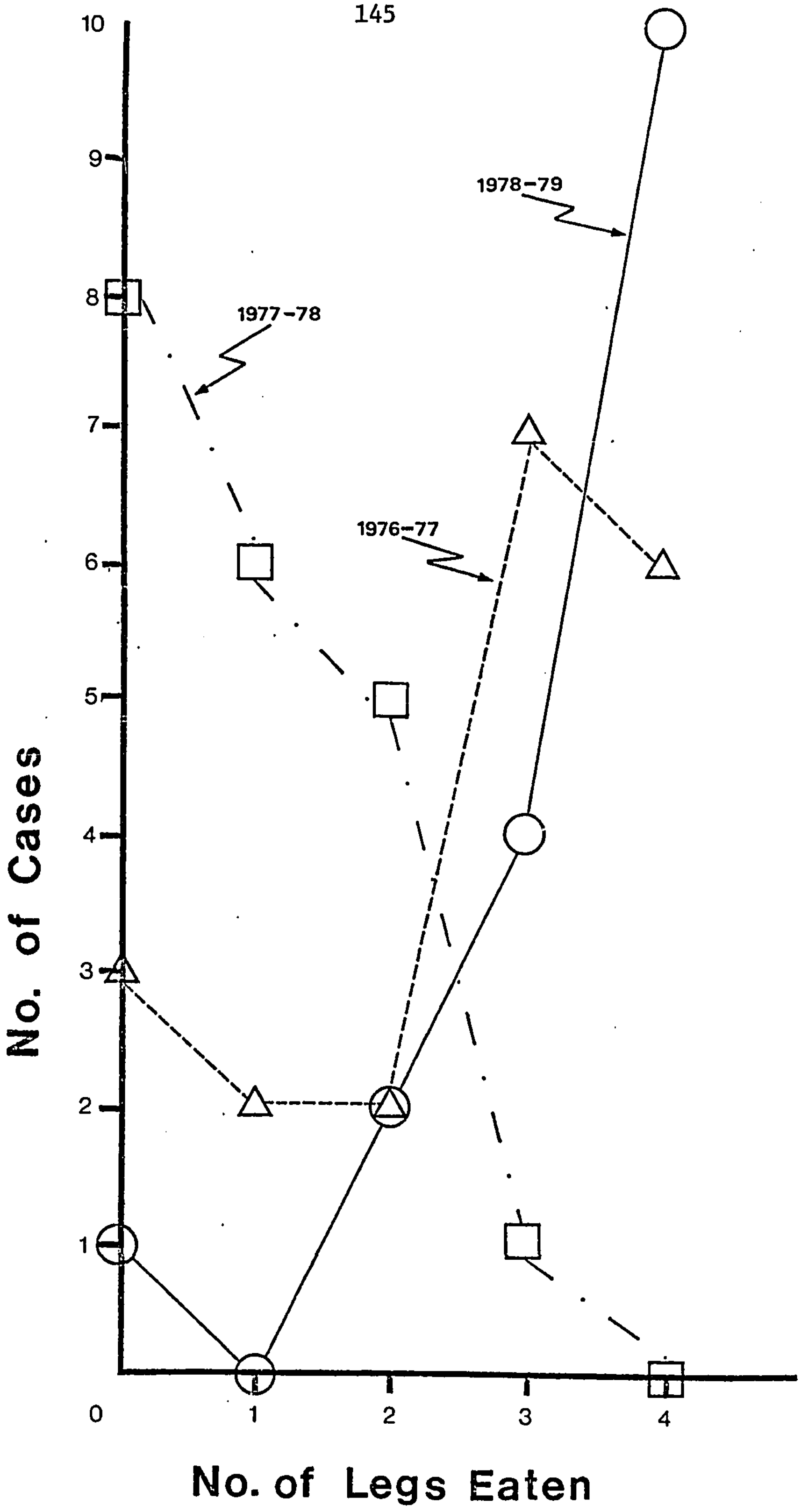


Figure 13. Graph of number of lower legs of Whitetail Deer eaten by wolves each year.

Table 6-1

<u>Mean pack sizes per recorded kill per year and mean number of lower legs eaten per kill and per wolf per year:</u>

Mean pack size	Mean number legs eaten	Mean pack size	Mean number legs eaten	Mean pack size	Mean number legs eaten
4.6	3.4	4.8	1.7	2.8	2.5
n=15		n=26		n=20	
0.72 leg per wolf		0.35 leg per wolf		0.89 leg per wolf	
1976-77		1977-78		1978-79	

productivity has been low. Whatever the cause, the effect is that pack sizes remain relatively large but carcass utilization becomes relatively low.

Note the distinction is made between prey vulnerability (high likelihood of being killed) and prey availability (simple existence of any prey within a wolf territory or catchment area). Also note that a greater availability of prey usually means there will be a greater number of vulnerable prey, such as the old, the sick, or the very young (Pimlott *et al*. 1968; Mech and Frenzel 1971; Mech and Karns 1977), if the age structure of the population remains consistent (that is, the proportions of age classes in the population do not undergo major changes).

Subtle differences in feeding strategies are suggested by the graphs of Figures 11 and 13. In Figure 11, the 1977-78 scattergram would have a nearly horizontal regression line, indicating that all size packs spent nearly the same low amounts of time at each kill (a bit more than one day on the average). This was observed during the same time that carcass utilization was relatively low, as seen in Figure 13. The following year, 1978-79, carcass utilization was high (see Figure 13), and Figure 11 shows that smaller packs spent more time at each kill than did larger packs. These trends are similar to those shown in Figures 11 and 13 for 1976-77: high carcass utilization, longer amounts of time spent at each killsite.

Table 6-1 tabulations can be used to illustrate that the mean number of lower legs eaten per kill per wolf is lowest for year two (1977-78), when pack size was still large on the average. The mean number of legs eaten per kill per wolf rises in year three (1978-79), and is over two and one-half times greater than in year two; pack size has dropped in year three to only about 2/3 of the year two level.

At this time it is not known if deer numbers in the study area are holding steady or are declining still, but they probably have not increased in the last four years (Floyd _et_ _al_.1979). Wolf numbers may have remained stable from 1976-77, and then dropped between winter 1977-78 and winter 1978-79 (Mech 1979 pers. comm.).

The paleoecologist at this point must realize that high utilization of carcasses can be explained either by low vulnerability of prey or by greater relative densities of predators. Unfortunately increased predator numbers (as measured per kill, as the size of the feeding group) for all practical purposes makes each unsatisfied wolf just as hungry as would lower prey vulnerability or availability. Wolves might use the same changes in strategies to compensate for continuing prey decrease as they do to compensate for temporary, insupportable increases in their own numbers while prey numbers hold steady.

A simple index of deer vulnerability per killing pack can be computed by inserting mean values for wolf pack size per kill, and mean estimated carcass utilization (expressed as a percentage of uneaten deer) into the formula

$$V = \frac{\bar{w}}{u},$$

Where V is ease of hunt or vulnerability index,

$\bar{w}$ is the mean number of wolves per feeding pack,

and u is average utilization of carcasses.

It can be seen that if wolf numbers rise and utilization remains at the same level, the vulnerability index also rises, indicating that deer are probably becoming easier to kill, for whatever reasons, and are not necessarily more numerous. Obviously the numerical value of V is meaningless unless there is another V value to compare: a high utilization value associated with large packs could yield a V identical to that resulting from a low utilization value associated with small packs. V indicates only a relative ease of successful hunting.

The Quaternary paleoecologist eager to find some way to estimate relative numbers of predators affecting fossil assemblages could probably determine utilization easily enough, assuming minimal post-mortem disturbance, but would have to estimate prey vulnerability from evidence of pathology, age, size, or related indirect evidence. However, the vulnerability index formula begins with knowledge of predator abundance: wolf pack sizes and densities in a variety of ecologic communities can be confidently applied to the past (if past predators were comparable to recent predators: this is a crucial interpretive step). If social canids were not involved in the fossil assemblages, of course, figures for other carnivore types must be applied.

At this point in the interpretation of fossil bones it becomes necessary to distinguish carnivores responsible for gnawing damage. I think this can be done. A discussion of the characteristic gnawing damage done by different carnivore families is found in Chapter 4.

If wolves or closely related canids were involved with the fossil assemblage of bones under analysis, it is possible to assign probable pack sizes to feeding wolves, using analogues from recent communities: where moose (*Alces alces*) and bison (*Bison bison*) are main prey in winter, wolf packs often contain more than eight and fewer than 18 members, averaging probably nearer 10 (R.O.Peterson 1977:185; Oosenbrug and Carbyn in prep.); packs preying on mule deer (Odocoileus hemionus) and elk (Cervus canadensis) often number 6-14 members (Carbyn 1974); packs preying on moose and caribou (when seasonally abundant) may include up to 12 to 15 members (Haber 1977); the most common size for packs preying on caribou is 6-10 members (D.R.Miller 1979; Alaska Dept. of Fish and Game 1976:58); packs preying on whitetail deer may have seven or fewer members (Mech 1973, 1977b). It must be noted that mean pack size figures very often are not the same as mode figures. This is a subject for future investigation. These pack size figures may apply only during the main predation seasons in areas where human interference is minimal. In other times of the year packs are usually split and scattered for the rearing of young in family groups, and pack sizes may be cut by one half or more from the main predation season size. The sizes and vulnerability of preferred prey and factors of social interaction directly affect size of wolf groupings (D.Allen 1979; Carbyn 1974). Note that it has been shown that pack sizes will vary during times of ecosystemic stress. When calculating relative values of the Vulnerability index, it would be useful to insert minimal pack sizes in the formula, as well as the optimal figures given above. It probably takes no more than three wolves to bring down an adult bison or a moose, but four or five could do it with less effort and more often. A single wolf could kill a deer or a caribou, but three would stand a better chance of making a living at it, and would be far more likely to contribute carcasses and skeltons to the future fossil record.

After estimating wolf members and assessing carcass utilization, a paleoecologist can use the index formula to compare prey vulnerability over space or over time. When dealing with prey larger than deer, even single bone elements may provide all necessary evidence of degree of carcass utilization. Larger prey will be discussed in following chapters.

Even after computing possible relative vulnerability indices the paleoecologist will still be faced with the problem of determining the causes of changes in prey and predator relationships. At this point analogues from other experimental and empirical studies in ecology must be applied.

Returning to the data on hand, Table 6-2 presents available age and sex data for the sample. Aging and sexing data were unknown in more cases than they were known. For year two (1977-78) 32 deer were aged out of 46 reliably-documented wolf-kills. The fawn to adult ratio is 1:3.6. For year one (1976-77) only seven kills were aged out of 26 possible, and the fawn to adult ratio is 1:6. This latter figure must not be accepted without caution, because so few kills were aged out of a larger sample.

If these fawn to adult ratios are legitimate for years one and two, it is possible that wolves in the second year were preying more heavily on vulnerable fawns, thus allowing packs to remain relatively large and the time spent at each killsite to be short. Information on productivity in the study area is not yet unequivocally available; however, it is known that the winter of 1976-77, when the 1977-78 fawns were in utero, was the mildest since 1971 (Mech 1979 pers. comm.). It would certainly not be unreasonable to expect that productivity of deer could have shown an increase that year.

Of course, variance in the data may be accounted for by sampling error or by behavioral changes in the wolves. For example, if wolves in the study area were substituting moose for deer as preferred prey species,

Table 6-2

<u>Aging and sexing data:</u>

sex	age class	number identified 1976-77 n=26	 1977-78 n=48	 1978-79 n=29
unknown	under 1 year	1	7	4
male	over 1 year	4	15	---
female	over 1 year	1	4	---
unknown	over 1 year	1	6	3
	total identified	7 (27%)	32 (67%)	7 (24%)

then the utilization of deer carcasses may drop a great deal but pack sizes need not change. There is no evidence for this, however. If a sampling error is involved, at least it is provocative.

Synopsis of Observed Gnawing Damage to Deer Bones

Descriptions of element damage and body part dispersals are sequentially catalogued in a section above; to supplement the descriptions, summaries of bone damage are synoptically arranged in this section by bone units, these being articulated or disarticulated bones ordinarily fed upon or abandoned together.

These analytic units are:

(1) Head and first two cervical vertebrae (which eventually become disarticulated).

(2) Rib cage and some cervical and thoracic vertebrae articulated with sternum.

(3) Scapula.

(4) Lumbar vertebrae and pelvis.

(5) Leg, from femoral or humeral head to hoof.

Some killsites may contain no analytic units or complete elements, but almost always contain dozens of pieces of broken long bone shafts (Figure 14, top) vertebral processes, and ribs. I have examined six fully collected fragment assemblages containing 12 to 60 pieces altogether, and only two or three bone fragments in any assemblage show even slight tooth marking (scoring of compact bone, caused by cusps of cheek teeth drawn across bone, or scratching and crunching). Most of the fragments are clean of any surface damage except for a rare depressed and splintered notch along a broken edge, caused by crushing with tooth cusps. This latter damage incidentally looks very much like the results of impact fracturing by a blow from a small pointed rock or hammer, the kind of damage done by human beings splitting long bones to extract marrow (see Figures 55 and 60).

(1) Head and Neck

When carcass utilization is low, heads and necks may not be damaged, and usually remain articulated to the body. Nasal bones may be slightly gnawed - edges are roughened, scratched by teeth, or splintered. The angle of the mandible (on one or on both) may be broken off if the tongue of the deer is consumed. With well utilized carcasses only toothrows of the mandibles and cranium may remain. Most killsites in the sample (59%) contained no teeth. At one personally observed killsite a piece of mandibular tooth was found in scat associated with one uneaten lower rear leg. This particular kill on a lake had been utilized by two wolves, and the lack of more meat or hair scats nearby supports the suggestion that the wolves entered the woods 25 meters away after every feeding, there to rest or sleep or possibly continue gnawing on bones. No bones or bone fragments were found in the bedding sites left by these two wolves.

Mandibles may be broken apart at the symphysis or posterior to it on either side. There may be depressed fractures from tooth crunching, and lower borders may be broken off to expose marrow cavities.

(2) Ribs/Vertebrae/Sternum

The sternum is usually completely splintered and consumed. Ribs, perhaps six or eight on each side, may remain articulated to vertebrae, although their ventral (or sternal) portions have been eaten. This

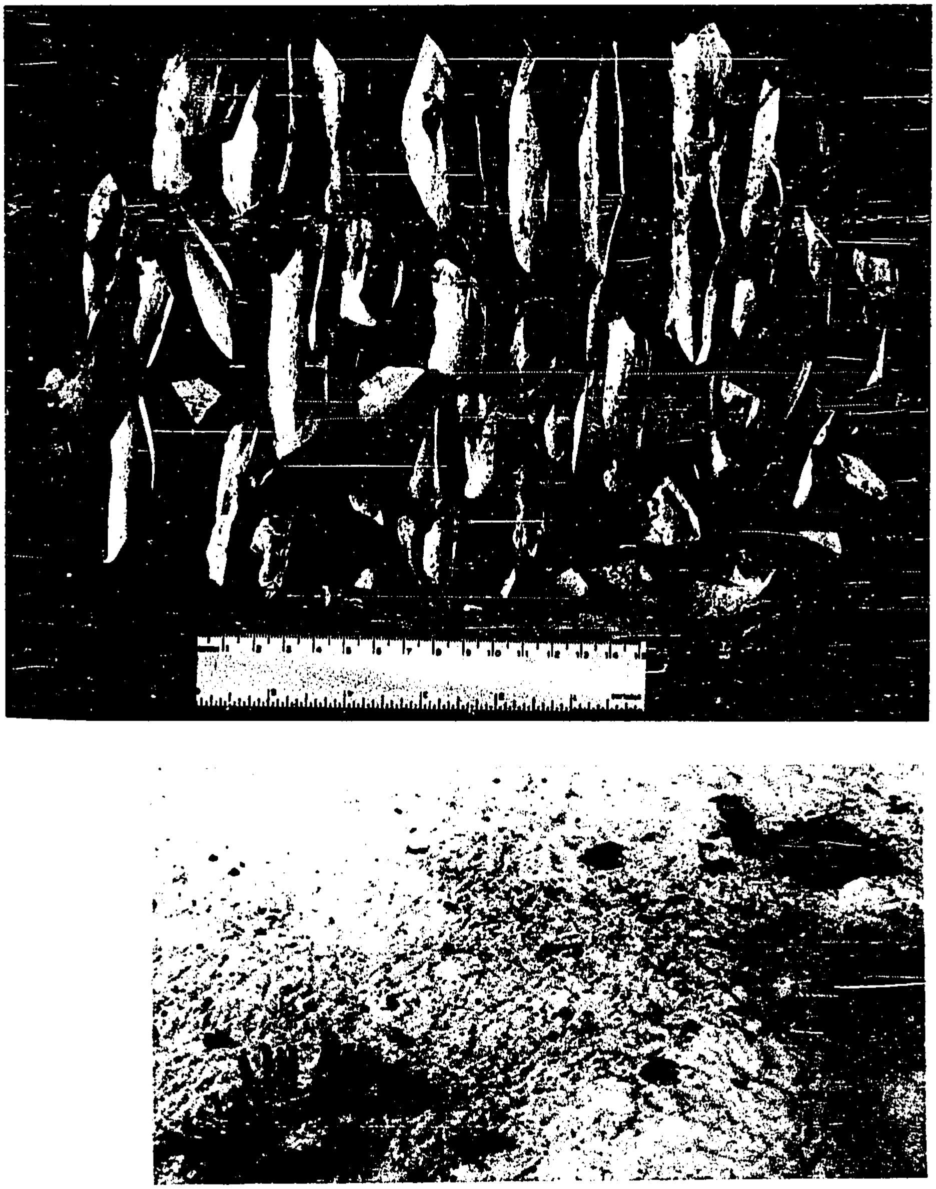


Figure 14. Deer bones from killsites.
TOP: Complete assemblage of bones from a single Whitetail Deer killsite.
BOTTOM: Rib-vertebrae unit and rear leg unit remaining at killsite of Whitetail Deer, lying on bloody, trampled snow which covers a frozen lake.

entire unit is detached from the head and from most cervical and lumbar vertebrae (Figure 14, bottom). All spinous processes on vertebrae are broken or splintered on well utilized carcasses. Most lateral processes also suffer breakage, and vertebral bodies may show isolated tooth marks (round bottomed depressions the size of tooth cusps).

(3) Scapula

One or both scapulae are disarticulated early in the consumption process. Only the vertebral borders may show damage, especially on lightly or moderately utilized carcasses. If a scapulae remains at the site of a well utilized kill, only the glenoid portion will usually survive.

(4) Lumbar Vertebrae/Pelvis

The pelvis may remain articulated to the sacrum and to several lumbar vertebrae, which have suffered loss of most processes. Ischial and ilial tuberosities and edges are almost always gnawed, and the pelvis may be split into right and left innominate halves. On better utilized carcasses, each half may be destroyed by gnawing down to the thicker bone surrounding the acetabulum.

(5) Legs

All legs are eventually disarticulated from the body; on very lightly utilized carcasses only one leg may be separated. At better utilized kills the surviving legs will be articulated from third phalanges (usually still in their hoof sheathes) up through metapodial, and often to midshaft of the tibia or distal end of the femur, or to distal end of the humerus. One upper long bone on every leg, fore or rear, is commonly broken (Figure 15).

In very poorly utilized kills the proximal tuberosities and head of the humerus, and the greater trochanter and trochlear rims of the femur may be damaged by gnawing. The olecranon process of the ulna usually appears bitten or broken off. Typical gnawing damage consists of tooth scoring and scratching on compact bone, removal of epiphyseal tissue, and gouging or furrowing of cancellous bone.

DISCUSSION

New Models from the Observations, and Propositions

The final approach in this research is to design ecological models based on logical propositions derived from observations. These propositions are concerned with the potential fossil bone representation of prey the size of deer, and slightly larger or smaller, killed and fed upon by wolves.

Killsites

(1) In geographic areas of low prey vulnerability, due to low prey availability, for the most part, or higher than optimal predator density, or combination of factors of unusual ecosystemic tension, social carnivores such as wolves would most likely devour nearly all the carcass of deer-sized prey (weighing up to 120 kg.); a number of bone fragments might survive at killsites, but tooth marks and unmistakeable gnawing damage need not occur on the bone pieces. Lower legs might survive as articulated units, but rarely or never would all four legs be present at killsites. The next most common surviving bone elements, although still rare, might be toothrows.

There is a very low probability of such killsites being discoverable as discrete sites by paleoecologists even if the sites occur in certain limited areas, such as wolves' winter territories or core hunting territories (see Mech 1977a), because kills tend to be more scattered as prey numbers drop (Mech 1977a:78-80). However, over decades of predation it is possible that certain lakes, for example, might accumulate relatively large bone assemblages within bottom and nearshore sediments. If these sediments are stratified and not subject to serious current disturbances, it might be possible to distinguish short term episodes of low prey vulnerability by separating out the levels containing extremely well-utilized carcass remains.

(2) In areas where the conditions of ecosystemic stress are less severe, but are still not near homeostasis, carnivore killsites might contain more lower legs more often, and might contain (in combination with at least one lower leg) other bones or units such as partially destroyed mandibles, ribs and vertebrae, and long bone fragments.

There is a low probability that these sites could be predictably located, but again the bone assemblages could be defined out of stratified deposits. Remains of kills that accumulate in nearshore sediments of lakes might actually be abundant in circumscribed spots, since deer are creatures of habits and wolves will also habitually hunt areas where past successes are remembered.

(3) In areas with optimal or "normal" ecosystemic conditions, killsites would be characterized by presence of lower legs (usually one or more), vertebral units (thoracic vertebrae with rib articular ends, and lumbar vertebrae with sacrum and pelvis), perhaps one or both scapulae damaged at vertebral borders only, some broken rib fragments,

spirally fractured long bone fragments, some bone chips and splinters, and most of the cranium and mandibles, or separate portions of toothrows (Figure 15).

If there is only one such unit present at a site there is a good possibility that the site is not the main locus of the kill, but is a nearby secondary feeding site.

Interassemblage Variations among Killsites Due to Minor and Temporary Perturbations of System Dynamics

During an occasional severe winter, prey might be killed in greater than normal numbers (Mech and Frenzel 1971:33), and the carcasses would be very lightly utilized (Mech and Frenzel 1971:45). However, kills made the following winters would reflect increasing utilization until prey numbers had recovered or stabilized. During a severe winter (1968-69) in the study area wolves killed more deer than they could effectively utilize fully, and the next year wolf numbers increased by about 30% (Mech 1977b:565). But because deer numbers did not also rise, and in fact were beginning a drastic decline, the wolf population subsequently fell to its earlier level by the following year, and continued to decline until 1974, when it rose again. During those years of decline, wolf utilization of prey carcasses was most likely very high.

As has been demonstrated by wildlife biologists (for example, Stelfox and Sturko 1977), an index of prey vulnerability can be estimated each season and each year based on contemporary animal observations and weather records; factors that need be considered would include Winter Severity Index (Verme 1968), proportion of typically vulnerable animals in the population (young of the year, sick or old individuals), and even the Winter Severity Indices from the preceeding years, since animals born or in utero during hard times may be less sound, smaller, or simply more vulnerable than normal counterparts (R.O. Peterson 1977).

It has been suggested here that there is also a simple osteological method to estimate vulnerability for whole prey populations in carnivore hunting territories. This method requires calculation of the observed average value for carcass utilization each winter, and rating of an average value for wolf pack size each winter for particular prey species. However, the size of wolf packs preying on any species may vary due to changes in the prey population over a very short time. The dynamic changing nature of predator-prey relationships must be kept in mind.

Consumption Sites

Secondary sites are created by wolves during resting and eating apart from the main carcass site. Parts of the kill may be carried up to 30 meters away from the killsite, especially by low-ranking wolves with limited accesibility to the main carcass (see Mech 1970 and Klinghammer 1979 for discussions of social ranking). Other higher-ranking wolves may gnaw pieces in secondary sites to gain some solitude, but they would usually be much nearer the main kill area.

No systematic recording has been done for such sites, but it is the impression of L.D. Mech (1979 pers. comm.) that usually no more than one analytic unit of the carcass would be found in single consumption sites, and that most consumption sites would be in peripheral parts of the killsite itself, within an irregular circle of 30 meters diameter. Bones or body parts of a kill may be carried about after gnawing, and may be saved, buried or stored, or abandoned at any point after gnawing; in summers when there are homesites to return to, wolves may collect bones (see the section below on dens). A random distribution of a few small carcass parts may occur in discrete places near single killsites (the randomness of the distribution may be open to question), but there would never be a compact association of such parts within a radius of about 6 meters except at killsites or homesites. On the margins of lakes, and over the course of many years, bones from secondary sites may accumulate.

Very few elements damaged from sustained gnawing have been observed at killsites, so I would predict that bones which have been relatively well gnawed are from secondary sites. "Gnawing" is defined here as the continual wearing away or breakage of bone through forceful application of the teeth, and occurs as part of ordinary feeding or as a pastime unto itself. The distinction between sustained gnawing and simple feeding will be brought up again below in the discussion of den sites.

Den Sites and Rendezvous Sites

Where wolf dens are re-used each denning season, there may be representation of several prey animals (Kuyt 1972:14; Haber 1977). Dens that are traditionally re-used are often located in geographic regions where main prey availability varies seasonally due to migrations and changes in herd structures. Dens in tundra and plains are generally re-used over and over again for generations (although some of those generations may be skipped) (see Novikov 1956 and Kozlov 1964), whereas dens in woods and forests may either be occupied only a single year (Mech 1970; Pulliainen 1965) or may be re-used (R.O. Peterson 1977).

Dens are occupied by wolves from late winter through mid-summer, until pups have been weaned (Mech 1970). Dens may be burrows which have been excavated underground, or they may be old beaver lodges, hollow logs, rock cavities and overhangs, or den burrows which were abandoned by other animals (Mech 1970; R.O. Peterson 1977). Rendezvous sites are occupied after dens are abandoned, as places where growing pups remain while adults hunt (Joslin 1967). Several such spots may be used between denning season and the fall and winter, at which time pups can accompany adults on their wide-ranging hunting journeys through the territory. Bones found at rendezvous sites are usually well-gnawed (R.O. Peterson 1977:110 and figure 71,p.109; Haynes unpublished data). Any kind of prey part may be found at rendezvous sites, from antler in velvet to long bones.

Elements at homesites will be much more gnawed than elements at killsites, and will probably show more edge rounding (actually a gnawing polish on broken edges, produced by continued licking and chewing), more linear and longitudinal fracturing of long bones (see Chapter 10), more tooth marking of compact bone, more gouging and furrowing of cancellous bone, and more crunching and splintering of thin bone.

Scavenging Sites

Gnawing damage to bones that have aged a season or more or that have little flesh on them is relatively slight. There may be no tooth scoring on long bones perpendicular to the long axis, and epiphyses are not gnawed as heavily as they are in fresh kills or fresh carrion. Damage may appear similar to that inflicted by small gnawers such as foxes or coyotes (Haynes 1978a).

The entire carcass of a scavenged animal may be much more intact than carcasses or skeletons of kills (photographs are in D. Allen 1979 and R.L. Peterson 1955). Wolves may gnaw bones discarded by human hunters following butchering, in which cases the bones are damaged often in the same places as they would be damaged in if gnawed when fresh; the damage is usually much less severe. Recent evidence for the existence of wolves in Glacier National Park, Montana, is rather scarce (Singer 1979), but I have observed probable damage from wolf gnawing on butchered mule deer bones which were collected in the park. I have also seen wolf scavenging damage on bones of bison that have died from drowning and disease in northern Canada, and again there is a difference between gnawing damage done to remains of these carcasses and damage done to kills actually made by the feeding wolves (see Chapters 7 and 8).

Bones of whitetail deer may be too easily eaten by wolves to be passed up, especially when live prey are relatively hard to come by. Scavenged bones from smaller animals will not be as well gnawed as bones in homesites, but will share some characteristics with them, such as longitudinal fracturing as a result of drying cracks that develop in compact bone parallel to the long axis of the element (see Chapter 10).

CONCLUSIONS

The position taken throughout this research is that today's predators are creating osteological sites; that these places where animal bones are found characteristically lack certain elements and show certain types of damage to elements because of behavior patterns of the predators; and that these behavior patterns, whether explained by factors of the environment or factors of the predator's own genetic predisposition, will correlate with aspects of the preserved bone assemblages.

The study area has undergone a severe decline in bone production, so to speak, over the last decade, and the ecological conditions under which this research is performed can hardly be idealized into a steady state. But this transformation of relationships in an animal community had provided clues to the nature of predator-prey interactions (as expressed in bone assemblages) under a number of different natural circumstances, ranging from near homeostasis to severe disruption. The biological characteristics of this changing system have been documented in reports and personal communications from wildlife researchers, and their data have been invaluable for this study.

My observations of carnivore modifications to deer skeletons differ in many significant aspects from observations on bison and moose as prey species. Under comparable ecologic conditions, single bones of large prey animals each show reliable indications of degree of carcass utilization, whereas entire surviving assemblages of caribou, antelope, or deer bones must often be examined to determine degree of utilization. Unless lower leg bones of deer-sized prey animals show breakage or gnawing damage, data must be available on the presence or absence of most other elements of the skeleton before many of the propositions discussed in this paper can be validly referred to by a paleoecologist.

The degree of utilization of any bone from a large carcass is related to a number of factors, including (1) species and numbers of carnivores involved in feeding, (2) season of carcass use, (3) type of site (home or kill), and of course (4) hunger of the carnivores, based on ease of the hunt and availability and vulnerability of prey in the catchment area. These four factors can be analytically distinguished on the basis of bone damage and skeletal modification.

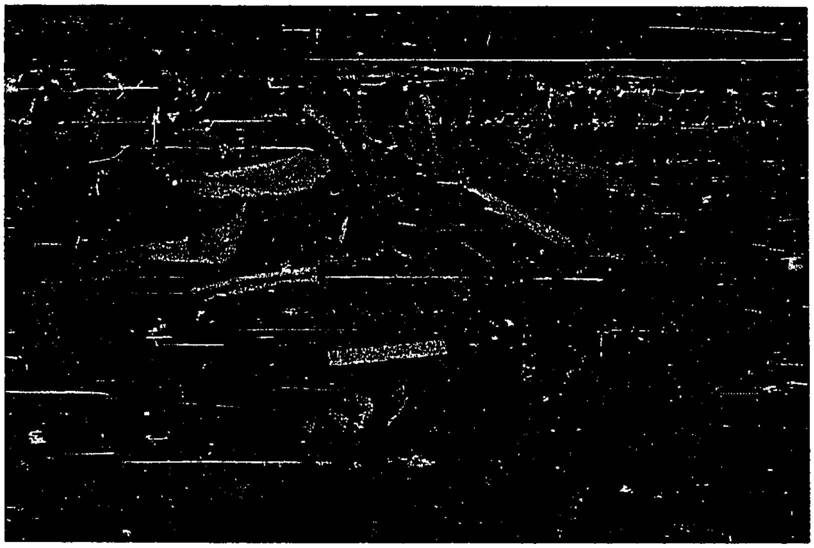


Figure 15. Remains of Whitetail Deer from moderately- to lightly-utilized wolf-killed carcass. Head and cervical vertebrae have been removed by biologist.

Figure 16. Bull Moose at edge of Lake Superior in September, Isle Royale National Park. Adult males may weigh over 600 kg., and adult females may weigh up to 360 kg.

VII. Field Study of Bone Damage and Carcass Utilization by Wild Wolves: Case Studies II and III. Isle Royale National Park and Wood Buffalo National Park Descriptive Data

INTRODUCTION

In these following sections, a slightly different approach has been taken for the presentation of data. The two study areas are each described in much greater detail, because a larger part of the research was concerned with documenting environmental effects on deposited bones *after* most carnivore and scavenger activity has ceased. Therefore, data are presented with the following organization: first, a substantial study area description; second, a brief discussion of background research on wildlife; and, finally, descriptions of selected carcass and skeleton sites. In the following Chapter (8), I present a summary discussion of observations on body dismemberment by carnivores, bone damage due to gnawing, bone distribution in carnivore killsites, and element survival in killsites. Chapter 9 presents a series of observations on decay of soft tissue in various micro-environments of the study areas, stabilization or continued decay of bones in various micro-environments of the study areas, weathering deterioration in the areas, and miscellaneous processes of bone deterioration, burial, and preservation under different local conditions.

CASE STUDY II: ISLE ROYALE NATIONAL PARK

Introduction

Isle Royale National Park is an archipelago in Lake Superior, the world's largest body of fresh water. The main island of the group, itself named Isle Royale, is an elongated and relatively narrow land mass characterized by many parallel, linear ridges and intervening valleys oriented in a northeast-southwest direction. All the other islands in the group are quite small, most of them being only slightly elevated extensions of the main island's otherwise submerged ridge systems. The greatest length of Isle Royale is about 72 km., and its greatest width is about 14 km. The mainland of Canada is approximately 24 km. away; it was most likely from the Sibley Peninsula of Ontario that timber wolves first came to colonize the island in 1948 or 1949, crossing the ice bridge between the two land masses (D. Allen 1979; Mech 1966). Prior to this time, the island had been populated by occasional woodland caribou (which disappeared in the mid 1920s), snowshoe hare, red fox, coyote, red squirrel, lynx, beavers, and several other mammalian species (see Mech 1966:7, table 3). Moose were becoming common by the second decade of the 20th century, probably slowly immigrating from Canada. However, because there were no real predators, throughout the next 40 years the numbers of moose tended to fluctuate between environmentally insupportable highs and subsequent lows following overbrosing of available vegetative food, leading to die-offs (Mech 1966:table 4,page22). The population fluctuations have not been so extreme since timber wolves became established predators (R.O. Peterson 1979). Today moose numbers may be somewhat declining.

yet the wolf population is the most dense (per land area and per prey animal) known to exist anywhere in the world (Peterson and Scheidler 1979; Peterson and Stephens 1980; R.O. Peterson 1979).

Over-logging and disastrous man-caused fires cleared large areas of the main island in the 19th century, and recovery has been slow since the soil and litter cover on the island's bedrock is so thin. Over half the forest area on the island is in subclimax recovery stage (Shelton 1975:32). In 1940 the archipelago was established as a National Park. In 1958 D. Allen of Purdue University initiated a planned longterm research program on wolf and moose relationships; the study has continued uninterrupted to the present day (see Mech 1966; D. Allen 1979; R.O. Peterson 1977,1977a,1979b; Peterson and Scheidler 1979; Peterson and Stephens 1980). Currently R.O. Peterson of Michigan Technological University has assumed leadership of the study program. In winter a research team flies daily aerial surveys of the island's moose and wolf populations, and maps and investigates all dead animals and confirmed kills made by wolves. During the summer months study teams continue investigating on the ground all known dead moose and other species. Over 600 moose carcasses have been autopsied, or their skeletal remains have been examined in the 22 years of the study.

Location and Physiography

Isle Royale is administratively located in the state of Michigan, although the mainland of Minnesota is much closer. In the summertime there is regular boat and floatplane service to Michigan and Minnesota. The park has no roads, but much of its interior is made accessible by miles of foot trails, some quite rugged. There are several developed campgrounds and shelters for campers located in the park, many of them tucked within the elongated harbors and bays of the Lake Superior shores. There are also campsites located on several of the numerous inland lakes. The island is completely closed to visitors from November through May, when it is under snow and its lakes are frozen. In spite of a heavy summertime influx of campers in summer, most of the island is genuine wilderness.

The long parallel bedrock ridges which run along a southwest and northeast axis are often bare of vegetation at the crests, but are usually thickly wooded on sloping sides. The valleys between these ridges are often flat-bottomed and poorly drained. The elevation at the Lake Superior edges of the island is a bit over 181 meters asl, and ranges up to nearly 419 meters asl at the top of Mount Desor. Thus, relief is not extreme, although the island is extremely rugged to travel.

Most of the island's bedrock is volcanic in origin, derived from lava erupted underwater in Precambrian time (over one billion years ago); the oldest of these rock formations lie in places underneath conglomerates containing minor lava flows, which in turn underlie or are interbedded with sedimentary rocks (Huber 1975). The sandstones, shales, and conglomerates of these sedimentary formations are not commonly exposed, and usually are buried in depressions under surficial deposits (Huber 1975:15). The sedimentary rocks include a wide range of consolidated gravels and sands. All the bedrock formations are tilted from 5° to 50° to the southeast, stacked one on another with the uppermost edges of the beds forming the parallel ridges which run the length of the island. The intervening valleys were formed by erosion, and some are now filled with lakes. The north sides of the ridges are much steeper than the south sides which follow the dip of the bedrock layers (see Huber 1975:7 and Shelton 1975:8 for figures). Vegetation, like drainage, directly reflects these differences in topography.

There has been much erosion, folding, and deforming since the rocks were originally laid down in Precambrian times. Prior to Pleistocene glaciation, the Lake Superior region probably was part of a broad river valley that also included the other Great Lakes. Beginning about two to three million years ago, the ancestral Isle Royale land masses were overridden by glacial ice four times, each glaciation removing direct evidence of the preceding episodes (Huber 1975:41). As a result, the exposed rock on the island today is not as deeply weathered as one would expect in deposits of such great age. There are many rounded, polished, and striated outcrops exposed on the island, most of them bare of any vegetation except for patches of lichens and mosses. On the west end of the island there are till deposits which cover bedrock and somewhat even out the ridge and trough topography. There are also rounded cobble beach deposits far above today's shore levels, remnants of times when the island sat lower in the lake; the island has been steadily uplifted since the last ice retreated 10-11,000 years ago (Huber 1975). The island also contains drumlins (ridges of till) and recessional moraines; however, it is the long bare ridge lines and the lowlying wet valleys between them, as well as the irregular, thin fingers of land forming deep protected bays that most impress the visitor to Isle Royale. These features also directly influence the distribution of animals, the nature of plant communities, and ultimately the distribution of animal bones and bone sites.

Climate

The islands of Isle Royale National Park are subject to weather influenced not only by regional, subcontinental patterns, but also by the localized presence of such a large body of water as Lake Superior. The surface water of the lake never warms up much above 15°C in the summertime. Thus, there is always a layer of cooled, moist air surrounding the islands at lower elevations. When it is foggy on the islands, the rest of the Lake and the mainland may be clear, or vice versa. Wintertime low temperatures seldom are as low as they are on the mainland because of Lake Superior's modifying influences, nor is there as much snowfall as occurs on the Michigan mainland (R.O. Peterson 1977:7). Day to day weather on the island varies considerably in the spring, summer, and autumn, but in general days are cool to warm, and nights are much cooler. Clear skies may cloud over very quickly. Mosquitoes and other insects flourish in the bogs, lakes, and wet depressions until the first irregular sub-freezing temperatures begin in September. However, even in June or July, nighttime temperatures may once in a while dip below 5°C. There are constant breezes off the lake, with winds from the northwest usually bringing precipitation as they cross Lake Superior in the summer (R.O. Peterson 1977:7-9). South-facing slopes are heated quite intensely by the summer sun, with the earth or rocks sometimes reaching temperatures as high as 60°C. Evaporation on these slopes is consequently great (Linn

1962:2). The island's interior uplands, because of fast runoff, drainage, and warm ridge-top conditions, possess a relatively hot and dry climate, as compared to the cooler and moister climate of shore-level areas (Linn 1962).

Average annual precipitation is probably between 70-80 cm., including about 60 cm. of snow (R.O. Peterson 1977:10,13). Snow depths may vary from year to year, and also may vary in open areas and areas of deciduous or coniferous canopy (R.O. Peterson 1977:13). Length of sunlight per day varies greatly over the year. In mid-winter there are far fewer non-overcast days and far fewer hours of sunlight per day than in summer. In wintertime Lake Superior waters usually freeze along all the shores of the islands, and once in a while the Lake entirely freezes over, linking the U.S. and Canadian mainlands to the islands.

Vegetation and Soils

Soils on the islands are usually very thin and not zonal, as a result both of glacial scouring and erosion, and of destruction by fire. Yet many of the slopes, ridges, and valleys of Isle Royale are densely wooded and deeply shaded. Every winter and fall strong winds blow down many shallow-rooted conifers growing on rocky soils. Diseased trees, being much weakened, also blow down. As a result, many of the interior forests of the island are thick tangles of snapped-off treetops, blown down branches, and uprooted trees. Ridge tops and rocky slopes may be bare of trees, but may be covered with shrubs, flowering plants, and annuals.

In areas near the shores which have not been burned for at least 30 years and which are not excessively well drained, the predominant forest species are paper birches (Betula) and quaking aspens (Populus), with scattered dense stands of spruce (Picea). On drier ground, spruce and jack pine (Pinus) may be found as pioneer species (Shelton 1975:34). Fir (Abies) growing in the shaded aspen-birch woods may be overbrowsed by moose, and therefore may not become an important element in later successional stages of forest growth (Shelton 1975:34).

In the final successional stages, spruces and firs would be dominant over deciduous species, although aged birches may survive for a time in the deeply-shaded woods.

Where the climate is somewhat warmer, as in the central and western uplands of the island's interior, sugar maple (Acer) and yellow birch (Betula) have become the dominant (climax) species. There are thus two entirely different kinds of climax forests on the big island, the cool and moist spruce-fir association, and the warmer and drier sugar maple-yellow birch association. In valley bottoms and on north-facing slopes there may be transitional zones of spruce and fir woods. Swamps and bogs are common in many valleys, and in these wetlands are found black spruce, tamarack (Larix), and white cedar (Thuja) (Linn 1962:18). There are many other types of trees on the islands, including, among others, Yew (Taxus), mountain ash (Sorbus), elder (Sambucus), willow (Salix), oak (Quercus), dogwood (Cornus), and hazelnut (Corylus) found in varying associations.

Yew, a favored browse species of moose, has been practically eliminated from most of its natural habitat by moose feeding. Beavers contribute to the death of many aspens and birches when they dam water to create ponds. These beaver-created openings in the woods may subsequently become spruce and fir groves during forest recovery (Shelton 1975:40).

A transect moving across the big island from Lake Superior shore to inland valley would cross the following vegetation and soil zones:

(1) The rocks of the shoreline, which in the drier areas support a few mosses and lichens growing in cracks, and which in wave-washed areas grow long tresses of submerged algae.

(2) Rocks of the supra-shore zone, supporting some low-growing junipers on an extremely thin and localized mantle of humic sediments.

(3) Nearshore flat areas and rocky ground beginning to slope upwards away from the shore. This zone supports white cedar in wet spots and scattered trees, shrubs, low-growing ground cover, and berry bushes on a thicker mantle of soil.

(4) Gentle and steep slopes upwards towards the interior, where the soil mantle is more than a few inches thick, and which support fir, spruce, and birch successional or climax forests (Shelton 1975:46-47).

(5) On the other side of the first set of slopes and ridges, after descending through a similar series of forest and soils types, the climax and subclimax forest gives way to bog forests in the wet valleys. These forests include tamarack, black and white spruce, paper birch, alder, and balsam fir. A thick humus layer caps the sediment mantle.

(6) A mat zone forms between the bog forest and the wettest parts of the depressions. In this zone grow sundew plants (<u>Drosera</u>) and heathlike plants such as Labrador tea (<u>Ledum</u>).

(7) A sedge zone rings the water, and the humus layer pinches out on the surface but continues submerged as a layer of peat.

(8) Finally, in the water itself are found water lilies and bottom-rooted or floating aquatics (Shelton 1975:81).

If the transect is continued, the entire sequence would be reversed back through zone 4, then reversed again as another slope is climbed and another valley is crossed, and so on until the transect ends on the opposite Lake Superior shore. Some of the wet valleys, which may be high in the uplands, contain water courses, some contain deeper lakes that lack bottom-rooted vegetation towards their centers, and others contain beaver-dammed ponds in all stages of the natural sequence of infilling.

For each of these zones, potential bone preservation and fossilization will differ substantially. Availability of shade and moisture varies locally; in some locales, bones may remain cool and wet for months, with minimal circadian temperature fluctuations, while in other locales bones on the ground surface may suffer severe day to night differences in temperature.

<u>Wildlife Resources and Research</u>

Isle Royale National Park is essentially a closed ecosystem insofar as mammal populations do not habitually and freely move away from the islands to other land areas. Many mammal species on the island seem to have established at least a temporary balance with their environment. Deer mice have no competing species on the island yet they are still "rather thinly distributed" (Shelton 1975:112). The red squirrel population appears to have stabilized at a recognized level, even though no efficient squirrel predators exist (Shelton 1975:112). Lynx are extremely rare on the island (Peterson and Stephen 1980:18), but red foxes are not uncommon, and are important predators on snowshoe hares. Hare population levels fluctuate cyclically, and red fox numbers reflect the abundance or scarcity of these prey animals (Peterson and Stephens 1980:18; Allen 1979). Wolves also kill snowshoe hares and beavers, but depend for the most part on moose.

For a number of reasons, the population level of moose never truly stabilizes. Moose numbers respond to environmental pressure that may be different each year. Unusually severe winters may cause increased mortality of calves and older animals; however, some unusual winter conditions might result in increased productivity of the herd. For example, high winds in 1977-78 blew down twice the usual yearly number of trees, whose upper branches had been far out of reach of browsing moose prior to that time. As a result, more forage became available to breeding-age adults, and increased calf production may have resulted (Peterson and Scheidler 1979:4). At the present time, "the moose population seems to be slowly declining" (Peterson and Stephens 1980:14). An increase in calf productivity continues (1979-80), but it is not yet known if this will eventually reverse the downward trend in moose numbers (Peterson and Stephens 1980:4).

Wolf numbers have risen and fallen several times since censuses were begun in midwinter 1958-59. The overall trend since 1969 is towards increase, with one drop occurring between the winters of 1976 and 1977.

There were 50 wolves living on Isle Royale in 1980. Of these, 39 were distributed in 5 different packs (containing 14, 10, 7, 4, and 4 members) and 11 wolves were loners or members of "small, transient groups without a territory" (Peterson and Stephens 1980: 11). At the same time, there were 650-700 moose on the islands (Peterson and Stephens 1980:14). The previous year, 1979, there were 43 wolves on the island: 34 wolves were in three large packs (11, 14, and 9 members) and nine wolves were associated in duos, trios, or wandered as loners. During 1979, there were about 800 moose on the island (Peterson and Scheidler 1979:1).

Each pack did not have the same size territory nor the same numbers of moose available in their particular territory. The averaged kill rates for 23 packs observed during 1971-80 was one kill per 4.3 days, made by an averaged size pack of 10.5 wolves (Peterson and Stephens 1980:16). Obviously, because actual pack sizes varied and actual kill rates varied (due to local differences in availability and vulnerability of moose), the figures for any pack in any one winter will seldom completely match the figures for any other pack. Both the moose and wolf populations on the island are in a state of flux. Because the numbers of wolves and numbers of packs seem to be growing (although unsteadily) (Peterson and Nelson 1980:figure 7), while the number of moose seems to be steadily declining and the number of kills made per year is also dropping, carcass utilization is undoubtedly greater recently than in the past. Larger packs do not necessarily kill more moose than do smaller packs; but do utilize their kills more fully (up to a point, that is) (Peterson and Scheidler 1979:13; also see D.R. Miller for similar observations of wolves preying on caribou). Thus, when larger packs feed, nearly the same amount of food has to go farther than when smaller packs feed.

Distribution of Skeletal Sites and Bones

In 1934, Adolph Murie described some of the habits and range of Isle Royale moose. At that time, prior to the establishment of National Park status, hunting by humans was the only real predation pressure on moose. Coyotes may have occasionally killed moose calves, but for the most part moose population numbers were affected only by extremes of weather and availability of vegetation (Murie 1934). The sight of moose carcasses or skeletons was apparently not unusual when there were no timber wolves on the island. Today it is exceptionally rare for the off-trail traveler to find carcasses of moose that have died from causes other than predation; it would appear that moose are no longer allowed to die undisturbed in salt licks, bogs, or lakes to the same degree that they once did when they lacked predators.

The opposite situation may be seen on the Slate Islands in northern Lake Superior, where for generations woodland caribou have lived and died without having any major predators. Some of the land suffaces on the island are littered with caribou skeletons and bones (B. Lieff and M. MacDonald 1980 pers. comm.). In contrast, on Isle Royale today moose bones are extremely scattered, and are difficult to find even when detailed maps and notes are available.

In the winter of 1958-59 L.D. Mech became the first field researcher involved in the intensive wolf-moose study program directed by Durward Allen. Mech determined several criteria for recognizing evidence of wolf feeding at moose carcass sites, including (1) scattering of moose bones, (2) vertebral column broken into two segments, and (3) presence of gnawing damage to scapula, the gonial angles of the lower jaws, and long bone epiphyses (Mech 1966:116). He determined that wolves not only kill prey animals, but also readily eat carrion. However, scavenged carcasses were characterized by far less gnawing damage and bone scattering than characterized carcasses of animals originally killed by feeding wolves. Allen (1979:362[photo]) and Peterson (1977:29) also distinguish scavenged from freshly killed moose using the same or similar criteria. Therefore, it is possible today to determine that predation was the cause of any particular death or that there was no predation associated with any particular moose death on the island. It is known that in winter wolves on Isle Royale kill most of the moose on which they later feed (Peterson 1977: 29). Any and all skeletons on the island are potential sources of useful information about predator and prey dynamics or about the relative health of the prey population.

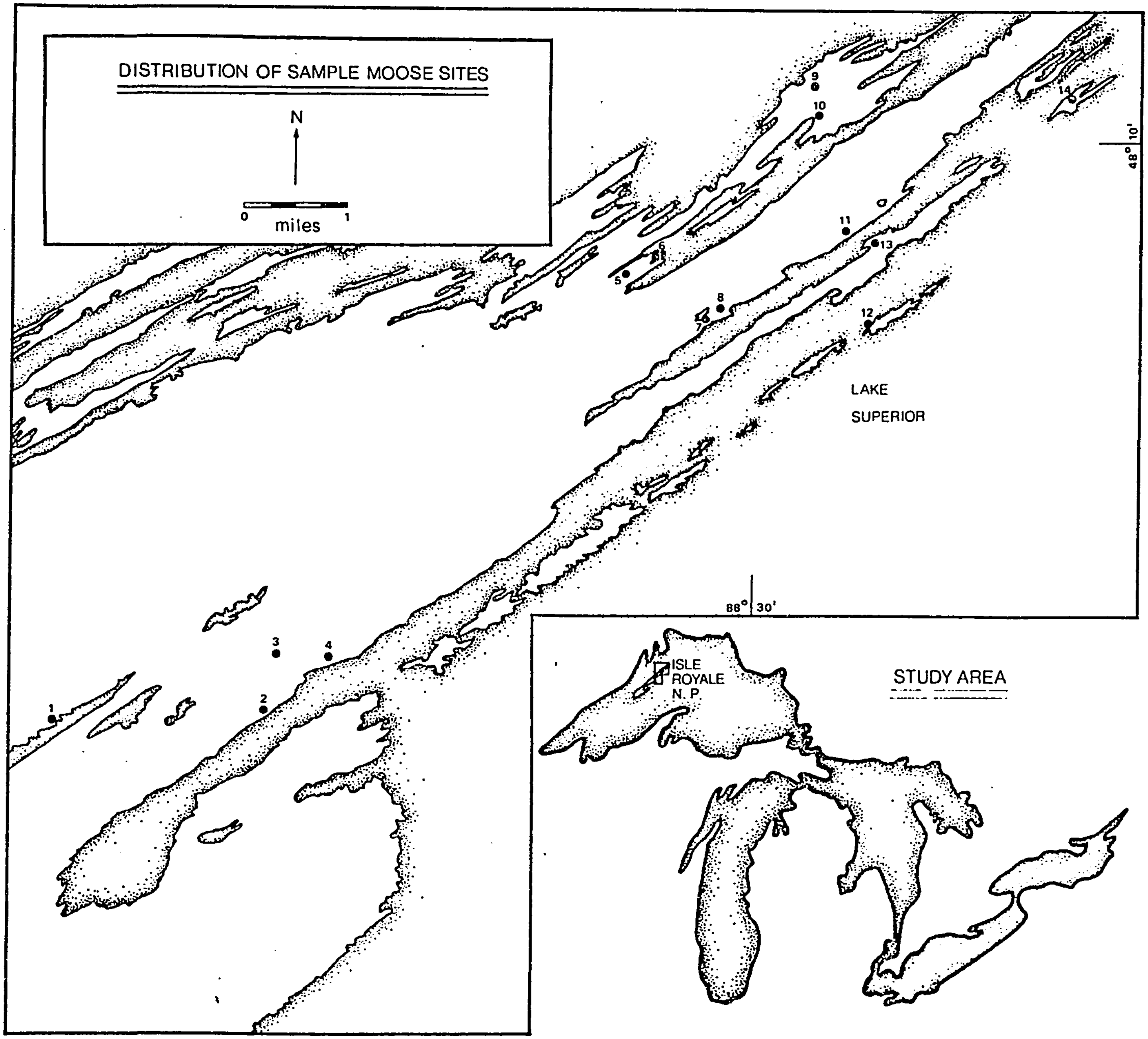
Moose, Wolves and Bone Sites

In habitats where the preferred (or only realistically available) prey is moose, wolves have little reason to hunt or wander in only one restricted part of their territories. On the other hand, in habitats where preferred prey animals herd together and feed communally, wolves would spend more time in limited portions of their hunting territories. Moose, like deer, are not gregarious and spread themselves out in their ranges (Figure 16), by no means randomly but still in a rather scattered manner depending on availability of forage and cover (R.L. Peterson 1955). Therefore, of course, some parts of the range would most likely be much preferred by moose, such as for example some shorelines and protected harbors on Isle Royale (R.O.Peterson 1977:figures 78 and 79; Peterson and Stephens 1980:figure 12); for this reason (moose numbers are highest, densities are greatest), wolves would produce more kills in these preferred areas, just as wolves create more kills in primary bison ranges where bison commonly spend more time. When mapped, the long term distribution of killsites in moose range definitely appears clumped (Peterson 1977:appendix J; Peterson and Stephens 1980:figure 14; Peterson and Scheidler 1979: figure 9), yet on Isle Royale for over 22 years of study there has been no recorded instance of two different moose kills being located in the same spot or in closely overlapping sites (using an arbitrary areal measurement of 30 meters x 30 meters as a definition of a killsite). It is possible that single bones from a particular skeleton, when subject to scatter (due to wolf or fox transport, kicking by moose, and redeposition by gravity or water) may eventually de deposited nearer the bones of other kills than the rest of the bones from their particular skeleton. However, due to the presence of thick undergrowth on most of Isle Royale's woods, single bones are extremely hard to detect, even when their general location is known from maps. Single bones are simply not common or not commonly detectable on the ground surfaces of Isle Royale. Bones are quickly overgrown and covered with leaf litter, blowdown trees, or decaying organic debris, especially in recovery forests where there is deciduous cover.

For years skulls, mandibles, and metatarsals have been collected from moose skeletons by researchers on Isle Royale. In addition, at least one (and sometimes two) long bones are deliberately fractured by biologists in order to check the condition of the animal's bone marrow. Thus, after the biologist's initial visit, the moose carcass or skeleton has been well-disturbed by human activity in addition to carnivore or scavenger activity. In contrast, only one half mandible is collected from bison skeletons in Wood Buffalo National Park, and one long bone is deliberately fractured for marrow check. The human disturbance of moose remains on Isle Royale is too severe to make it worthwhile for intensive revisitation monitoring of body part or bone dispersal; however, the mapped sites (Figure 17) will be re-inspected from time to time in order to record weathering deterioration of bones, or other incidental changes to remaining elements.

Figure 17.

Map of sampled moose carcasses in study area on Isle Royale National Park.



Moose Skeletal Sites

Most moose carcasses are located from the air in the winter; the dates of death for these carcasses and skeletons can be estimated either from the air or upon later examination on the ground. Most of the known carcasses or skeletons are from wolf-kills, and are usually discovered within a very few days of the kill date. The presence of wolves or their tracks are the most important factors leading to discovery of remains. In many instances observers have actually watched wolves kill moose and feed on the carcasses. Over the past five winters, the number of moose killed on the entire island has dropped from a high of 51 in 1976; in the midwinter of 1978-79, there were 30 kills made by a population of 43 wolves; in the midwinter of 1979-80, there were 28 kills made by 50 wolves.

Wolves kill moose twelve times more often in winter than in summer (R.O. Peterson 1977).

Carcass 79-9 Female, estimated age 7.5 years.

(Moose Site #10 on map).

This animal was killed by two or three wolves on 29 January, 1979; its remains were utilized by the small killing pack and later (both before and after the biologist's visit) by an 11-member pack. The four lower legs, the skull and mandibles, one scapula, and articulated vertebral units remained at the site when it was examined at the end of January.

I visited the site in June, 1979. The remains lay in a spruce-fir woods, about 30 meters from the Lake Superior shore (at an inner bay). A hair mat, 3-4 meters in diameter, a single small rib fragment, and the distal end of a humerus were the only remains that could be found. Other bones may have been lying on the ice nearby and fallen through earlier in spring. The humerus had been fractured by the biologist during visual check of the animal's marrow condition, and had been subsequently gnawed by wolves.

Carcass 79-18 Male, estimated age 10-12 years.

(Moose Site #5 on map).

This animal was probably killed by two wolves on 10 February, 1979. I visited the site in June, 1979. Its remains lay in wet, closed-canopy bottomland woods. The animal had suffered slight necrosis of the upper teeth and jaw, and arthritic hips (involving the femora and acetabula) and vertebrae.

The right foreleg was not found. A hairmat was found about 6 meters from whole bones. On and around the mat were numerous splinters and fragments of ribs and vertebrae. The articulated or free units included the head and mandibles articulated to all cervical vertebrae and six thoracic vertebrae with rib articular ends attached, six thoracic and six lumbar vertebrae attached to the sacrum and pelvis, the left scapula, the left foreleg, the right femur, and the left rear leg (from hoof through femoral head in articulation, cleaned of soft tissue down to the tarsal bones). All processes on vertebrae were broken. All caudal vertebrae were missing. The ilia and ischia were almost entirely gnawed off the pelvis.

The left rear leg was located about 16 meters from the head-vertebrae unit and the pelvis vertebrae unit (the latter two units laying side by side). The left foreleg was found about 13 meters north from the hairmat, or about 18 meters from the spine units. On both legs, the hooves had been gnawed and the dewclaws (hoof sheath and phalanges) were missing. The right femur lay near the pelvis unit. Both femora retained their head, but on both the greater trochanters were gnawed off and the trochlea and condyles were well-gnawed or completely gone.

Gnaw damage to femora, the one tibia, and the one humerus was moderate to heavy. Joints on the legs were still in strong articulation from soft tissue, and there was much hide left on lower legs. However, vertebrae, ribs, the skull, the pelvis, and exposed long bones were dry and white, although they had been lying in shaded swampy areas for four months.

Carcass 79-19 Female, estimated age 6.5 years.

(Moose Site #1 on map).

This animal was killed by the 11 member East pack probably on 8 February, 1979. The remains were found 45 meters from an inland lake in thick alder-spruce-birch wood, with semi-open canopy. I visited the site in June, 1979.

Only two legs were found, including the articulated left foreleg and the articulated right rear leg only. The right scapula was found. The left humerus head had lost its lateral tuberosity to gnawing, and the olecranon was gnawed off the left ulna. Below the ankle joint hide still encased the bones. The first and second phalanges on the lateral side of the lower leg were well gnawed, with the horny sheath coming off the third phalanx. Medial segments of rib and rib fragments were found lying on the 7 meter diameter hairmat, only a few meters from the foreleg. About 16 meters away a vertebral unit, articulating all thoracic and lumbar vertebrae with the sacrum and pelvis, contained four attached nearly whole ribs and many rib articular ends. Parts or all of all vertebral processes had been broken off. The pelvis was whole but gnawed at all edges. The head lay nearby articulated to seven cervical vertebrae. The angles of the mandibles had been broken off by feeding wolves. About 6 meters away from the head the right rear leg was found, articulating the hoof through the femur proximal end. The bones of this leg were cleaned down to the mid metatarsal. The hoof had been gnawed a bit; the femur was moderately gnawed, while the tibia was lightly gnaw-damaged.

Carcass 79-25 9 month old calf, sex unknown.

(Moose Site #13 on map).

This animal had been killed by the 11-member East pack about 14-15 February, 1979, and the remains were visited by the biologist on 17 February. The carcass lay at the edge of a lowland swale in alder-spruce-birch woods. The biologist found the two forelegs connected by hide, one complete mandible, and one rear leg. Bones of all legs were cleaned down to the tarsals or carpals.

I visited the site in June, 1979. At the time I found a few scattered bones or bone fragments and a hairmat. Five meters from the mat was the pelvis, and part of the sacrum still in articulation to it; two scapulae were also found, as well as many rib fragments, parts of single vertebrae, some pieces of teeth, and one petrous portion of the skull. On both scapulae, the glenoid portions were well gnawed or broken off. All bones were clean and white although scraps of soft tissue remained in places, except for the pelvis which was covered by "ribbons" of soft tissue.

If February the biologist had collected the mandible and one metatarsal, and had broken the tibia and femur for marrow check. No femur or tibia fragments could be found in June. I gathered most of the remaining bones together, and I mapped and photographed the new distribution. I returned in September to record further disturbances. No bones or fragments had been removed since June, but some pieces had been moved 3 cm. or less or flipped over, possibly by ravens. The hairmat could still be seen, although it was overgrown and much of the hair was rotted. Some soft tissue (no more than 10% of periosteum) still adhered to the bones, which were laying on mossy wet vegetation. The bones were out of water atop soil or vegetation, and were exposed to open sky. Articulated bones (that is, unfused epiphyses or pelvic bones) were still attached. Bone surfaces, where exposed, were very clean, smooth, and greaseless.

Carcass 79-27 Female, estimated age 8.5 years.

(Moose Site #9 on map).

This animal was killed by the 11-member East pack on or about 20 February, 1979. A day or two later the tracks of two other wolves were seen at the site. The remains lay under scattered spruce on open ground, less than 3 meters from a lowland alder thicket. Hair, stomach contents, and cleaned bones could be seen from the air. I visited the site in mid June, 1979.

At that time the remains consisted of the skull, the pelvis, two metacarpals, the left mandible, one femur, two humeri, one radius and ulna, one phalanx, an articulated hoof lacking keratin sheath, and two tibiae, all lying within a 6 meter diameter area. The angle was broken off the mandible, one olecranon was well gnawed on the ulna, the partial hoof was ungnawed, the tibiae were moderately to heavily gnaw-damaged, both humeri were moderately gnaw-damaged, and the femur was moderately damaged. There was no hide found. All long bones (except the radius and ulna) were disarticulated and not lying in association with each other (that is, all were 2/3 meter apart or farther). One ankle unit (tarsals and metatarsal) was articulated without calcaneus or astragalus. Some bones were slightly greasy, especially where they had been lying on wet ground. There was water standing 3 meters away from the bone scatter, and other bones may have been in it.

The upper cheek teeth showed severe necrosis, and the humerus was slightly arthritic.

Carcass 79-28 Male, 9 month old calf.

(Moose Site #14 on map).

This animal was killed about 20 or 21 February, 1979, by three wolves. On the date it was found, 22 February, a cow moose (presumably the mother) was seen standing over the remains of the calf. The bones lay in dense fir woods on an island off the north tip of the main island. I visited the site on 16 June, 1979. At that time the remains consisted of a hairmat about 2 meters square, the well gnawed skull (the front of the brain case had been broken open), many rib fragments, both scapulae, a hoof sheath, a rear leg, a foreleg, both mandibles, and six cervical vertebrae. The foreleg consisted of articulated bones from humerus through hoof, with hide cleaned down to the mid-radius; the proximal end of the humerus had been broken off. The rear leg consisted of the femur articulated through to the distal part of the metatarsal shaft. The lower part of the leg had been broken off. The proximal end of the femur had been gnawed and broken off. Both scapulae were only lightly gnaw-damaged. One mandible was broken at the alveolus of the third premolar. The other mandible had lost the angle of the ascending ramus. All processes were broken off the vertebrae.

On the skull, the rostrum was gone, the occiput was broken off, and there was a large puncture (5 cm. across) into the frontal bone. All teeth were present. Most of the rib fragments were heavily gnaw-damaged.

All bones and bone units were found in a linear scatter, in an area about 13 meters long within a geologic fault which appeared similar to a sunken road.

Carcass 79-31 Male, estimated age 6.5 years.

(Moose Site #8 on map).

This animal was killed by the 10-11 members of the East pack on 22 or 23 February, 1979, and its remains were found on 24 February. It originally lay on the north side of a ridge in spruce cover, but all bones had been pulled by wolves down into a wet swale. I visited the site on 15 June, 1979.

Three distinct hairmats were found, including one on the ridge slope near the top, 6-10 meters above the slough bottom. This 1.5 x 1.5 meter mat probably marked the original kill and feeding site, since stomach contents and rib and vertebrae splinters and fragments were found there. A faint trail led through brush from this hairmat down to the bone scatter in the slough area. Twenty meters from the upper hairmat was another mat, spread out in a 5-7 meter diameter area. Both forelegs, five articulated cervical vertebrae, and rib and vertebrae splinters were found on or within 1 meter of this second hairmat. The articulated skull, mandibles, and first cervical vertebra were located 10 meters from the edge of the hairmat, all these bones and hair being in a low, wet area containing shallow standing water (Figure 18). The forelegs were 3 meters apart from each other; both were articulated from humerus through hoof, both were tightly flexed. Both humeri lacked proximal ends due to gnaw-damage; both were encased in hide from carpals through hoof.

The left articulated rear leg lay 27 meters from the skull; most periosteum remained on the femur, tibia, ankle bones, and upper metatarsal, which were cleaned of hide. The femur had been gnaw-damaged moderately, as had the tibia. The tuber calcis of the calcaneus was lightly gnawed. The metatarsal showed a very few tooth scratches on the shaft. The hoof keratin showed biting damage. This rear leg lay just out of the wet flat area. Medial rib segments lay scattered in the low places.

The third hairmat was found 16 meters from the second one, on the opposite edge of the lowland-ridge transition, in a dry area. Three meters away was the other rear leg, articulated from femur through hoof. Its condition was similar to that of the other rear leg, except the tibia showed heavier gnawing damage. The pelvis, the scapulae, and most rib pieces were not found.

The skull and mandibles were articulated; a pronounced underbite was visible, so severe that the upper first premolar were not worn at all except on the posterior-most upper surface; the upper third right premolar was offset laterally, and also showed unusual wear.

I revisited the site in September, 1979. At that time the low area was much wetter than it had been in June. Much of the surrounding undergrowth had been recently trampled, probably by feeding moose. Old gnaw damage on the remaining bones showed up as greying, moldy, and drying out; fresher gnaw damage appeared ivory colored. The bones had been shaded and subject to much recent rain. On some specimens periosteum appeared to have been recently peeling off.

An articulated distal femur-proximal tibia lay at the edge of the wet area, surrounded by fragments of the shaft and other ends of the bones; these pieces resulted from the biologist's fracturing for visual check of marrow at the time of the June visit. Little disturbance had taken place with these fractured pieces. A disarticulated metatarsal was found 5 meters from the knee joint, and the calcaneus was found 19 meters from the metatarsal. These pieces (knee, metatarsal, calcaneus) lay linearly on a game trail. Eight meters away, in the center of the low area but not lying in water, was an articulated foreleg, from proximal end of the humeral shaft through second phalanges, and one articulated third phalanx (without sheath cover). The skull and mandibles had been collected.

The right femur was found under trees at the edge of the swampy area, 16 meters from the foreleg. Two meters from this bone was the rest of the rear leg tightly flexed, articulated from proximal and through the hoof (with keratin sheath attached). One meter away lay a second phalanx. The other half of the hoof (third phalanx and hoof sheath) lay 2 meters from the femur. Hairmats were still visible. The femur appeared to have recent gnaw damage to the trochlea, in addition to the older damage done to the greater trochanter and lateral condyle. The tibia had no apparently recent gnaw-damage. The tooth marks from old or recent gnaw damage were virtually identical (in depth, width, and length of scoring on compact or cancellous bone tissue).

Carcass 79-48 Female, estimated age 8.5 years.

(Moose Site #4 on map).

This animal was probably killed by wolves in the late winter of 1978-1979. A trail crew found and reported the remains on 30 May, 1979. The carcass lay in a dry, flat, open area with very scattered birch and spruce trees. I visited the site on 16 June, 1979.

At that time, several dozen live ticks were seen on branches of trees above parts of the remains or in the low brush nearby; these insects had crawled off the dead animal when the carcass cooled.

The stomach contents and intestines were present, laying under a spruce tree. All legs were present, scattered 20-25 meters from each other and up to 10-15 meters from the stomach contents and associated hairmat. No bones were heavily gnawed. The sternum survived nearly whole. The skull and mandibles were articulated to all cervical vertebrae and nine thoracic vertebrae, which were also articulated to ribs or rib articular ends on both sides (Figure 19). Five to seven other ribs were still whole, articulated to the sternum. Next to this unit lay the pelvis-sacrum-vertebrae unit, consisting of a very lightly-gnawed pelvis, articulated sacrum, and 11 articulated vertebrae (Figure 20). All lumbar spinous processes were undamaged, but lateral processes on one side were all broken. All vertebrae were present at the site except caudals.

Both forelegs were found 10 meters from the killsite (stomach content locus), articulated from scapula through hoof, with very light gnaw-damage to scapulae and humeri. Long bones were cleaned down to the lower radius shafts.

The right rear leg was found 2 meters from the stomach contents; bones were cleaned of flesh and hide down to the tarsals. On the femur only the greater trochanter showed gnaw damage. The other rear leg was located 10 meters apart from the hairmat-stomach contents, and was similar to the first rear leg in damage and hide cover.

I re-visited the site one week later. The stomach and gut contents were still undecomposed and undisturbed. Most of the rear leg long bones had been broken by the biologist for marrow check. The two spinal column units remained next to each other. No further gnaw damage was noted on vertebrae, ribs, or sternum. Both articulated forelegs and scapulae remained next to each other, about 15 meters from the spine sections. Most bones were still covered with periosteum. The pelvis was covered with much soft tissue, and its edges were mostly undamaged by wolf gnawing. Far fewer ticks were seen in the brush.

I also revisited the site in September, 1979. The stomach contents and guts were still apparent under the spruce tree. The fractured halves of a femur and a tibia (unarticulated) lay together on the ground where discarded by the biologist. The articulated forelegs had been minimally disturbed, although the scapulae had separated from humeri. Below the left scapula lay a dewclaw sheath, a third phalanx, and a carpal bone. A gnaw-damaged third phalanx lay atop the scapula. Carpals lay scattered near the right scapula, which was 2/3 meter from the left scapula. Most phalanges were detached and lying separated. Both humeri were still attached to each radius-ulna by only thin strips of ligament, although all bones still had cartilage and periosteum cover. Several ribs and vertebrae had detached from the anterior articulated unit (the head and mandibles had been collected earlier).

Long bones were still greasy near epiphyses, but marrow was nearly all gone from shaft cavities. Shaft fragments from the other tibia and femur were found near the stomach contents, but epiphyses of these elements were not found (these bones may have also been broken by the biologist for marrow check).

Carcass 79-58 Female, estimated age 6-7 years.

(Moose Site #11 on map).

This carcass was found and reported in June, 1979. The animal probably was killed by wolves in winter of 1979. Its remains lay in an open spot on a south-facing slope wooded densely with fir and birch trees.

I visited the site in June, 1979. The cleaned skeletal units lay scattered in an area of about 25 meters x 12 meters. Free rib segments, the sacrum, and one scapula were not found at the site. All four legs were found, as well as the mandibles, all vertebrae except caudals, the left scapula, and the skull (attached to the spinal unit, which also included the pelvis).

One rear leg was located 10 meters from the Lake Superior Shore, and about 10 meters downslope from the rest of the bone scatter. The femur was moderately to heavily damaged by wolf gnawing, and the articulated tibia was lightly to moderately damaged. The leg bones were cleaned of flesh down to the tarsal bones, which were ungnawed. There were many logitudinal drying cracks in the tibia shaft, most being a few inches long and appearing as linear grease stains. The bones were mostly cleaned, with dry periosteum and soft tissue enclosing epiphyses.

Upslope from the rear leg was a hairmat and the right foreleg, articulated from humerus head through hoof. The humeral proximal end was moderately gnaw-damaged. Hide on the lower bones was decaying but the articulated bones were still firmly held together, tightly flexed. The olecranon of the ulna was mostly gnawed off. Tiny greasy longitudinal cracks ran the length of the cleaned bones which were lying in a typically sunny area.

Forty meters away, directly upslope from the first rear leg, was another hairmat and the other foreleg with hide peeled off and hanging around the carpal joint. The bones were solidly articulated, flexed at the wrist. Two meters above this leg lay the pelvis and the attached spinal column articulated through the skull. Only four articular ends of the ribs were attached to vertebrae; all processes on vertebrae had been broken off. The pelvis was whole but gnawed along its crests and edges. On the skull the nasal bones were gnaw-damaged, as well as the edges of the orbits, the occipital region, and the zygomatic arches.

Five meters upslope from the first foreleg and hairmat were found both cleaned, articulated mandibles. Both had gnaw damage on the angles. All teeth were present.

The second rear leg was situated 5 meters from the first foreleg (the right) and hairmat. This unit was tightly flexed only at the tarsal joint. The calcaneus had been lightly gnawed, the femur was moderately to heavily gnaw-damaged, and part of the keratin hoof sheath was damaged. The proximal end of the tibia was moderately to heavily damaged.

The left scapula was found two meters upslope from the left foreleg; its vertebral border had been broken, and was very ragged from wolf gnaw-damage.

I revisited the site a week later, after biologists (and scavenging wolves) had visited it. The spinal column, minus the skull and pelvis, was in two pieces. The scapula was unmoved. The right foreleg had been flexed at each joint. A femur still in articulation with a tibia was located about 5 meters upslope from the left scapula. A humerus, a broken distal end of a femur, a sawn off lower leg (hoof and part of metatarsal), and a calcaneus lay about 8-10 meters from the first hairmat. A tibia lay 3-5 meters away and somewhat downslope from this bone cluster.

I also re-visited the site in September, 1979. The hairmats were still visible on the open slope, but no bones or bone units were found in them this time. The downslope rear leg was not found. The left scapula had not been much disturbed. Fourteen articulated vertebrae (second cervical through thoracics) were located next to the scapula. Three rib articular ends were still attached to the vertebrae at first and second thoracics. Seven thoracics contained only partial spinous processes. There were several isolated fragments of long bone shafts found, as well as epiphyses with some attached shaft from long bones fractured both by wolves and by the biologist during marrow condition check. Both tibiae were broken by wolf-gnawing; one femur had been broken earlier by the biologist but most parts of either femur were not found on my last visit. Bones of one foreleg were also not found, although they had been present in June.

Carcass 79-56 Male, estimated age 8.5-10 years.
(Moose Site #6 on map).

This animal was a near-senile bull that probably died in the fall (after September, before January) at the edge of a small bay in semi-open woods. It had suffered moderate necrosis in the upper cheek teeth, severe arthritis in the right acetabulum and slight arthritis in the left, and arthritic ankylosing of two vertebrae; one polished antler was aberrant, and the other was only a knobby growth on the pedicel. I visited the site in June, 1979.

The site consisted of a compact bone scatter, with no articulated elements except 11 vertebrae in one unit and six thoracic vertebrae in another unit. The mandibles lay atop a single, very heavy hairmat spilling over the bank edge, and the skull was about 13 meters away up a mild slope. All bones were bright white and mostly cleaned of periosteum and cartilage, although somewhat greasy at epiphyseal ends. Some ribs were complete, but scattered, and there were two with possible healed fractures. Two ribs were seen in the water below the bay, about 2 meters off shore under 1 meter of water.

The left femur, atop the hairmat, was arthritic. It had extremely light gnaw damage. The humerus lay 5 meters up the bank from the hairmat, its tuberosities lightly gnaw-damaged. One radius-ulna lay 2/3 meter from the humerus. The sacrum law 3 meters from the radius-ulna, 5 meters up the bank from the hairmat. The pelvis was complete, but its edges had been lightly damaged by wolf gnawing. The element showed severe arthritis on the left acetabulum, and advancing arthritis on the right. A single splint bone lay next to the sacrum, about one meter from the pelvis. Two or three meters to the east lay an ungnawed scapula. Three ribs lay 2 meters east of that. Two-thirds meter south of the scapula was the other humerus, its tuberosities lightly gnawed.

On the skull, the aberrant antler had been gnawed at the palmate portion. The nasal bones were slightly scored by gnawing. The atlas lay next to the skull, as did a metacarpal articulated to both first phalanges and both second phalanges. The skull had been collected earlier by campers but replaced by a park ranger; therefore it is probable that the other bones lying with it were also taken from the original bone scatter and later replaced in a different spot.

Carcass: Moose Lake Calf, estimated age 9 months.
(Moose Site #7 on map).

The remains of this calf were found by hikers who visited Moose Lake in June, 1979. The animal had probably been killed by wolves in the winter of 1978-79. The bones lay on grassy mud, 10 meters from thick woods and a few meters from open water of a large beaver pond (Moose Lake). The hikers had reported one leg, the skull, and the mandibles of a yearling moose; however, I visited the site in June and found instead part of a scapula, the right rear leg (femur articulated through second phalanges, without hoof), a hairmat, and the pelvis of a calf.

Most of the scapula blade and spine had been broken off. The leg bones were cleaned of hide. The femur lacked proximal epiphyses, and was lightly gnaw-damaged. The calcaneus had heavy gnaw damage on the tuber tip. The tibia had its proximal edges gnawed moderately. The pelvis was well gnawed, with the ilia and ischia mostly gnawed or broken off.

Other bones may have been in the lake water or in the thick woods, but none were found after a search was made.

Raspberry Island calf- female, estimated age 11 months.

(Moose Site #12 on map).

This animal died in late winter 1978-79 in the lodge and campground complex on the main island's north end. Park personnel removed the carcass prior to the summer opening of the area to the public. The remains were bloating when removed. The remains were put on the gravel "beach" of Raspberry Island where it was hoped that they would decompose quickly and be eaten by scavengers. The waters of Lake Superior are too cold to encourage underwater decay and scavenging.

When I first visited the site 18 June, 1979, the carcass lay in 4 meters of water nearly under the dock, about 1-2 meters from the shore. Wave action had apparently moved the remains into the lake water. A biologist had earlier removed the entire head and disarticulated and collected one lower leg. One front lower leg (from metacarpal midshaft through hoof) had been sawn off and collected before the carcass was towed away (by a cable attached to one rear leg) from the lodge area, and pulled across the bay to Raspberry Island. My main goals with this site were to witness daily how non-wolf scavenging affected the remains, and to determine how water action might modify bones and bone distribution.

The remains lay on the right side. Much of the hair had fallen out, and the hide was slipping away from the ribs (Figure 21).

When I next vistied the site (24 June), the remains had moved out 13 meters from shore, about 1 meter away from the dock. All up-side ribs were now exposed. Most hair on the legs (three of which were recognizable, bones of the fourth visible) had fallen out. The up-side scapula had slid down the ribs and rested on bunched hide. The bottom upon which the carcass lay was a cobble pavement, and about 2 meters of water covered the body. The slope of the bottom on which the remains were sliding into the lake was not severe (drop off of 2 meters in distance of 13 meters) and the remains would not of their own weight alone been moving downward even if partly buoyed, except in times of higher wave activity. I used an underwater viewing apparatus to study the remains.

I returned to the site 25 June, after park personnel had replaced the carcass on the pebble beach 20 meters west of the dock. The remains now lay with the head end towards the water, which was about 1 meter away.

The bones of the pelvis had begun separating. The left femur was whole and clean. There was a hole in the hide on the lower left leg, and the exposed metatarsal was fractured in that spot. The distal end of the right (up-side) humerus was abraded. A mass of hide lay under one mandible piece (chopped off by the biologist) and a vertebra. The sawn end of the left metacarpal showed edge rounding. The tibia of the right leg was broken in midshaft (probably done earlier by the biologist for marrow check). The femur of the right leg had a square hole chopped into it.

Both rear legs were not articulated to acetabula, but were held to the trunk by hide.

The only hair remaining on the hide was directly above the hooves. The bones had been stained from a light brown to a yellowish, ivory hue. Waves were mostly mild, lapping in a 10 cm. surge every two to three seconds on calm days. The remains lay in the lee of a rocky point 10-12 meters out from the beach, four meters west, and in the lee of the dock, about 15-20 meters east.

My final visit to the site was 28 June. All bones had been disarticulated and scattered, except for three groups of two vertebrae. Possible dispersal agencies were birds, foxes, rodents, people, and (least probably) waves.

Daisy Farm calf.

(Moose Site #2 on map).

This animal had been killed on a hiking trail by wolves during the winter of 1978-79. Its slightly scattered articulated bones lay about 13 meters off the trail in an open area, rocky and grassy land surrounded by scattered spruce trees and aspen seedlings. I visited the site in June, 1979. A 3-4 meter wide hairmat and stomach contents mat directly in the trail marked the original kill and feeding site. A second hairmat was located about 15 meters from the first one, between the first hairmat and the main bone area. One foreleg lay nearest to the trail; the humerus through hoof was articulated, flexed and covered with hide from the radius-ulna through hoof. The humerus had been very lightly damaged by gnawing. One scapula lay nearby, showing a ragged gnaw-damaged vertebral border. Ten meters from the foreleg was found the spinal column, articulated from first cervical vertebra through pelvis (the head had been collected earlier by biologists). Twelve ribs were articulated and complete from vertebral articular ends to sternal ends. The pelvis was whole but gnawed at the edges. Only six or eight vertebrae had whole or nearly whole spinous processes. On all other vertebrae lateral and spinous processes had been broken off.

The bones of the second foreleg lay 20 cm. from the first foreleg, but they may have been disjointed and disturbed by the biologist. The scapula remained articulated to humerus. All bones lay disarticulated, but nearly in anatomical order. The missing rear leg had probably been collected earlier by the biologist.

The carcass site was situated on and next to a moderately used foot-trail. Mid-summer use of the trail was not especially heavy at any one time of the day, but traffic was rather consistently flowing or expectable (probable rate about one walker every couple of hours).

Smaller scavengers such as ravens, foxes, or weasels would be able to visit the site briefly and depart during daylight hours or dark hours, but may have been discouraged by the unexpected passage of humans at irregular intervals. Wolves would probably have stayed well away from the trail when human use became clear after the island was opened to summer visitors. Thus, the remains would have been minimally disturbed, even by passing humans, many of whom reported the hairmat but did not seek the nearby bones. Utilization of the carcass of this calf, aged about nine months, was unusually light, suggesting that scavenging or delayed feeding by wolves on Isle Royale might account for a great deal of bone dispersal and damage at any particular site. Such feeding need not necessarily be considered garbage dining or simple carrion utilization, since wolves had originally produced the resource, the feeding site, themselves and had voluntarily abandoned it for a time, with the clear implication being that _if possible_ it would be returned to eventually for further utilization.

Experimental site

(Moose Site #3 on map).

This site was created in June, 1979. I laid out some clean, degreased, unweathered _Alces_ bones, carefully mapped them and photographed them in a wet area some distance from a foot trail, in order to determine if bones that lacked the odor of fresh animal flesh would appeal to scavengers, and to see how moose trampling might break or disperse bones.

On a small floodplain I laid out a right scapula, humerus, radius-ulna, and metacarpal in articulation. The bones lay on wet dirt, amongst young Joe-Pye weed which was growing 20-30 cm. apart. A small stream was flowing 3 meters away. About 13 meters away along the edge of the water I positioned a pelvis articulating with a left femur, a tibia, an astragalus, and a calcaneus. These elements were laid on mud where recent moose tracks were visible. The grass growing sparsely on the surface reached about 10 cm. in height.

In September, 1979, I revisited the experimental site. At the first locus, the scapula had been moved 15 cm. away from the humerus. The other bones, however, were unmoved, and still lay abutting at articular surfaces. At the second locus, the pelvis was gone, but the rest of the bones were unmoved and still in articulation. Recent moose tracks could be seen in the mud all around the bones. It is possible that moose walking along the narrow shore kicked the bulky pelvis into the stream, whose waters are opaque and deep at that point. The other bones did not appear to have been pressed into the mud or stepped on.

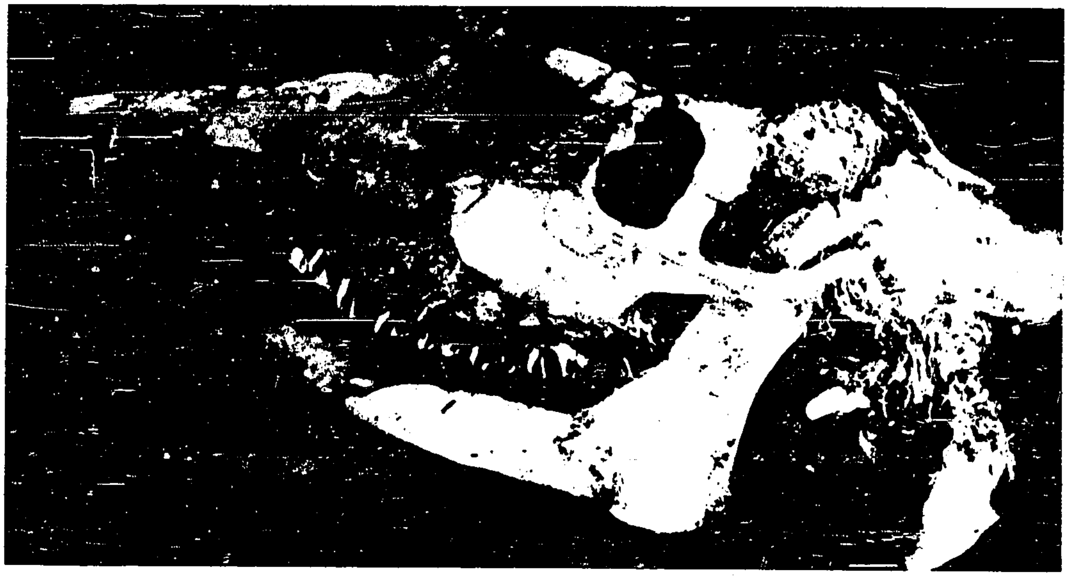


Figure 18. Articulated skull, mandibles, and first cervical vertebra of male Moose killed by wolves in February, 1979, on Isle Royale National Park, photographed June, 1979.

Figure 19. Articulated bones of female Moose killed in late winter or early spring by wolves, photographed four months after death on Isle Royale.

Figure 20. Articulated pelvis, sacrum, and vertebrae from same animal illustrated in Figure 19.

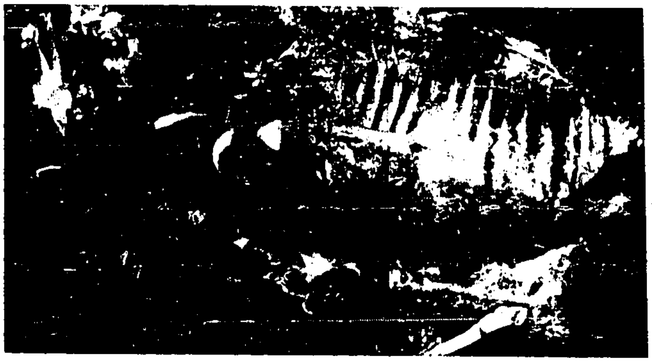


Figure 21. Remains of female Moose calf, winter starvation or disease mortality, photographed underwater in June, 1979, Isle Royale. Head has been removed by biologist.

CASE STUDY III. WOOD BUFFALO NATIONAL PARK

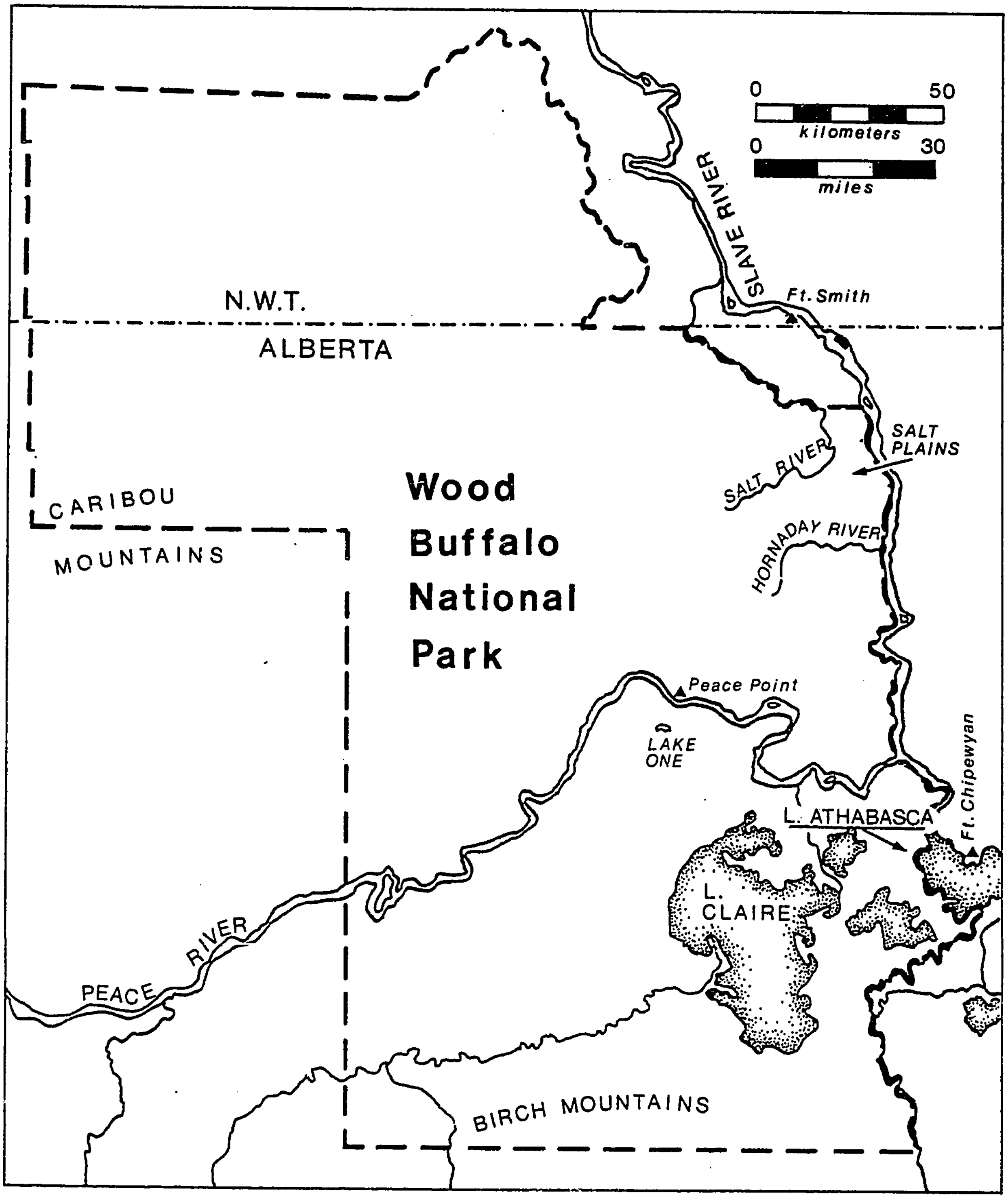
Introduction

Wood Buffalo National Park is an enormous wilderness preserve that spans the eastern part of the border between the Northwest Territories and the province of Alberta, Canada (Figure 9 and Figure 22). The park contains a number of distinct landforms which have characteristic bedrock geology and topographic relief (see Physiology section below). The area of the park is greater than that of any other national park in the world - 44,807 $km.^2$ (17,300 $miles^2$). The variety and magnitude of its biophysical resources are staggering. The greatest length of the park is nearly 290 km. (180 miles), and its width varies from around 128 km. (80 miles) to 166 km. (over 100 miles). Much of the ruggedly dissected uplands in the park's western regions have been rarely (if ever) visited, and much of the rest of the park is seen only occasionally from the air. Most of the main study areas of the park are characterized by low relief and high water tables.

There are several settlements in or around the park, including the town of Ft. Smith on the Slave River, Ft. Chipewyan on Lake Athabasca, and a native settlement at Peace Point on the Peace River. A single loop road enters the park near Ft. Smith, passing through Peace Point and linking up to a seasonal road to Ft. Chipewyan, but most of the road is practically impassable except in wintertime when the ground is solidly frozen. In summer, Ft. Chipewyan can be reached only by air or water travel. A small number of foot trails enter and cross some of the country in the park.

A limited number of native residents are allowed to trap fur-bearing animals inside park boundaries, using registered traplines.

Figure 22. Map of Wood Buffalo National Park, Canada.



Mammals inhabiting the park include the world's largest wild and free-roaming herd of bison (Bison bison), woodland caribou (Rangifer tarandus) in small scattered groups, a few deer (Odocoileus virginianus and perhaps hemionus), black bears (Ursus americanus), wolf (Canis lupus), moose (Alces alces), snowshoe hare (Lepus americana), red fox (Vulpes vulpes), beaver (Castor canadensis), lynx (Lynx canadensis), and others (see Soper 1935,1945). Bison hunting is not allowed, although there are numerous instances of poaching each year. Wolves are trapped for furs, but not very intensively (see Loranger 1979). The world's last wild Whooping Cranes nest in the remote northern section of the park. In autumn and spring a tremendous number of waterfowl pass through the Peace-Athabasca delta region.

All mammalian species have probably been historically and prehistorically resident, although the aboriginal wood bison population was artificially augmented early in this century by release of several thousand Plains bison transported north from central Alberta. At one time barren-ground caribou probably entered the park from the northeast during winter migrations, but as of late the herd moves no closer than about 80 kilometers from Ft. Smith.

The park was formally established in 1922 and enlarged in 1926. The bison herd has been under occasional or sustained scientific observation for much of this century (see Seton 1911; Kitto 1924; Raup 1933; Soper 1935,1941,1945; Novakowski 1961; Fuller 1960,1966). In 1972 Parks Canada and Canadian Wildlife Service personnel began making total counts of bison numbers (see Stelfox 1976,1977); in 1978, a Canadian Wildlife Service study was initiated to examine wolf-bison interactions. From 1978-81 the field work was performed by S. Oosenbrug in cooperation with the Park Warden Service, under the overall direction of Dr. L. Carbyn of the Canadian Wildlife Service. In the three years of the field work, 35 wolves were live-trapped, fitted with collars that contain radio transmitters, then released and monitored from fixed-wing aircraft (Oosenbrug 1980). Thirty-three bison carcasses were located that were suspected or known to have been killed by wolves. Total numbers of wolves inhabiting main bison ranges could never be counted, although a minimum of 68 were observed during the winter of 1978 (Oosenbrug *et al.* 1980:53). Winter field work consisted basically of locating the radio-collared and associated wolves, and ground-checking bison carcasses by means of snowmobile or ski treks into the back country. During the rest of the year field work consisted of wolf scat collection, ground surveys of selected areas to determine density and distribution of wolves, observations of bison behavior and biology, and further examinations of bison carcasses. By far the greatest part of all the research was performed by S. Oosenbrug, and I am indebted to him for cooperation, kindness, and assistance. Most of the data used in this study was collected by him and shared with me, and he also acted as my field guide.

Physiography

The Wood Buffalo area has been called a northern extension of the Great Plains, with geomorphic, edaphic and biotic intrusions from the Laurentian plateau to the east (see Kitto 1924:434); it has also been defined as a distinct boreal flatland and wetland area bordering the Canadian Shield (see Rowe 1959 and AAA 1979). The geographic region may be very grossly defined as the lands bounded by the Slave River on the east, the Caribou mountains on the west, Great Slave Lake on the north, and the mammoth Peace-Athabasca delta and the Birch mountains to the south. Within the park, four land districts may be defined on the basis of geology and relief, including (1) the lowlands of the Peace and Slave rivers and Lake Athabasca; (2) the Slave River plain; (3) Cretaceous uplands to the south and west (Birch mountains and Caribou mountains, respectively); and (4) the Buffalo Lake lowlands and Robertson Lake uplands to the west (AAA 1979:313).

All these areas were overridden by about 2-3 km. of ice during the last glaciation of the Pleistocene. The ice mass advanced from the northeast and retreated in that direction after 8-9000 years ago (AA 1969:12).

On the west side of the Slave River the bedrock is Devonian limestone, dolomite, and gypsum. On the east side, outside the park, bedrock is Precambrian igneous and metamorphic rocks which are the foundations of Shield landforms. The Athabasca-Peace areas are plain-like, as is the vast central park area where primary bison ranges are located. The Peace-Athabasca lowlands contain sand plains and level or depressional expanses, where surface deposits are alluvial, deltaic, or lacustrine in origin (AAA 1979:314,368). Elsewhere, north of the Peace River, outwash deposits, lake deposits, and wind deposits of sands and gravels can be found, as well as silts and clays of lacustrine origins (AA 1969:8).

Near the Peace River are sand plains containing linear dunes on broad expanses of fen or bog terrain (AAA 1979). The dunes are sometimes irregular in shape, and the sands have sometimes been reworked by wind and water due to historically fluctuating lake levels in the surrounding delta area (AAA 1979:328). Old lake beds have been exposed where water levels have fallen, leaving black soils supporting sedge and willows, the latter on somewhat elevated, drier ground. The banks of rivers and streams may have high levees which contain stratified mineral and organic layers as a result of recurrent flooding and imperfect drainage (AAA 1979:368). Abandoned channels and old terrace are not uncommon on the alluvial lowlands along the Slave River and Lake Clair-Peace River drainages (La Roi _et_ _al_. 1967).

The major study area is characterized by broad, open sedge-grass "prairies" or meadows containing scattered, dense wood stands of spruce or poplar, or scattered willow thickets.

Climate

Very general trends in climate have been determined for the Ft. Smith area, which is located north of the northernmost primary bison ranges. The mean annual temperature for Ft. Smith showed a general increase from 1910-32, a decline for 1932-36, a rapid increase between 1936-45, and a decrease since 1945 (Scace and Associates 1974). The difference in maximum and minimum averaged temperatures is about 3°F, although nearby areas showed up to a 5°F difference in mean annual temperatures over the same measured time periods (Scace and Associates 1974).

The following data are from Longley (1967:53-67), the Atlas of Alberta (1969:14), and Canadian Department of Transport and Atmospheric Environment Service records:

Mean January temperature (averaged for 1931-60) measured between -24°C to -27°C for the entire park, although the Lake Athabasca area was at the higher end. In the overall park area, mean April temperature (1931-60) measured -3°C - -2°C, mean June temperature (1931-60) measured 21°C - 24°C, mean July temperature (1941-70) measured about 18°C and mean October temperature measured 0°C - 2°C. The average dates of the latest spring frost (based on records from 1951-64)for Lake Athabasca were 1-15 June, while for the northern Ft. Smith area the latest spring frosts occurred between 16-30 June. Total annual precipitation (1951-60 period) averaged about 40 cm., while mean annual snowfall (1931-60 period) averaged about 152 cm. or less. Summer rain fall (1931-60) averaged about 15-20 cm. and autumn precipitation (1931-60) averaged about 10 cm. or more.

Scace and Associates (1974) summarize available data on soil temperature measurements made at Ft. Vermillion, which is outside the park but nearby (290km. distant from Ft. Chipewyan). The annual temperature fluctuations at 150 cm. depth below surface may be less than 10°C while at 1 cm., 5 cm., and 10 cm. below the surface the soil temerature may fluctuate up to 40°C over the year. Mean air temperature, as seen above, may fluctuate 50°C over the year. Real air temperature fluctuations, of course, may surpass this latter, averaged figure; maximum air temperatures may exceed 25°C in summer, and minimum temperatures may drop below -40°C in winter. However, in summer, there are probably fewer than 15-25 days when air temperature reach or exceed 25°C (AA 1969:15).

The deep soil (at 150 cm.) is not permanently frozen, but is probably cold year-round (very near freezing temperatures), so that anything deeply buried is well refrigerated. Fluctuations in ambient temperature will directly affect bones lying on or within the ground. The degree of weathering or preservation of bone tissue will reflect the length and severity of periods of dry warmth or refrigeration. Extremes in freezing and thawing temperatures, because the existence of such conditions leads to the growth and quick reduction of ice crystals within bone pores or interstitial or interlamellar spaces, will often produce damage to bone tissues. While frequent freezing, thawing, and re-freezing may not burst bones or completely splinter them, as a result of ice crystal expansion, it is nonetheless probable that the degree of weathering damage to shallowly buried or unburied bones will be affected by even day to night temperature and humidity variations, as well as by longer-term seasonal variations. The gradient in soils' temperatures is not constant throughout the year: in January the coldest temperatures are at the 1 cm. and 5 cm. depths below surface, while in April the minimum temperatures are at 50 cm. and 100 cm. below the surface, as the temperature of the upper soil layers rises with rising air temperatures. Thus, even relatively deeply buried bones are affected by seasonal temperature fluctuations.

The number of frost-free days (averaged for 1951-64) in the southern lake and delta area is between 100-120, in the Peace River area between 100-80 days. Elsewhere in the park the average is between 80-60 days. Therefore, no more than three months of the year may be free of freezing or subfreezing air temperatures in a large part of the study area. Of course, it is not this measurement alone which is significant for bone weathering studies; once bones are solidly frozen they are in a state of suspended deterioration. It is both the freezing and thawing of bones as well as extremes in drying and re-wetting under warm conditions that most damage bone tissues.

In winter the study areas have on the average fewer than 10 days when air temperatures rise above 5°C (based on 1955-64 measurements in AA 1969:15). Thus, once frozen in midwinter, bones on the ground surface will probably stay frozen or nearly frozen until spring. Bones lying on the ground in autumn will be frozen and thawed several times until early November, when daytime air and ground temperatures fall below freezing.

Bones deposited on the ground in winter will remain practically fresh until warm temperatures resume in early or mid-June. If bones remain moist their deterioration will be slowed considerably after thawing. In the Wood Buffalo study area there are between 90-120 days with precipitation during the year, with 120 more common near Lake Claire and 90 days more common in the northern part of the park (AA 1969:16). Bones in the southern part of the park not only may stay wet longer, but may not be subjected to as cold average air temperatures. In other words, bones in the south may not freeze and thaw as often in autumn and spring, and may not dry out as quickly as do bones in the north. These north-south variations in moisture and temperature may or may not prove to be very significant in the long run as far as bone deterioration or preservation is concerned. Future periodic checking of mapped bone sites, planned for 1981-1995, will be designed to note possible north-south distinctions.

Average rainfall in May is about 0.4 to 0.6 cm., in June is about 0.6 to 0.8 cm., and in July is about 0.8-1.0 cm. However, there may be up to ± 35-40% annual variability in precipitation (AA 1969:16). Some years may be over 1/3 drier, while others may be 1/3 wetter. Potential and actual evapotranspiration measurements indicate another factor in bone deterioration: loss of moisture from bones causes tissue shrinkage and cracking (see Miller 1975; Tappan 1971). Extremes in length of exposure to sunshine and drying conditions will cause extremes in bone weathering. Unscreened sunlight of course encourages moisture loss. In the study area in March, 55-60% of the sky may be covered by clouds in daylight hours; in August up to 60-70% of the sky may be covered by clouds in daylight hours. Since August is usually much drier than March, the slight increase in sun screening cannot affect bone weathering rates very favorably. Also, in summer the <u>length</u> of sunlight hours is much increased, adding to an accelerated decay of bones. According to Johnson and Hartman (1969: plate 23), there are 19 hours of sun-above-horizon daylight hours on 21 June at 60° N lat., while there are only six hours on 21 December. Average actual evapotranspiration in the park is about 25-36 cm., the greater moisture loss occurring in the south part of the study area. These figures are somewhat lower than average potential evapotranspiration, which is a measure of how much moisture could be lost through available heat. Overall the study area's moisture index may be characterized as dry subhumid (AA 1969:19).

Vegetation and Soils

Vegetation in the study areas varies a great deal locally. In general the vegetation of the whole area is boreal to subarctic in aspect. In the southern delta region, around the margins of Lake

Claire, the landscape is mostly treeless, made up of muskeg and sphagnum moss ground cover. West of the Lake there are wooded muskegs also possessing heavy moss cover, and the trees for the most part are black spruce (*Picea mariana*). . Willow (*Salix*) and aspen (*Populus*) scrub forests are found immediately north of the lake and its muskeg margins. Most of the rest of the park is a mosaic of aspen-poplar-spruce forests, black spruce muskegs, willow and aspen thickets, jackpine (*Pinus banksiana*) forests, occasional lichen barrens and treeless muskeg, and northern wet site grasslands (AA 1969:28). Jackpine grows on sandy and well-drained soils, while black spruce and tamarack (*Larix laricina*) grow in organic and boggy muskeg. Riverine forests are found along the Slave River and Peace River, consisting of spruces and broadleaf species such as birch (*Betula*) and poplars. On the Slave River and in the Lake Claire area, the vegetation of broad lowlands and deltas is characteristic of boreal/subarctic alluvial zones. Immediately southwest of Ft. Smith there are boreal/subarctic mixed wood forests, with mixed white spruce and poplars. The vegetation of this latter area is subject to slow growth conditions and frequent fires. Around Lake Athabasca alluvial wetlands surround upland mixed wood forests and woodlands (LaRoi *et al.* 1967).

Soils of course differ according to local conditions and parent materials. The following data are from AAA 1979:

Sandy soils, if well drained, are generally podzolic. That is, as typical of cool and moist conditions, iron and calcium leach out of the upper soil zones, and noticeable zonal color changes are present in the profile. Old exposed lake beds are usually made up of degraded black soils (highly humic sediments with upper layers eroded away) developed in silts and clays.

The sandplains south of the Peace River are characterized by elongate or irregularly shaped dunes, most of them under 20 meters high, isolated in broad open muskeg or organic terrain. The dunes are made up of fine or very fine sands, well- to excessively well-drained, and are probably underlain by lacustrine sands and silts. The sides of most dunes slope 15-30°. Fens lie between the dunes, these being low wet ground containing shallow standing water. Aquatic vegetation oftentimes surrounds the water, whose depth rarely exceeds 1.5 meters (AAA 1979:330) (Figure 23, top). Organic soils in wet spots are very poorly drained, and decomposition of plant materials is poor to intermediate (AAA 1979:333). The pH of sand on dunes is usually less than 5 at the surface, increasing with depth (AAA 1979: 333). When the vegetation cover is disturbed, wind erosion may be great on the dune features. The low pH and high hazard of erosion are factors that greatly discourage bone preservation on elevated sand surfaces. Indeed, the only bones I have found on any unprotected dunes are archeological materials recently exposed through deflation. However, if quickly buried by blowing sands, modern bone may be sufficiently protected to be preserved and fossilized. Blowouts are actually rare except at bison wallows; some recent bones have been found partially buried in wallow sands between dune ridges, but generally in poor condition (very weathered, abraded, and splintering).

In some interdune areas, black spruce forests are developing over sphagnum. Willow/alder thickets on drier ground may rapidly develop into black spruce/mixed wood forests, or into aspen/poplar or jack pine-dominated forests where fires are common. The increasing woody canopy in these areas greatly reduces environmental stresses that unburied bones must undergo. However, the lowering of the water table (or an increasing in thickness of surface sediments above the water table due to overbank deposition or humic buildup) which encourages tree growth also serves to lessen a bone's chances of enjoying perfect preservation, by allowing freer circulation of air and allowing oxidation to occur. Bones within an anaerobic fen environment have potential preservation advantage over bones in a willow thicket or spruce wood. Some of the interdune areas may be wet and open meadows, but seasonally these wet meadows may dry up. At Lake One in recent years such drying occurs by August. Bison wallows and ponds that were filled with water earlier (Figure 23,bottom) are dusty by late summer, and bones that were once well-protected from weathering are abruptly exposed to the harsh conditions of hot and dry subaerial weathering.

In the Peace-Athabasca delta area silts and sands are generally stratified, and are most often of deltaic origin. The pH of levee soils may be around 7.4-7.8; these soils are naturally wooded, and contain a high proportion of silt (AAA 1979:368,371). Bone preservation in these shaded areas is much better than it is in the occasional open meadows away from watercourses. The bones found on levees most often derive from transported carcasses, deposited during spring flood or overbank episodes, while bones in woods and meadows most often derive from _in situ_ deaths, wolf kills, poaching kills, or animal densite or lair accumulations.

Another major soils type in the study area is that found in the so-called Salt Flats between the Hornaday River, the Slave River, and the Salt River to the southwest of Ft. Smith. This is a vaguely defined region of 300-400 $km.^2$, located on a mildly sloping apron of saline sediments, extending eastward from the base of an escarpment cut by the ancient Slave River meandering across the area to its present position several kilometers east. Boulders of Precambrian age rocks lie scattered on the exposed flats, transported there by the ancestral Slave River, and are subjected to intense chemical erosion by salt weathering (AAA 1979). Saline meadows and willow/alder thickets are found around bare mud flats whose surfaces are crusty with salt precipitates. The underlying bedrock is impermeable. Drainage is poor, and the water table is within 1/2 meter of the surface (AAA 1979:394). Spring water, draining from the surface of the Alberta Plain to the west of the escarpment, travels underground some distance before emerging very saline on the flats. The soils ringing the saline meadows and flats are silty clay loams, with pH of 7.6 at the surface and 8.0 at about 40-50 cm. below the surface (AAA 1979:395). The most saline near- or over-surface waters are found only where ground surfaces are unvegetated; vegetated soils are much less saline. Some of the vegetation is unique, and includes maritime species growing around and in salt marshes in undrained depressions (AAA 1979:397). The least saline soils support meadows of wheatgrass, swamp birch, and willow/scrub thickets. Black and white spruce, aspen, and jackpine are found in distinctively-shaped tree islands within open meadows.

Figure 23. Terrain in Wood Buffalo National Park.
TOP: View of grassland. In the background is a linear sand dune, about 6 meters high. In the lower left of the photograph is the edge of a drying wallow pond. The two skulls were gathered by a biologist.
BOTTOM: Bison bull and calf standing in a water-filled basin (wallow pond), and a female standing in grass in the Lake One area, August, 1979.

Figure 24. The Salt Plains, seen from the west escarpment, Wood Buffalo National Park.

Figure 25. Bones of Bison skeleton number 10, lying on dried lakebed, July, 1979.

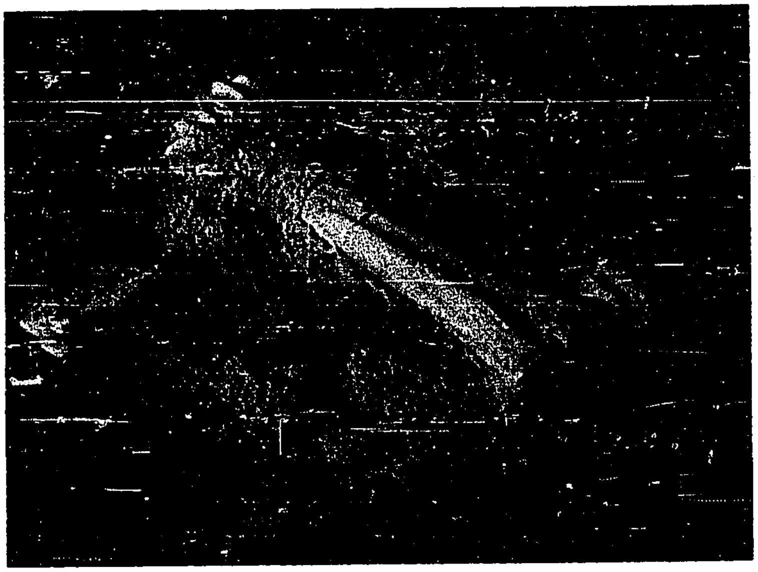


Figure 26. Lower leg bones of skeleton number 10, and part of a rib, lying on and partially in dried lakebed sediments, July, 1979.

The salty mud of the flats is a suitable matrix for bone preservation, until it dries out, which it tends to do in later summer of drier years (such as 1979 and 1980) (Figure 24). Some years are much drier than others. A single season of unusual drying will lead to a great deal of peeling and exfoliation of surface bones, due to the shrinkage of tissue and also due to the rapid growth of salt crystals precipitating within bone pores or interstitial spaces (see Cooke 1979 for a discussion of factors pertaining to salt weathering of porous stone). When saturated with water in spring and early summer the salt flat sediments do not readily flow around bones deposited there. The bones are eventually buried in organic and mineral sediments if they lie in shallow ponds or lakes (Figure 25, Figure 26). When the sediments dry they crack apart in reticulated patterns and become very hard or dusty. But because the water table is so high even in dry periods, most of the exposed flats only dry out in their upper few centimeters, so that shallowly-buried bones remain well-protected (and difficult to find).

Hydrology and Drainage

Several important aspects of hydrology have already been discussed above, such as actual and potential evapotranspiration compared to available moisture, seasonal amounts of precipitation, different drainage characteristics of various sediments, and average yearly variability in levels of precipitation. There is one more important point on hydrology that must be discussed in this section regarding the park's large freshwater delta area: historically the ecological conditions of the vast Peace-Athabasca delta were maintained by a spring-summer increase in water levels of about 1.7 meters each year. Over fall and winter the water table gradually lowered (Dirschl 1972; PADPG 1973; also see Stockton and Fritts 1971 for reconstructions of water levels for 1810-1967, using tree-ring analysis). Fluctuations in water levels left large parts of the delta in early plant successional stages due to the regular creation of thick silt deposits and the flushing out of plant materials (Dirschl 1972). This produced an extremely favorable circumstance for many kinds of wildlife including waterfowl, muskrats, bison, and moose. Grasses and sedges and aquatic plants could grow anew each year on ground that would otherwise support willows or other species with low nutritive value for wildlife (Fuller and La Roi 1971). Because the area is so flat, even slight changes in water levels will profoundly affect plant succession over large areas (the delta covers over 4700 $km.^2$).

In the late 1960's a dam was constructed upstream from the delta on the Peace River. Due to the existence of this impoundment and also to unusual weather conditions, from 1968-71 the delta had extremely low water levels. During these years many of the once deep lakes froze to the bottom in winter, killing fish and resident muskrats (PADPG 1973; Cordes and Pearce 1977). Lake water flushing during flood season was minimized, leading to poorer water quality and the creation of very large exposed silt flats at the margins of shrinking lakes (see Dirschl 1972:figures 7-10). These flats were colonized by grasses and sedges, and willow-alder scrub thickets would eventually have developed on many of them. However in 1971 there were two major floods on Lake Athabasca, including an ice-jam backup and consequent overflow from the west in April, and a summer flood in July (PADPG 1973:129).

High water levels were maintained in the 1972 spring floods, when an ice jam on the Peace River caused the damned water to overflow onto the delta (Cordes and Pearce 1977:18). The delta also flooded in 1973, and in 1974 the water levels of the Peace-Athabasca delta were raised to a high exceeded only two other times in the preceeding 44 years (Cordes and Pearce 1977:20). At freeze-up in late 1973 delta water levels had been about two meters above normal, and much of the winter bison range was iced up over winter (Tempany 1974). During 1974, flood waters did not recede until the end of summer. In October, 1974, strong westerly winds skewed the high water levels of Lake Athabasca enough to wash out a weir, leading to the steady drainage of the lake into the Slave River system until ice-up later in the year (Cordes and Pearce 1977:21-22).

In 1971, during the flood which ended the period of unusually low water levels, at least 48 bison were drowned, out of probably 8000 or 9000 animals in the area. These animals were most likely caught in the rising waters while foraging in areas of low topographic relief. In earlier years bison had also been known to drown in spring floods: for example, in the thaw of 1961, at least 1100 animals died, and possibly as many as 3000 (Novakowski 1961). However, about 30-50 drownings a year was thought to be the typical figure (Soper 1941:403 ; PADPG 1973:72; Couchie and Loranger 1979:7) (Figure 27). This is a relatively small number when compared to the estimated total number of bison in the park before 1974 (8-10,000). But an unusually great flood following unusual water levels, such as occurred in 1961, 1971, and 1974, can kill thousands of bison in a short time. Whereas in normal years less than 1% of the total bison herd does from drowning, in extreme years nearly 30% of the population can be destroyed. The bone assemblages resulting from the most recent cataclysmic flood will be discussed more fully in later chapters.

Wildlife Resources and Research

In 1907, Ernest Thompson Seton set off on a 6 month, 3300 km. canoe journey into the northern prairies and tundra, inspired by an urge to see great herds of caribou before civilization began its overwhelming advance down the Athabasca River towards the arctic. He visited Lake Athabasca, Ft. Chipewyan, and the Ft. Smith area (Ft. Smith Landing), and reported on the range conditions of the Wood Buffalo area (Seton 1911).

Civilization has still not penetrated very deeply or profoundly along many northern rivers which flow to the arctic. The Wood Buffalo area and environs are rarely seen by man. The area's wildlife, however, continue to be of great concern to civilized and uncivilized man. Seton thought the idea senseless that wolves were destroying the bison herd, instead placing the blame on indiscriminant killing by local natives. Seton recognized that carcasses fed on by wolves, as opposed to those utilized by Indians, were characterized by the presence of the big bones and lack of breakage of the skull (Seton 1911:44). Kitto (1924:437) also did not believe local wolves were inflicting serious damage on bison numbers, which at the time he wrote seemed to be increasing. Soper (1935) speculated that during pre-European settlement times there may have been one wolf per 2.6 $km.^2$ in the area; later Soper (1945) attempted to trace fluctuations in local wolf numbers. In 1925, according to local residents and park wardens, wolves began increasing in numbers within the park, became perceptibly more numerous between 1932-1934, and since then (up to 1945) steadily increased in numbers. Soper noted the same recorded population trends for large areas of the north, stretching from central Alaska to Ontario (Soper 1945:19). (Munro [1947] in Central British Columbia noted a considerable increase in wolf numbers after 1926, with frequent sightings from 1932-34, and steady increases through 1947.) Note that these periods of increase are broken down into intervals similar to the intervals for changes in local mean annual temperature trends (see discussion above). It is possible that wolves were increasing in numbers due to an increase in prey numbers, prey vulnerability, or prey availability. Soper postulated that during the early decades of this century wolves may have been following migrating caribou herds near the Wood Buffalo region, and then migrated into bison range to stay. Soper (1945) advocated artificial control of wolves, since moose and deer numbers seemed to be declining as wolf numbers increased, the justification for interference in natural affairs being that the park is unique, and its native residents are dependent on available wild meat for their subsistence.

Soper (1945) also observed several natural factors in the region which could be disastrous to wildlife, especially bison; these factors would include unusually deep snow with midwinter thawing and refreezing, and consequent formation of thick, hard crusts through which feeding or travelling would be difficult. He mentions (Soper 1941:404) several years in the last century when such weather conditions were recorded, such as 1820, 1840, and 1866. In those years bison winter die-offs must have been unusually great.

Fuller (1960,1966) offered excellent observations of bison behavior and biology, based on his studies in the park during the 1950's when there were annual slaughters of bison for commercial sale of meat. Later, after all commercial enterprises were discontinued, some slaughtering was performed for disease control. For example, in 1967 120 bison were killed or disposed of at Lake One for anthrax control (Oosenbrug *et al.* 1980:5).

Beginning in 1971, actual counts of total bison numbers are available for the delta area and the entire primary bison range of the park (Kuyt 1971; G. Masson 1971; Lyster 1972; numerous other manuscripts on file at headquarters of Wood Buffalo National Park) as performed usually in one day helicopter or fixed-wing aircraft survey flights. On March 25, 1971, the total count for the entire primary range was 9869 animals, whereas the count for September was 9561 animals. For any survey flight some animals may not be counted because they are in heavy cover, while others may be counted twice. However, total counts since 1971 have been in general agreement year to year, although abrupt declines have been noted after spring floods (Allison 1982). Variations in counted totals of up to 10% may have been due to sampling and counting errors and not to changes in actual bison numbers. The total count for February, 1979, was 5539 animals (estimated total of 6100 after adding 10% error of possibly uncounted animals), while the total for February, 1980, was 4512 animals (with correction to 4963 after addition of 10% possibly uncounted) (Anions and Lukiwski 1980, Anions 1979b).

It is evident that there has been a significant decline in the size of the herd since 1971, perhaps precipitated by the disastrous

1974 spring flood in the delta which may have killed 3000-4000 bison (Lyster 1979;Cooper 1974; Tempany 1974). Harsh winter conditions, heavy opportunistic predation by wolves (taking advantage of increased bison vulnerability) and disease may have since depressed the recruitment rate of the herd. Aerial counts in November, 1979, show that only 7.9% of Area I bison herds and 10.8% of Area II bison herds were calves, and in February, 1980, only 5.8% of Area I herds were calves (Area II count unavailable)(see Anions 1979a and 1979b and Anions and Lukiwski 1980). Once the proportion of calves in the herds drops below 10% in winter, the herd may not noticeably increase the following spring, and may in fact be in a declining phase.

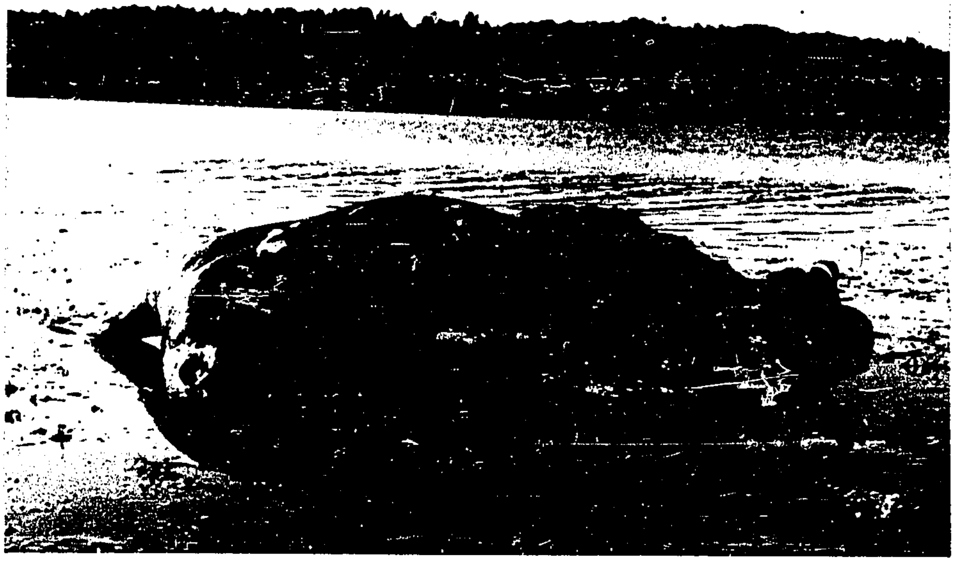


Figure 27. Dead male Bison floating in thick, bottom-rooted vegetation in North Arm of Lake Claire, August, 1979. Sweetgrass Island is in the background.

Bison Skeletal Sites

One of the aims in conducting most of the field research in distant northern areas was to ensure that human behavior would have minimal (or preferably no) influence on animal remains under observation. No humans live in the park, except a very few natives who temporarily reside in private cabins while engaged in winter fur-trapping. In other seasons of the year, park wardens and scientific researchers occasionally visit many remote parts of the park, and a small number of hikers may from time to time venture into back country. The main carcass and skeletal sites (Figure 28) were deliberately selected out of many alternatives because none are near roads, passable trails, trappers' cabins, trap lines, or commonly visited areas of the park interior. It is improbable that humans will encounter and disturb the remains.

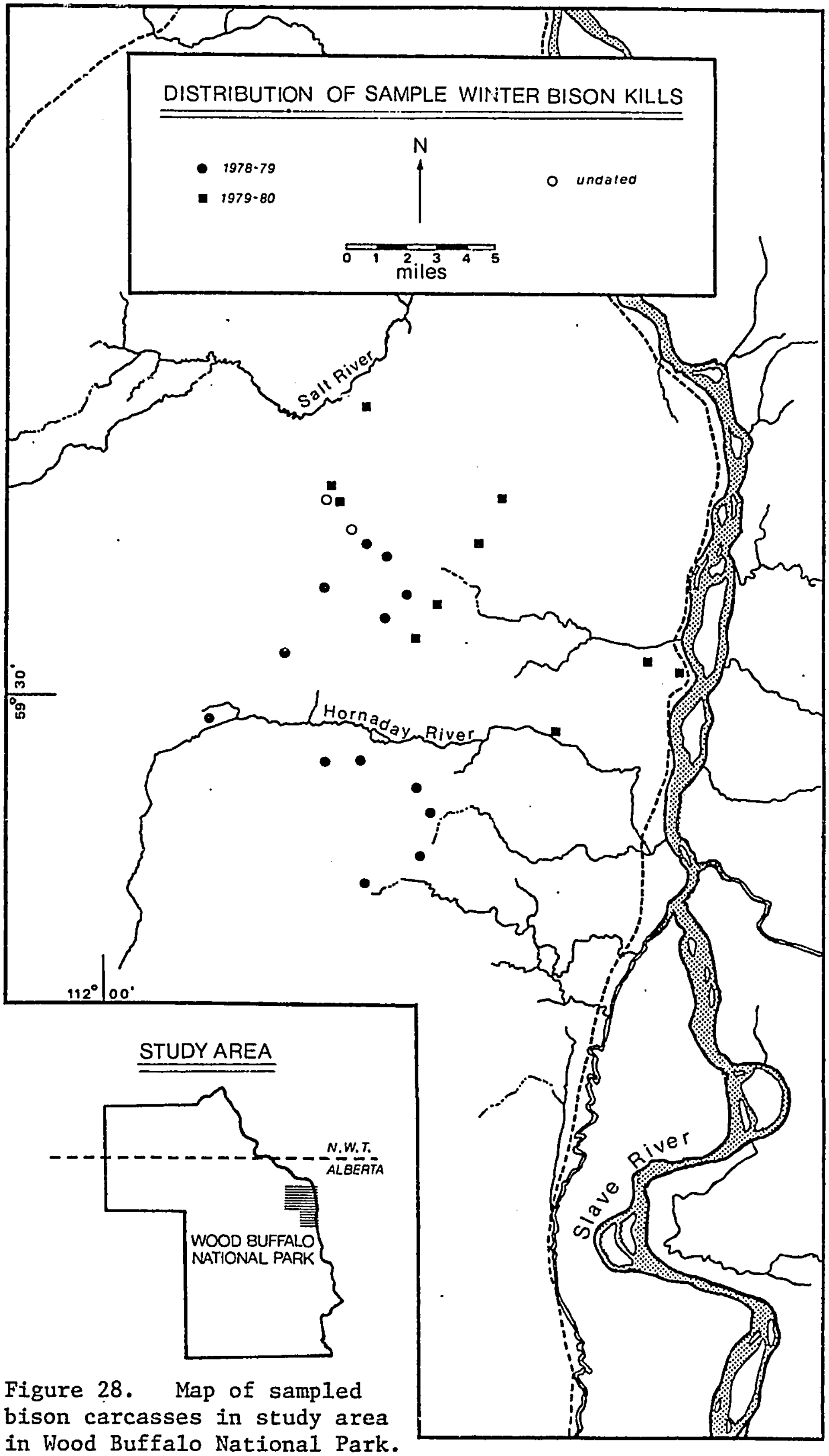


Figure 28. Map of sampled bison carcasses in study area in Wood Buffalo National Park.

Introductory Notes

The distribution of ungulate carcasses (carnivore-killed) in any part of Wood Buffalo National Park is positively correlated, for the most part, with the distribution of live animals. In some cases, floods might carry articulated skeletons away from their places of deposition, but because there are so many tree stands interrupting open meadows in Wood Buffalo National Park, I doubt that carcasses will be more than a few kilometers removed from their original sites before being hung up in trees (Figure 29). Therefore, in the following discussion, wolves and bison are considered as examples of interacting predators and prey wholly responsible for the creation of many sites.

Wolves are often found very near bison herds, which usually move slowly while feeding or searching for feed (Figure 30). Daily migrations may take bison several kilometers, while seasonal migrations may take them several dozen kilometers or more (see Raup 1933; Fuller 1960, 1966; Soper 1935; and numerous manuscript reports on file at the headquarters of Wood Buffalo National Park). Bison carcasses from wolf kills would not necessarily be accumulating in any one restricted area over short periods of time, but may do so over relatively long periods of time because primary bison ranges (which possess the most abundant preferred feed resources) do not change their character quickly or often. Where bison aggregated perhaps only half a decade ago, they may not be scarce, due to a drying trend in the summer weather of the Wood Buffalo area; in these cases, succulent plant feed may have been replaced by less-preferred species in normal seral progression. However, most of the primary bison ranges are good and appealing to bison for many years (compare Raup 1933 and Stelfox 1978).

There are few meadows or prairies in Wood Buffalo National Park that stretch more than three to five km. between tree stands. Bison may move in and out of the same discrete prairies many times over the year (Collingwood 1977; Cooper and Tempany 1974), or they may visit any only once. Wood Buffalo bison attach themselves in smaller feeding and breeding groups than did the historically known Plains animals of more southerly regions, whose ranges were vast and uninterrupted by tree stands and pockets of different edaphic and botanic characteristics (see J. Allen 1877; McHugh 1972; Roe 1970; Catlin 1844). Wolves that preyed on open-ground-dwelling Plains herds, whose numbers may have swollen to several hundred thousands on certain ranges and at certain times of the year (see Roe 1970; McHugh 1972) may have moved about differently and established different kinds of hunting territories than do wolves whose prey is not so abundant or uniformly distributed (as characterize Wood Buffalo area bison). Moose and deer, while not as plentiful or available in any one spot as are bison in herds, are actually more uniformly distributed in their range than are bison. Wolves that hunt cervid prey do not usually follow or harry animals at great length, but instead may explore their territory and be assured of eventually encountering a prey animal somewhere else (Mech 1966,1970).

The bison of the Wood Buffalo area are a clumped but nonrandomly distributed resource, whose patterns of dispersal are in between those of the Plains bison and the woodland moose. Over the course of a year these bison never move more than 180 km. in any one direction (a distance a pack of wolves can cover in a day and a night of travelling if snow conditions are favorable), and so are always available and nearby to predators. Yet, these bison also occur in clumps (bands or herds, although there are quite a few lone bulls in winter) whose presence or absence cannot be predicted at any one prairie or complex of prairies from day to day or week to week. Wolves will often spend days near the same feeding bison herd, bringing down members from time to time (Figure 31, center and bottom left). Yet wolf packs also leave the herds to wander the rest of their territories, possibly because they are feeling well-fed and restless to explore traditional hunting areas, even though they risk losing touch with immediately available prey. Wolves are capable of spending several days travelling without food, especially after they have eaten well.

The Hornaday River wolf pack in the park hunted an area of about 1345 km.^{2} in the winter of 1978-79. The size of the pack ranged from 14 members in early winter to 10 members in late winter. During this time there were approximately 200 bison wintering in their territory (Oosenbrug and Carbyn in prep.). In the winter of 1979-80, their hunting territory was even larger, the southernmost boundary being 40 km. beyond the 1978-79 boundary, possibly because it was easier to travel greater distances due to milder weather conditions (Oosenbrug et al. 1980;Oosenbrug and Carbyn in prep.; Oosenbrug 1979, 1980 pers. comm.). There were 11 members in the pack during the second winter of my study. Over this winter of 1979-80, about 473 bison were wintering in the wolves' territory (Anions and Lukiwski 1980:4). Within the main area of the hunting territory, where more bison would usually have been found, the pack killed or visited 33 carcasses during the winters of 1978-79 and

1979-80 combined. In 1980, most (or all) of the carcasses that the wolves visited were probably killed by the pack; in 1979, some were considered unconfirmed kills, and may have been winter deaths that were scavenged (Figure 31, bottom right). In 1978-79 most of the bison in the area were bulls who kept themselves solitary or who aggregated in small bands that usually contained fewer than a dozen members. In 1979-80, the bison in the area were found mostly in mixed herds, with many more females and calves in the area than in the previous year. Thus, data on the age and sex of bison killed by the Hornaday pack were quite distinct each year. In 1978-79, the pack killed or scavenged carcasses of nine adult males, three adult females, and no subadults. In the following winter (1979-80), the pack killed or visited carcasses of adult males, adult females, calves, and yearlings.

Figure 28 depicts the distribution of carcass sites that I inspected in winters and other seasons. Killsites are not uniformly distributed on the map, even though several years of kills are visually represented. However, the killsites do cluster where prairies are largest and most often visited by wintering bison. Wolves test their prey by running after them and attacking, and so successful kills (even from the same, nearly sedentary feeding herd) are often scattered. Wolves test far more animals than they bring down (Oosenbrug 1980 pers. comm.), and so they make herds move about quite a bit. Bison are not very easy to kill (as can be deer or caribou, especially in harsh winters); the dropping of a single adult animal may take considerable time and effort, and is only accomplished if the bison is separated from other animals (Figure 33, bottom left).

The dropping of a calf, which is a highly preferred prey type, is relatively simple if the animal is separated from the rest of the herd; however, bison in herds or bands usually defend themselves as a group. They will flee attacking wolves in a tight mass, and they will wheel about to confront pursuing wolves while still bunched shoulder to shoulder (Oosenbrug 1980 pers. comm.; Haynes unpublished data). It is not easy for attacking wolves to scatter bison. Several steaming carcasses are not going to be found at the same killsite at any one time, unless whole bands are suffering severe disease, malnutrition, or wintering stress.

In fact, I have never found more than one skeleton per killsite (using an arbitrary spatial definition of a killsite as an area 30 meters by 30 meters). Wolf or fox dens, and the edges of ponds or traditionally used bison wallows may contain single bones representing more than one individual bison, but very rarely have these bones weathered or aged for identical lengths of time. Most of the bones in ponds or wallows do not appear to be from kills, but from winter deaths _in situ_ or from retransport of single bone elements by foxes, wolves, or bears to the site of another scavengeable carcass.

Most bison are killed when there is snow on the ground. In new killsites I have never found older bones at a site left from prior kills, after I have returned to inspect the sites in the spring or summer. It is conceivable that bones from several kills could accumulate in lake or pond sediments, especially in nearshore areas which are subject to high sediment addition rates from annually dying bottom-rooted plants and organic debris. Many of the numerous interior lakes of the Wood Buffalo region are not subject to high-energy drainage currents or flood disturbances, and so whole articulated skeletons or bone units may actually be settling into sediments atop earlier skeletal deposits. However, since these ponds are popular with live bison, it is probable that traffic in the muds works to disarticulate and mix bones that lie on bottoms or within bottom mucks.

Most kills on land surfaces occur in wooded areas, but are within a few hundred meters of open meadows. This is due to the fact that attacked bison often flee into wood cover, which is usually nearby except in the southern Delta region, where tree stands or shrub bush are sometimes very widely situated. Bison often try to feed near woods in winter, because of the shelter from winds that is offered.

By the time that spring scavenging is complete, kills lying in grasslands or woods are usually disarticulated. Perhaps vertebrae subunits remain together, and perhaps the bones of lower legs above the hooves lie in anatomical order. Gnaw damage to long bones is patterned at scavenged killsites (see Table 8-2). At death sites (not kill or predation sites) many times the bones are in anatomical order, and much more of the carcass is articulated than at killsites (Figure 32). There even may be several skeletons lying close enough together to overlap (assuming a "normal" scatter of about 6 meters by 6 meters, in the absence of much scavenging by large carnivores). Bones at these sites are of course little damaged by carnivore gnawing. Where several animals perished together (or where their remains eventually rest) wolves produce little to no gnaw damage on most bones, but where only one skeleton is found, the gnaw damage may vary from heavy to light. The remains with light damage are most likely scavenged winter deaths (Figure 32, bottom); the remains with heavy damage are most likely scavenged summer deaths.

Where there are several skeletons found together (the result of mass deaths), some may be fully or semi-articulated, most will show little or no articulation, most will have missing elements, and a few will be quite complete. Any gnawing damage seen on such clustered remains will not fit neatly into the sequential damage chart (Table 8-1). Ribs will seldom be broken off vertebrae at or near articular ends; vertebrae spinous processes will rarely be broken or even moderately damaged.

Density of bones or skeletal units is very low at any kind of site except mass death sites such as drownings, when floating carcasses are wind-rowed along levees or gallery tree lines. I have never seen carcasses or skeletons piled atop each other, even when hundreds of animals drowned and floated _en masse_ into thick trees lining narrow creeks. Piling apparently occurs only when single bones or units of articulated bones are deposited by floodwaters into slack-water areas or natural detritus traps, such as log jams.

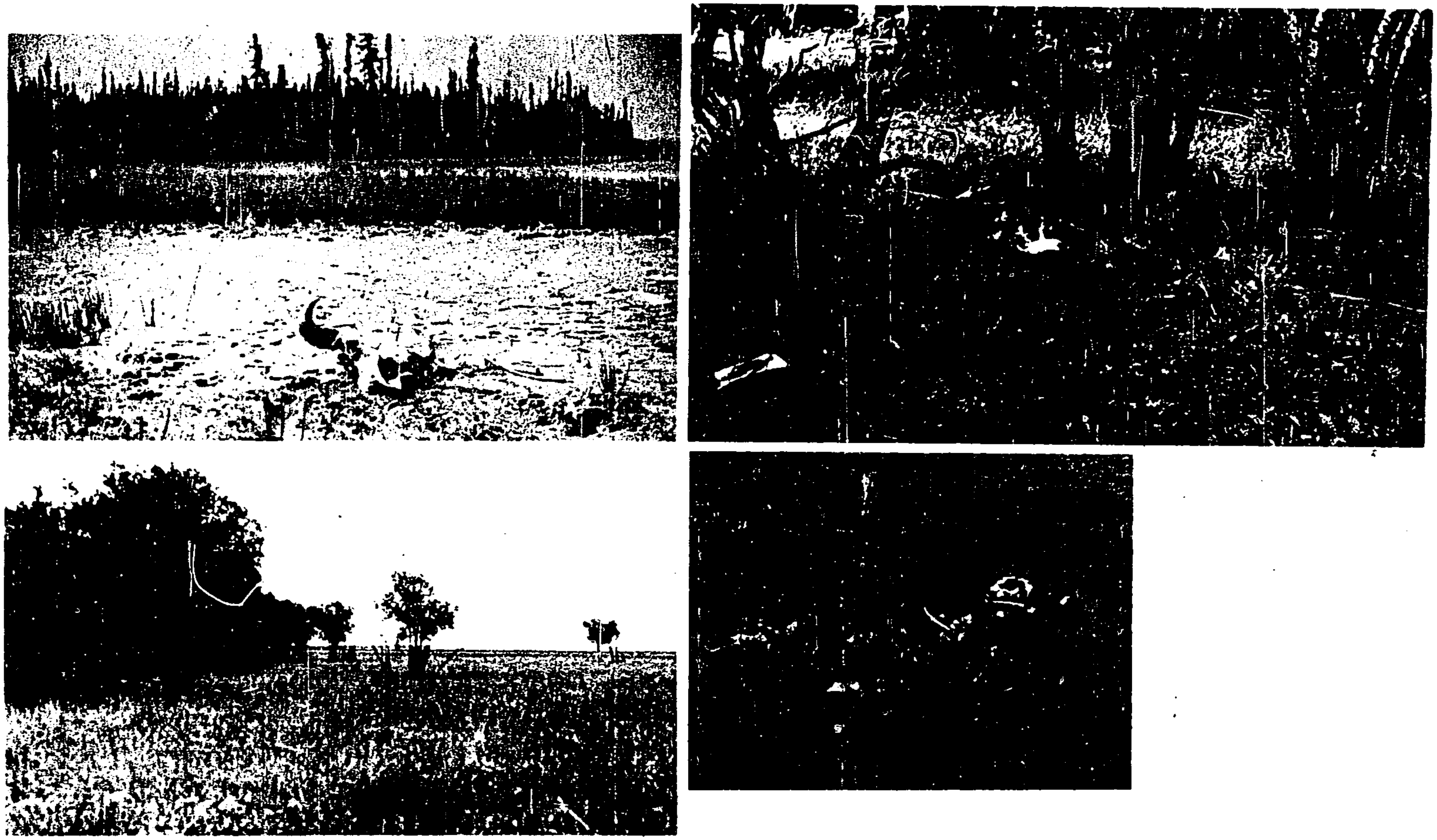


Figure 29. Lake and pond sediments, and shores.

TOP LEFT: Salt Flats. Dried saline lakebed with grasses and sedges growing in middle distance, and willows growing around stunted spruce in foreground. Carcasses floating in the lake would not be carried far into the trees.

TOP RIGHT: Bones of Bison lying at edge of prairie-willow bush, where floating carcasses settled after floodwaters receded.

BOTTOM LEFT: View of willow bush (to left) and extensive prairie (to right) which forms the shore of Lake Claire.

BOTTOM RIGHT: Bison bones on dried bed of Malheur Lake, Oregon. Skull is inverted (to left). Photographed by G. Benson, February, 1931. Courtesy U.S. National Archives, negative number 22-WB-37504.

Figure 30. Bison feeding in dispersed fashion on Lake One prairie. In the distance are large wooded sand sunes. Photographed by S. Oosenbrug in midsummer, 1978.

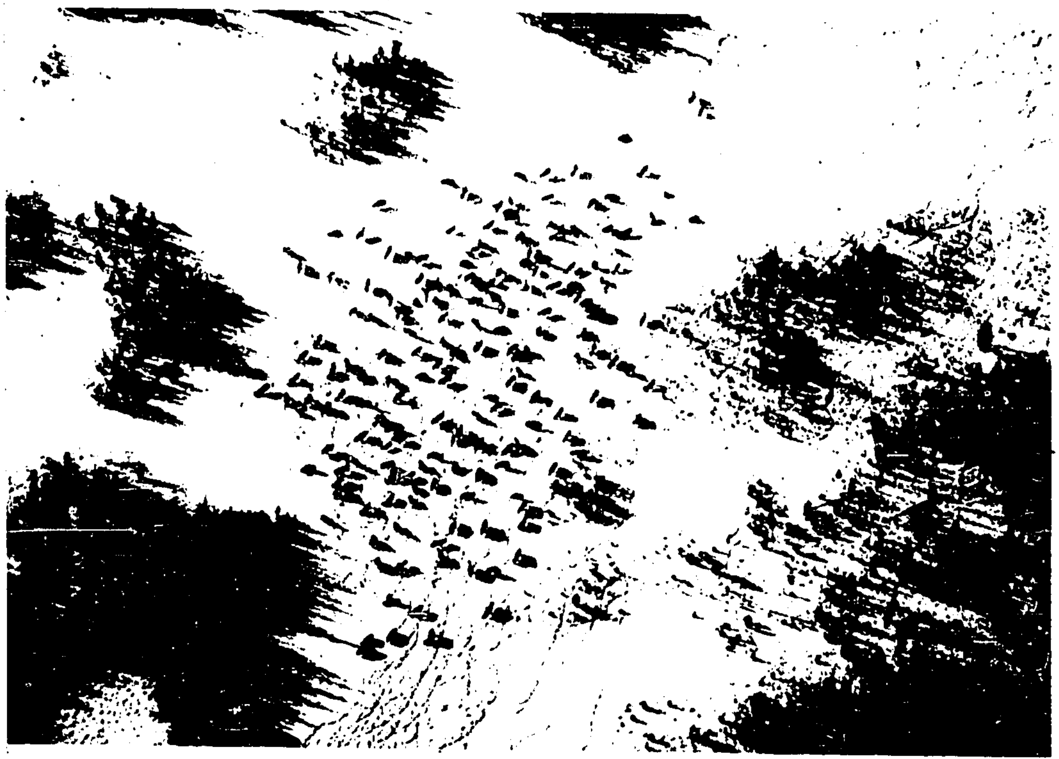
Figure 31. Research strategy and techniques.

TOP: Small plane used to locate wolves and carcasses of prey.

CENTER: Feeding mixed herd of bison, photographed in midwinter, 1980, in the Hay Camp prairies area.

BOTTOM LEFT: Bison bull under attack by 11 wolves (Hornaday pack) (one wolf is not in the photograph).

BOTTOM RIGHT: Author taking notes at scavenged carcass site 1w79-7 in midwinter, 1979.



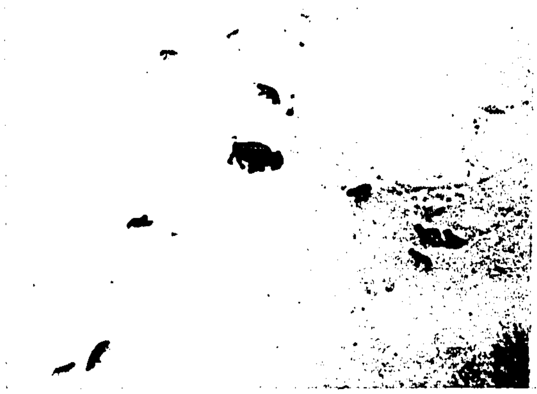


Figure 32. Scavenged carcasses.
TOP: Bison bull that died from unknown disease in Lake One prairie, recently scavenged by wolves, summer, 1979.
BOTTOM: Remains of carcass site lw79-2, after spring scavenging in 1979.

Figure 33. Wolf-killed Bison.

TOP LEFT: Bison bull lw79-5, midwinter, 1979.
BOTTOM LEFT: Bison bull lw79-6, midwinter, 1979.
TOP RIGHT: Bison bull lw79-1, just after wolves had killed it, midwinter, 1979.
BOTTOM RIGHT: Remains of lw79-1 a month later.

Skeletal Sites

Carcass 1w79-1 Male, estimated age +7 years.

This carcass was found during aerial tracking of the Hornaday River wolf pack. The animal had been killed by the 14 wolves of the Hornaday pack on 19 January, 1979, after a 200m pursuit and a fierce struggle in the woods that broke down several trees and sprayed blood high on trunks. The carcass lay on its brisket and its left rear side (Figure 33, top right). The biologist collected one mandible and a femur. I visited the site on 8 March, 1979.

Most remaining bones were quite clean, except those of the head and lower legs. All vertebrae had been well gnawed (vertebrae were articulated from skull through sacrum). All ribs on both sides had been broken off. Only five medial segments of ribs remained, all the rest had been broken near articular ends. Several rib segments lay about the site. The right scapula was gone. The pelvis was well-gnawed. Much fresh snow covered all lower legs, which had been encased in packed and icy snow already (Figure 33, bottom right). Humeri and femora were well-gnawed.

Carcass 1w79-2 Male, estimated age 9-10 years.

This carcass was discovered on 16 January, 1979, during aerial tracking of 10 wolves of the Hornaday Pack nearby. The animal had died sometime earlier (estimated date November or December, 1978, based on snow and ice accumulation) and its remains were very lightly utilized. It lay about 40 meters from a prairie within an open woods. It was lying on its right side, all legs extended, and some of its left ribs were broken out and its insides exposed. The only bones out of anatomical order were the broken ribs. I visited the carcass on 2 March, 1979; it lay exposed but partially buried by snow. The left nasal bones had suffered very light damage during wolf-gnawing of the nose. The left ear had also been eaten. Hide was removed at the rump, the upper left rear limb, and the ribs and sternum on the upper (left) side. The tail had been eaten. The left femur's greater trochanter had been gnawed down a bit, and the left scapula had been very lightly gnawed at the vertebral border. Many tracks and urine stains, and a great deal of wolf scat was found in the area, indicating recent wolf feeding on muscle tissue or viscera.

The site was revisited 26 July, 1979. A hairmat and a mat of gut contents were found where the carcass had been lying in the winter; the ground had been disturbed by bison moving along a migration trail that passed within 2 meters of the original carcass position. The carcass itself had been moved 10 meters into a willow thicket; wolves or bears were most likely responsible. Mandibles, the skull, some ribs, the scapulae, two articulated vertabral units, a phalanx, and bone fragments were scattered between the new carcass location and its original spot. As for the carcass itself, all muscle meat and viscera were gone; 17 vertebrae were in articulation through the sacrum and pelvis. The left and right forelegs were complete from hooves through humeral proximal ends, and were attached to the vertebral column by hide. All ribs had been snapped off from the vertebrae at least 1 cm. from their articular ends. The skull was completely cleaned of flesh, and lay upside down below the vertebrae and pelvis. The left ilium and ischium and left humeral head had been somewhat gnawed (Figure 32, Bottom).

A fragment of bone (rib?) with chronic osteomyelitis was found in the bone scatter. The severity of infection indicated on this fragment may have been the main cause of the bison's death; later, in winter, wolves found the carcass and ate some meat, but because the remains were solidly frozen carnivores did not utilize the carcass until the following spring and summer.

Microscopic examination of sectioned M^1 from the animal indicated death following the rut, but before winter (late fall, very early winter - November, 1978).

1w79-3 Female, 7-8 years old.

This animal's remains were found 19 February, 1979, during radio-tracking of the Hornaday Pack. Date of death was estimated as early winter, 1978-1979 (possibly December or January). The bison lay on its right side in the open, on a level prairie several hundred meters from trees, within or on top of less than 10 cm. of packed snow. Little or no meat remained on the bones, and several elements were missing.

I visited the carcass on 2 March, 1979.

The right side hide (the down side) was unconsumed, and all that remained at the site were the left rear lower leg from the proximal tibia through hoof, the right foreleg from proximal humerus through hoof, and the well-gnawed head (skull, horns, and mandibles). The left mandible had been collected earlier by biologists. The maxilla showed gnawing damage, as did nasal bones, the auditory bullae, the palate, malars, pelvic bones of both sides, the right humeral head, and the left tibia proximal end. The tibia shaft was lightly scored by gnawing.

No vertebrae or ribs were found, although segments or whole elements may have been nearby but covered by snow.

The site was revisited and photographed by Park Warden D. West on 29 July, 1980. The leg bones were gone, and only the skull, right mandible, hide, and some bone fragments could be found.

lw79-4 Male, estimated age 6 years.

This carcass was found 21 February, 1979, during aerial radio-tracking of the Hornaday Wolf pack. Fresh evidence of a struggle and the fresh look of the carcass indicate that it was a kill made by the wolves about a week before its discovery. The animal was a very large bull lying on its left side in the trees about 15 meters from an open prairie. During the first visit (21 February), the snow in the woods was shallow and packed. Most bones of the carcass were exposed, and several were well-gnawed. Some chips and fragments of long bones, vertebrae, and ribs lay scattered about. I visited the site on 2 March. At that time, most ribs were broken off the vertebrae; the spine was broken into two articulated units. All spinous processes of all vertebrae had been gnaw-damaged. The head had been removed from the spine by a biologist, but wolves had apparently returned to the site and dragged it 10 meters away. The nasal bones had been gnawed. Both rear legs were moved up to 30 meters away from the spine, most of which was lying on the uneaten, downside part of the hide. The mandibles were disarticulated from the skull by the biologist on 21 February, and also damaged by chopping at that time. The rumen was untouched, and lay on the uneaten hide.

One lower rear leg had suffered a mid-shaft spiral fracture, undoubtedly the result of chopping damage done by the biologist to check marrow condition. The lower leg had been carried 30 meters away, where the hoof had been slightly gnawed. Much of the scatter of the skeleton may have been the result of wolves later carrying elements that the biologist separated upon investigating the carcass on 21 February; however, photographs taken of the carcass on 21 February show unusually heavy wolf utilization of some elements of the remains, so that disarticulation of remains by feeding wolves might have been possible even without the biologist's actions.

Many long bones were broken by the investigators for marrow check, or were collected. On 7 March, five wolves re-visited the site and fed or gnawed on remains. On 6 December, 1979, I revisited the site and found in the snow only the skull and horns, one of which had been removed from the horn core. Both horns had signs of light gnawing (previously noted 2 March).

1w79-5 Male, mature; unknown age.

This carcass was found 24 February, 1979, during aerial tracking of the 10 member Hornaday pack. The bison had been freshly killed in a small prairie which was surrounded by broken thickets of willows several hundred meters away. The animal apparently had been killed by wolves after a short pursuit in the open, and lay on its right side on packed snow. I visited the site on 8 March, when the legs on the downside had been buried in new snow that was packed by wind or by wolf trampling (Figure 33, top left).

All vertebrae except caudals were exposed and gnawed, and all remained in articulation; all ribs on the upper (left) side had been broken off at or below articular ends.

Hide and meat on the downside (right) foreleg were entirely uneaten. Head and throat hide was uneaten. The downside rear leg was partly cleaned (the femur and tibia were exposed) but no gnawing damage to the bones was noted. The left scapula was cleaned and very lightly gnawed; the left humerus, in articulation, was also partly cleaned but undamaged. The left half of the pelvis was cleaned and gnaw-damaged. The left femur was missing, having been collected earlier. Several 5-6 cm. long segments of ribs were scattered around the frozen carcass. The lower left rear leg was found about 200 meters away on a trail made by a running wolf, who had been surprised while feeding at the site. One mandible had been chopped out and collected earlier. Much ligament and soft tissue remained on the spinal column. Caudal vertebrae were missing.

lw79-6 Male, estimated age 7-8 years (not visited).

This carcass was discovered during aerial tracking of 11 wolves (the Hornaday pack) on 28 February, 1979. It was a suspected kill, with few or no fresh signs of pursuit or struggle. It lay on its left side at the edge of a willow thicket. Utilization by feeding wolves was only of the upside rump, shoulder, and ribcage meat (Figure 33, bottom left).

All ribs were broken off the up-side, and several fragments were scattered. The right hind hoof was gnawed, as was the tip of the right horn. The lower parts of the fleshy nose and of the ear flesh were eaten.

1w79-7 Male, age 20 years.

Scavenged remains, probably from a summer death dug out of the snow by members of the Hornaday pack on 5-6 March. Bones that were found included the skull (which was full of hundreds of fly pupae cases), the pelvis, an articulated femur and tibia, and an articulated unit of vertebrae (cervicals and thoracics).

1w79-8 Seen from the air - Probably adult male.

This carcass was spotted by me from the air during aerial tracking of radio-collared wolves on 15 March, 1979. Sixteen wolves had been seen nearby in the previous week. The articulated skeleton could be seen lying on its left side atop an uneaten "blanket" of hide, situated in an open prairie several hundred feet from willow bushes. All legs seemed to be present. Some of the up-side ribs were broken away, but the rumen was undisturbed. Head and neck hide appeared to be uneaten, as did hide on all lower legs.

1w79-9 Female, estimated age 6-7 years.

This carcass was spotted 15 March during aerial tracking of the Hornaday Wolf pack. The animal had apparently been encircled by the pack and killed in open woods no more than two or three days earlier. It lay on its front left side and on its belly (Figure 34). All of the right side ribs were broken off, these being the only bones at the site out of anatomical order. Most of the flesh on the right rump and upper rear leg and the right upper rear leg and the right upper foreleg had been eaten. Most caudal vertebrae were present. A large part of the hide had been peeled back from the upper side of the carcass. Some parts of the viscera had not been eaten (including a complete lung), and the rumen contents were untouched, although some of the gut walls had been eaten.

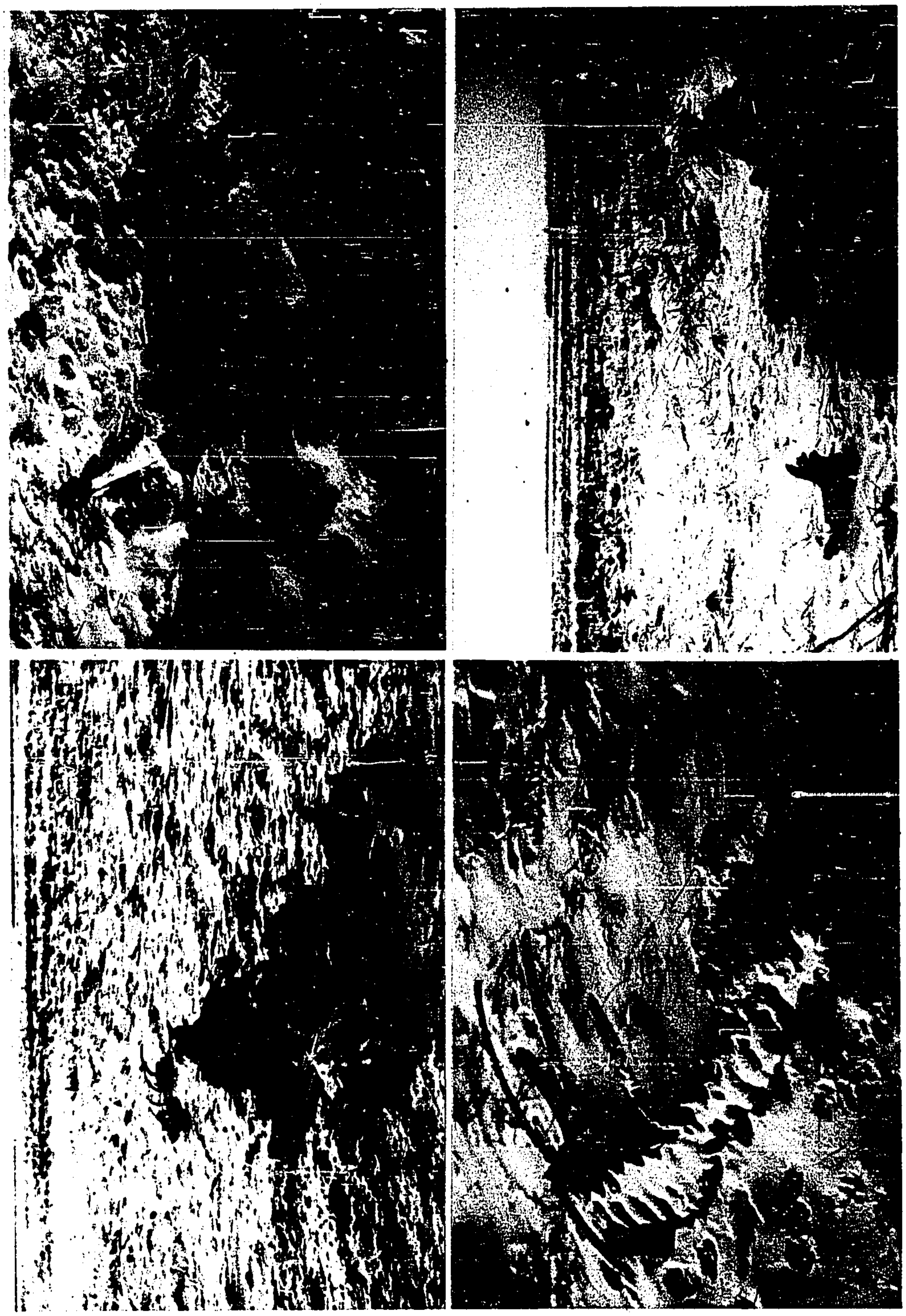
The right scapula was well gnawed; all vertebrae were cleaned and all processes were damaged or broken off. The vertebral border of the down-side scapula was also damaged by gnawing. Dozens of splinters and chips of ribs and vertebrae were spread around the carcass. The right ischium was well gnawed; the right femur's greater trochanter was gnawed off. The sternal ends of the down-side ribs were splintered and tooth-marked. The distal posterior facets of the right humerous were gnaw-damaged. Most major leg bones (tibiae,femora, humeri) were exposed and cleaned, even those on the down-side (the left).

2w79-1 Female, calf.

This carcass was sighted on the ground by a fur trapper traveling his trapline near the Hornaday River. The bison had been killed 14 November, 1979, and fed on by 12 wolves. I visited the site on 6 December; the remains were located in a very thick poplar bush, about 16 meters from a cleared trapline trail. No whole or partial long bones remained, only chips, splinters and fragments of bones. A biologist had collected the head, which had survived (well-gnawed) as did a bit of hide. On 6 December one chewed-up horn was collected; no other bones were seen in the snow.

Figure 34. Pilot M. Bailey at carcass of 1w79-9, about three days after wolves had killed it, winter, 1979.

Figure 35. Wolf-killed Bison.
TOP LEFT: Remains of 2w79-2, early winter, 1980.
BOTTOM LEFT: Articulated unit from 2w79-2 site, early winter, 1980.
TOP RIGHT: 2w79-2 bone units, hide to left, articulated right rear leg to right. Left tibia is bottom center. Left femur is missing.
BOTTOM RIGHT: 2w79-3 site, hide to right, articulated mandibles to left.



2w79-2 Female, age 13 years.

This carcass was sighted during aerial tracking of the Hornaday River wolf pack. The animal had been killed on 23 November; its remains lay on an open prairie several hundred meters from scattered willow bushes or spruce-poplar woods. I visited the site on 6 December. At that time the carcass had been pulled apart and somewhat scattered (Figure 35, top left). All legs had been disarticulated from the body; both scapulae were loose; the head and mandibles were articulated to all cervical vertebrae (which were cleaned) and the first three thoracic vertebrae were cleaned of meat and hide. Articular ends of ribs were articulated to the three thoracic vertebrae on both sides. On all four legs, hide remained uneaten from the proximal ends of metapodials through the hooves. Both forelegs were attached to the remaining hide/ head unit by hide (mostly the uneaten left side hide).

The right femur was well-gnawed, as was the proximal end of the right tibia (still in articulation). The left femur had been removed from the site by wolves (Figure 35, top right). Two meters away lay an articulated unit made up of sacrum, pelvis, all lumbar vertebrae and eight thoracic vertebrae, and six ribs (none complete, but one nearly so) (Figure 35, bottom left). Medical segments of ribs lay scattered about the main skeletal units, within an 8 meter radius from the head. All edible meat and viscera and over two-thirds of the hide had been consumed on this carcass within three days.

2w79-3 Sex unknown, calf.

This carcass was discovered during aerial tracking of the Hornaday River wolf pack; a calf had been killed 19 November in open prairie near a thin willow bush, several hundred meters from trees.

I visited the site on 6 December. Many rib and vertebrae fragments lay on and in trampled snow around a hairmat and the spilled gut contents, about 20 meters from the major remains. The only remaining bones were the skull, mandibles (unattached to skull), and both rear legs from broken mid-shaft of tibiae through hooves (Figure 35, bottom right). The head was attached to one-half the animal's hide, which was attached to the rear legs. The mandibles, articulated to each other, were entirely cleaned and lay a few meters from the head/hide/legs.

2w79-4 Female, estimated age under 3 years.

This carcass was discovered by wardens making a winter road patrol. A yound bison cow had been killed by wolves about 28 October; its tracks and remains were interpreted to have resulted from a kill made in a gully very near the road.

I visited the site on 15 December. The carcass lay in a spruce-alder bush next to a creek, approximately 10 meters from the actual killsite (which was in water, since frozen over). The skull had been dragged away by wolves, and could not be found. The mandibles had been collected by wardens. All vertebrae except caudals were present and in articulation to ribs, rib ends, and sacrum/pelvis (Figure 36). No long bones were found (one femur had been collected earlier). One scapula and one rib fragment lay next to the spinal unit.

lw80-1 Male, estimated age 5-6 years.

This carcass was spotted during aerial tracking of the Salt River Wolf pack. This pack, made up of six to eight members (numbers not stable from day to day) took two days (18-20 Feb.) to kill the bull in a poplar-willow bush with scattered spruce trees, then fed 5 days on the remains. The 12 member Hornaday pack discovered the carcass and also encountered the Salt River pack; a fight between wolf packs followed, during which three Salt River pack members were killed.

I visited the killsite on 5 March, 1980. The animal was lying on its belly (rear legs spread wide) and brisket, although the head had been flipped upside down. Belly hide was uneaten. Hide held the head and mandibles to the forelegs and lower rear legs. Nine vertebrae were in articulation with the head, and 15 were attached to each other and the sacrum/pelvis/rear legs. The left humerus and scapula were not found. All other long bones were present, most of the lower leg bones still encased in hide and frozen into packed snow. Femora were entirely cleaned of meat and were well gnawed. The right horn was somewhat gnaw-damaged at its tip. The left hyoid bone remained in the throat; although air temperatures were well below freezing (and had been for weeks), there was a very strong odor of rot at the carcass, probably the result of the spinal cord decaying in the warm body for a time after death. The pelvis was extremely well-gnawed, as were the femora. The buccal surfaces of the lower ramus on each side showed noticeable tooth scratching and incising.

lw80-2 Male, estimated age +17 years.

This carcass was discovered during aerial tracking of the Hornaday River wolf pack. A very large old bull had been killed 18 or 19 January, and its remains were first visited 15 February by the biologist; I visited the site on 4 March, 1980.

The carcass lay in a willow-poplar bush, about 20 meters from an open meadow. The animal lay on its throat, brisket, and belly, its bones articulated and in anatomical order (Figure 37). The skull and mandibles were articulated to all vertebrae through the last lumbar; the right half of the pelvis and the sacrum were missing, possibly due to the biologist who chopped the right femur out to collect it. Both forelegs were complete from humerus proximal end through hooves, although both humeral proximal ends were damaged by gnawing. The belly and lower hide were uneaten, and lay like a blanket under the skeleton. Both rear legs from tibia proximal ends through hooves were frozen into packed snow. The left femur was very well gnaw-damaged; the distal right femur (broken by the biologist) was also gnawed.

The hide of the neck and head had not been eaten; hair was missing from much of this skin, possibly due to disease when the animal was alive. A strong stench was present at the site, the result of spinal cord decay while the body had still been warm.

lw80-3 Female, estimated age +12 years.

This carcass was discovered during aerial tracking of the Hornaday River wolf pack. Twelve wolves were located near or at the killsite on 31 January, but the remains were first seen 1 February.

Figure 36. Articulated unit at 2w79-4 site, early winter, 1979.

Figure 37. Articulated unit at site of lw80-2, midwinter, 1980.

The carcass lay on an open prairie about 300 meters from a road on which traffic in winter is very light but consistent, and about 800 meters from a complex of buildings that are not used in wintertime.

I visited the site on 6 March, when drifting snow was beginning to cover the skeleton. One mandible and the left femur had been collected earlier by the biologist; the femur showed advanced damage due to gnawing. The carcass lay on its right side, and most hide on the up-side of its head had been consumed. The left side malars were gnaw-damaged. All vertebrae (except caudals) were articulated from the head through the pelvis, and all were gnaw-damaged. The down-side hide was uneaten. The right hyoid remained in place; the pelvis was very well-gnawed.

Because of the lack of pursuit and attack signs (tracks or struggle areas in the snow), the biologist considered this carcass to have been a scavenge, not a kill. If so, judging by the high degree of utilization, it was fed upon almost as soon as it died.

lw80-4 Male, yearling (1.5 years).

This carcass was discovered during aerial tracking of the Hornaday River wolf pack. The yearling was killed in the middle of February, and first visited 16 February. The remains were located in an open area near scattered willows and poplars. On 16 February, three lower legs were present, as well as rib fragments, hide, and the rumen. The skull had been carried by wolves 200 meters along a trail. The biologist collected the head, one cervical vertebra, six rib segments, and the right scapula.

I visited the site on 6 March. At that time, all that remained at the site was an area of hair, blood, bone fragments, and rumen contents in trampled snow, and a yard-square piece of hide 50 meters away. There were many recent wolf and fox tracks at the site.

Hay Camp Calf Male (9+ months).

This animal was killed 2 March while under aerial observation (during tracking of the Hornaday wolf pack). I visited the site 4 March.

The carcass lay in a willow bush near an unused corral-fence complex. The remains had been lightly utilized, then abandoned by the feeding wolf pack. Its killing may have been a reflex action performed by the wolves when the bison herd began to run in panic response to the circling airplane.

The carcass was twisted and flipped, so that it lay on its chin, with the belly up and the posterior back up. Over two-thirds of the hide was uneaten. The upper fore quarters, the back, and the belly hide had been peeled open. The rump meat was totally consumed. Rib and vertebrae fragments (up to 12 cm. long) lay scattered within three meters about the carcass. The skull and articulated mandibles were articulated to the first four cervical vertebrae. The lower part of the cranium showed gnaw-damage. Nine vertebrae were articulated to the sacrum and pelvis, and all tail vertebrae were also attached. Hide held together both separated parts of the spine; the left foreleg and scapula were missing; the other three legs were held to the rest of the carcass by hide or ligament. The lower legs (from hooves through mid-tibia or mid-radius) were still enclosed in hide. The right femur was gone. The pelvis had been mostly cleaned, but suffered little gnaw damage. There had been no horn-gnawing, and the nose and ears were uneaten.

Skeletons #10-#27.

Most of these are incomplete skeletons, the remains of animals that died in earlier years (Table 7-5). A few may have been wolf-kills. Numbers 14, 15, 17, 18, 19, 20 (includes eight different animals), 23, and 26 are believed to be the remains of animals that drowned in a large flood during the spring of 1974. None of these sites contains complete skeletons.

Only two of the suspected drowning death sites did not include a skull; in one case several skulls in a cache were found nearby; suggesting that apparently human travellers in the area had gathered skulls from various skeletal sites to mark a particular point on the ground. All skeletal sites from suspected drowning deaths contained at least one upper leg bone; only three of 14 sites contained lower leg bones other than phalanges. One suspected drowning death site contained most elements of the bison skeleton - in this particular case the bones of the two year old female were lying in a compact mass (in anatomical order) under a layer of duff, roots, and woods litter. The skull was 3 meters away from the bone pile, but there was no other scatter of elements. Nine of 14 sites contained at least two vertebrae.

In 35 of 42 cases of skeletal sites, whenever two or more bones were found lying within 16 meters of each other, a skull was also found, months (or years) after the date of death. In all but two cases where skulls were <u>not</u> found, the cause of their disappearance was most likely (or definitely) humans collecting study specimens or souvenirs. The two remaining cases where skulls were not found included a skeletal site located at a heavily used bison river-crossing, and a small scatter of bones from a very young bison calf probably drowned in the 1974 flood. In these cases, it is reasonable to suspect that natural disturbances account for the absence of skulls. At the river-crossing site, the bulky skull may have been kicked into the stream channel; the young calf's head may have been separated from the rest of its body during the flood. Alternatively, scavengers may have carried the head away.

Table 7-1

Suspected or Confirmed Wolf Kills:

Species	Carcass Designation	Sex	Age	Time Since Death When Inspected	Season of Death	Number of Wolves Feeding
Alces	79-9	Fe	7.5 years	5 months	midwinter	14
Alces	79-18	M	10-12 yrs.	4 months	midwinter	2
Alces	79-19	Fe	6.5 years	4 months	midwinter	11
Alces	79-25	?	9 months	4 months	midwinter	11
Alces	79-27	Fe	8.5 years	3.5 months	midwinter	13
Alces	79-28	M	9 months	3.5 months	midwinter	3
Alces	79-31	M	6.5 years	2 months	midwinter	10-11
Alces	79-48	Fe	8.5 years	1.5 months	late winter	?
Alces	79-56	M	8.5-10 yrs.	7-8 months	fall	?
Alces	79-58	Fe	6.5 years	3-4 months (?)	winter	?
Alces	Moose Lake	?	9 months	3-4 months (?)	winter	?
Alces	Rasp. Island	Fe	11 months	1.5 months	late winter	0
Alces	Daisy Farm	?	9 months	4 months	midwinter	?
Bison	1w79-1	M	+7 years	2 months	midwinter	14
Bison	1w79-2	M	9-10 yrs.	4 months (?)	early winter	10
Bison	1w79-2(visit 2)	M	9-10 yrs.	8 months (?)	early winter	10
Bison	1w79-3	Fe	7-8 yrs.	3 months (?)	early winter	10
Bison	1w79-4	M	6 years	2 weeks	midwinter	10
Bison	1w79-5	M	+6 years	2 weeks	midwinter	9
Bison	1w79-6	M	7-8 yrs.	not examined	midwinter	11
Bison	1w79-7	M	20 years	6-8 months	summer	6
Bison	1w79-8	M (?)	+5 years	1 week	late winter	10-12
Bison	1w79-9	Fe	6-7 yrs.	1 week	late winter	9
Bison	2w79-1	Fe	5-6 months	2 weeks	early winter	12
Bison	2w79-2	Fe	13 years	2 weeks	early winter	12
Bison	2w79-3	Fe	6 months	3 weeks	early winter	12
Bison	2w79-4	Fe	-3 years	1.5 months	late fall	8
Bison	1w80-1	M	5-6 yrs.	2 weeks	midwinter	18
Bison	1w80-2	M	+18 years	6 weeks	midwinter	12
Bison	1w80-3	Fe	+12 years	5 weeks	midwinter	12
Bison	1w80-4	M	1.5 years	1 week	midwinter	12
Bison	1w80-4(visit 2)	M	1.5 years	3 weeks	midwinter	12
Bison	1w80-5	M	+9 months	2 days	late winter	12

Table 7-2

Bison skeletal Sites (Drownings, Disease Mortality, Suspected Predation):

Skeleton Number	Sex	Age	Estimated year of Death
10	M	+10 years	before 1976
11	Fe	adult	before 1976
12	M	12-13 years	before 1974
13	Fe (?)	adult	1978-79
14	?	adult	1974
15	Fe	2 years	1974
16	Fe	16 years	1978-79
17	Fe (?)	under 1 year	1974
18	M	4.5 years	1974
19	Fe	+2 years	1974
20	(7 scattered skeletons)		1974
21	?	3 months	1979
22	Fe	8 years	1977 (?)
23	Fe	+3.5 years	1974
24	Fe	8 years	1974
25	M	8 years	1974-78
26	Fe	2-3 years	1974
27	M	3 years	1974

Table 7-3

Identification Code for Bones of the Ungulate Body:

S = Skull
M = Mandible
H = Horn
CV = Cervical Vertebra
TV = Thoracic Vertebra
LV = Lumbar vertebra
Sa = Sacrum
Pe = Pelvis
CaV = Caudal vertebra
Sc = Scapula
R = Rib
F = Femur
Calc = Calcaneus
A = Astragalus
T = Tibia
Ta = Tarsals
Mt = Metatarsal
1P = First Phalanx
2P = Second Phalanx
3P = Third Phalanx
Hu = Humerus
St = Sternum
U = Ulna
Ra = Radius
C = Carpals
Mc = Metacarpal
Innom=Innominate
Vert= Vertebra
epi= epiphysis
Podial= unidentified podial element
Hide= any skin
Splinters=rib or vertebrae fragments

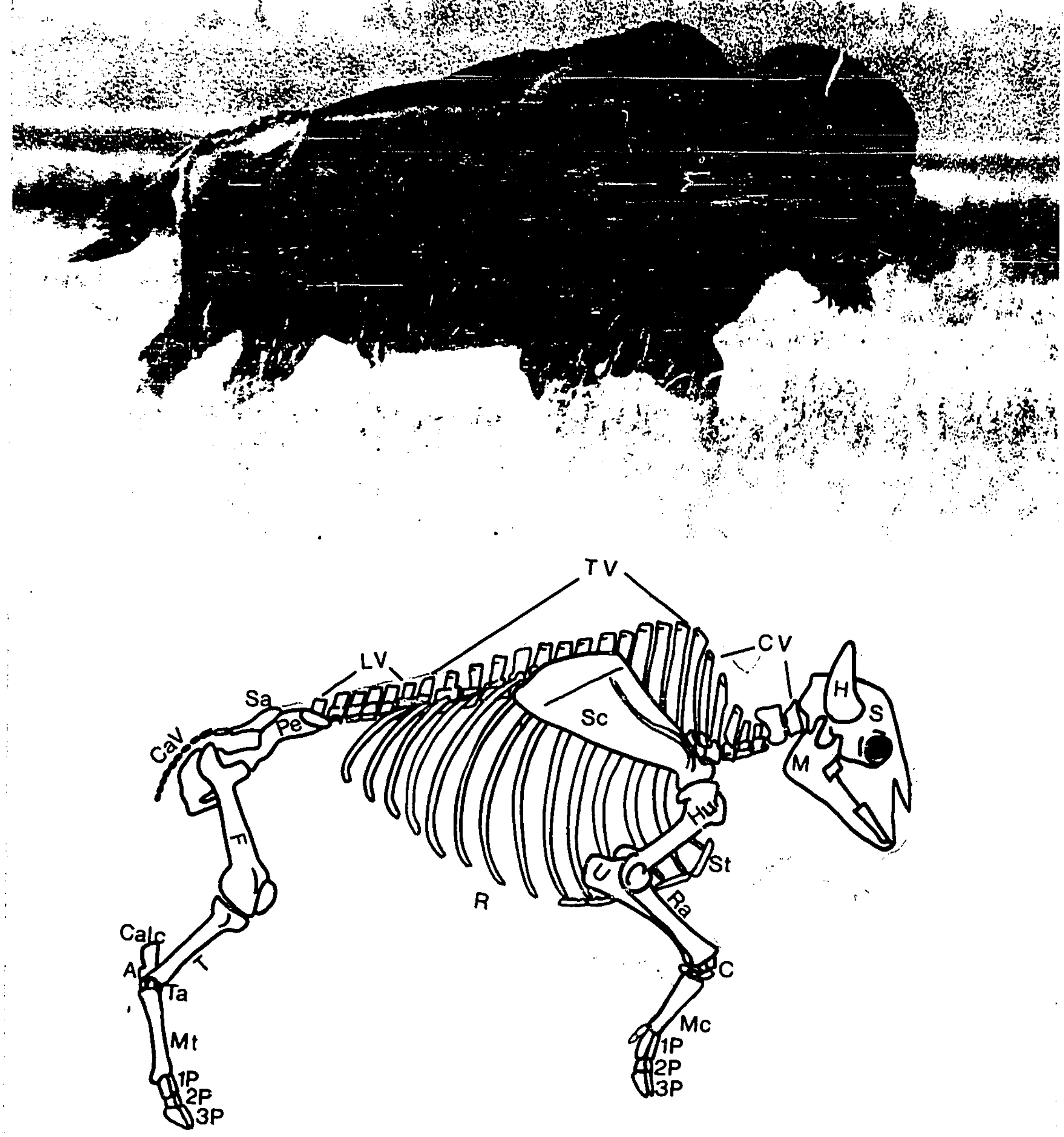


Table 7-3 continued: Bones of the ungulate body.

Table 7- 4

Site Inventory:
Species Bison   Carcass Designation 1w79-1   Visit 1

Element	Damage	Associated parts
S		
S w/horns	1	unit A
S w/1 horn		
S w/antlers		
H		
M L	6999	
R	6999	
CV 1	0	unit A
2	0	unit A
3	1	unit A
4	10	unit A
5	10	unit A
6	12	unit A
7	12	unit A
TV 1	20	unit A
2	20	unit A
3	20	unit A
4	20	unit A
5	20	unit A
6	20	unit A
7	20	unit A
8	20	unit A
9	20	unit A
10	20	unit A
11	20	unit A
12	20	unit A
13	20	unit A
14	20	unit A
R segment		
R epi L	12,20,20	unit A
R	12,20	unit A
LV 1	20	unit A
2	12	unit A
3	12	unit A
4	12	unit A
5	10	unit A
6	10	unit A
Sa	1	unit A
Pe	23	unit A
Innom L		
R		

Element	Damage	Associated parts
R (whole) L		
R		
Teeth		
Podial		
Bone		
Sc L	20	unit A
R		
Hu L	5	unit A
R	34	unit A
Ra L	0	unit A
R	0	unit A
C L	999	unit A
R	999	unit A
Mc L	999	unit A
R	999	unit A
Front hoof L	0	unit A
R	0	unit A
1 P		
2 P		
3 P		
Long bone frags		
F L	30	unit A
R	999	unit A
T L	10	unit A
R	999	unit A
Ta L	0	unit A
R	999	unit A
Mt L	0	unit A
R	999	unit A
Calc L	999	unit A
R	999	unit A
A L	0	unit A
R	999	unit A
Rear hoof	0,0	unit A
Splinters	999	unit A
CaV		
St		
Hide	30	unit A
Vert (any)		
Hyoid L		
R		
U L	999	unit A
R	999	unit A

NOTE: lower legs were buried in packed snow and ice.

<u>Explanation of Damage Codes:</u> (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:
Species Bison Carcass Designation 1w79-2 Visit 1

Element	Damage	Associated parts
S		
S w/horns	1	unit A
S w/1 horn		
S w/antlers		
H		
M L	0	unit A
R	0	unit A
CV 1	0	unit A
2	0	unit A
3	0	unit A
4	0	unit A
5	0	unit A
6	0	unit A
7	0	unit A
TV 1	0	unit A
2	0	unit A
3	0	unit A
4	0	unit A
5	0	unit A
6	0	unit A
7	0	unit A
8	0	unit A
9	0	unit A
10	0	unit A
11	0	unit A
12	0	unit A
13	0	unit A
14	0	unit A
R segment		
R epi L		
R		
LV 1	10	unit A
2	10	unit A
3	10	unit A
4	10	unit A
5	10	unit A
6	10	unit A
Sa	1	unit A
Pe	1	unit A
Innom L		
R		
R (whole) L		
R		
Teeth		
Podial		
Bone		
Sc L	999	unit A
R	6	unit A
Hu L	0	unit A
R	0	unit A
Ra L	0	unit A
R	0	unit A
C L	0	unit A
R	0	unit A
Mc L	0	unit A
R	0	unit A
Front hoof L	0	unit A
R	0	unit A
1 P		
2 P		
3 P		
Long bone frags		
F L	0	unit A
R	0	unit A
T L	0	unit A
R	0	unit A
Ta L	0	unit A
R	0	unit A
Mt L	0	unit A
R	0	unit A
Calc L	0	unit A
R	0	unit A
A L	0	unit A
R	0	unit A
Rear hoof	0,0	unit A
Splinters	1	units
CaV		
St	1	unit A
Hide	10	unit A
Vert (any)		
Hyoid L	0	unit A
R	0	unit A
U L	0	unit A
R	0	unit A

NOTE: carcass very poorly utilized.

Explanation of Damage Codes: (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:

Species Bison Carcass Designation 1w79-2 Visit 2

Element	Damage	Associated parts
S		
S w/horns	1	unit A
S w/1 horn		
S w/antlers		
H		
M L	0	unit B
R	0	unit C
CV 1		
2		
3		
4	0	unit F
5	0	unit F
6	1	unit E
7	1	unit E
TV 1	1	unit E
2	1	unit I
3	1	unit I
4	0	unit I
5	1	unit I
6	1	unit I
7	1	unit I
8	1	unit I
9	1	unit I
10	0	unit I
11	0	unit I
12	0	unit I
13	0	unit I
14	0	unit I
R segment	1,1	units D,G
R epi L	10	unit I
R	10	unit I
LV 1	0	unit I
2	0	unit I
3	0	unit I
4	1	unit I
5	1	unit I
6	1	unit I
Sa	1	unit I
Pe	1	unit I
Innom L		
R		

Element	Damage	Associated parts
R (whole) L		
R		
Teeth		
Podial		
Bone		
Sc L	0	unit J
R		
Hu L	1	unit I
R	0	unit I
Ra L	0	unit I
R	0	unit I
C L	0	unit I
R	0	unit I
Mc L	0	unit I
R	0	unit I
Front hoof L	0	unit I
R	0	unit I
1 P		
2 P		
3 P		
Long bone frags		
F L	6	unit I,L
R		
T L	6	unit L
R		
Ta L		
R		
Mt L		
R		
Calc L		
R		
A L		
R		
Rear hoof		
Splinters	10	unit H
CaV		
St		
Hide		
Vert (any)		
Hyoid L		
R		
U L	0	unit I
R	0	unit I

<u>Explanation of Damage Codes:</u> (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:

Species Bison . Carcass Designation lw79-3 Visit 1

Element	Damage	Associated parts
S		
S w/horns	45	unit A
S w/1 horn		
S w/antlers		
H		
M L	6	unit B
R	30	unit A
CV 1		
2		
3		
4		
5		
6		
7		
TV 1		
2		
3		
4		
5		
6		
7		
8		
9		
10		
11		
12		
13		
14		
R segment		
R epi L		
R		
LV 1		
2		
3		
4		
5		
6		
Sa		
Pe		
Innom L	40	unit A
R	40	unit A

Element	Damage	Associated parts
R (whole) L		
R		
Teeth		
Podial		
Bone		
Sc L		
R		
Hu L		
R	40	unit A
Ra L		
R	0	unit A
C L		
R	30	unit A
Mc L		
R	0	unit A
Front hoof L		
R	0	unit A
1 P		
2 P		
3 P		
Long bone frags		
F L		
R		
T L	34	unit A
R		
Ta L	0	unit A
R		
Mt L	0	unit A
R		
Calc L	0	unit A
R		
A L	0	unit A
R		
Rear hoof L	0	unit A
Splinters	23	units
CaV		
St		
Hide	23	unit A
Vert (any)		
Hyoid L		
R		
U L		
R	30	unit A

Explanation of Damage Codes: (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:

Species Bison Carcass Designation lw79-4 Visit 1

Element	Damage	Associated parts
S		
S w/horns	6	unit A
S w/1 horn		
S w/antlers		
H		
M L	6999	unit B
R	6999	unit B
CV 1	6	unit B
2	0	unit B
3	0	unit B
4	1	unit B
5	10	unit B
6	10	unit B
7	10	unit B
TV 1	12	unit B
2	23	unit B
3	23	unit B
4		
5		
6		
7		
8	20	unit B
9	20	unit B
10	20	unit B
11	20	unit B
12	20	unit B
13	20	unit B
14	20	unit B
R segment	20	units
R epi L	23	unit C
R	23	unit C
LV 1	20	unit C
2	20	unit C
3	20	unit C
4	20	unit C
5	20	unit C
6	20	unit C
Sa	0	unit C
Pe	6	unit C
Innom L		
R		
R (whole) L		
R		
Teeth		
Podial		
Bone		
Sc L	?	
R	?	
Hu L	30	unit B
R	?	unit B
Ra L	20	unit B
R	0	unit B
C L	0	unit B
R	0	unit B
Mc L	0	unit B
R	0	unit B
Front hoof L	0	unit B
R	0	unit B
1 P		
2 P		
3 P		
Long bone frags		
F L		
R		
T L		
R	6	unit D
Ta L		
R	0	unit D
Mt L		
R	0	unit D
Calc L		
R	0	unit D
A L		
R	0	unit D
Rear hoof R	0	unit D
Splinters	20	units
CaV		
St		
Hide	20	unit B and C
Vert (any)		
Hyoid L		
R		
U L	20	unit B
R	0	unit B
Rear leg L	?	unit E

Explanation of Damage Codes: (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:
Species Bison Carcass Designation 1w79-5 Visit 1

Element	Damage	Associated parts	Element	Damage	Associated parts
S			R (whole) L		
S w/horns	1	unit A	R		
S w/1 horn			Teeth		
S w/antlers			Podial		
H			Bone		
M L	6	unit A	Sc L	23	unit A
R	6	unit A	R	0999	unit A
CV 1	0	unit A	Hu L	1	unit A
2	0	unit A	R	0	unit A
3	1	unit A	Ra L	0	unit A
4	10	unit A	R	0	unit A
5	10	unit A	C L	0	unit A
6	10	unit A	R	0	unit A
7	10	unit A	Mc L	0	unit A
TV 1	12	unit A	R	0	unit A
2	12	unit A	Front hoof L	0	unit A
3	12	unit A	R	0	unit A
4	12	unit A	1 P		
5	12	unit A	2 P		
6	12	unit A	3 P		
7	10	unit A	Long bone frags		
8	10	unit A	F L		
9	10	unit A	R	20	unit A
10	10	unit A	T L	20	unit B
11	10	unit A	R	1	unit A
12	10	unit A	Ta L	0	unit B
13	10	unit A	R	0	unit A
14	10	unit A	Mt L	0	unit B
R segment	12	-	R	0	unit A
R epi L	10	unit A	Calc L	0	unit B
R	10	unit A	R	0	unit A
LV 1	1	unit A	A L	0	unit B
2	1	unit A	R	0	unit B
3	1	unit A	Rear hoof	0,0	units B and A
4	1	unit A	Splinters	20	units
5	1	unit A	CaV		
6	1	unit A	St		
Sa	0	unit A	Hide	10	unit A
Pe	20	unit A	Vert (any)		
Innom L			Hyoid L		
R			R		
			U L	1	unit A
			R	0	unit A

Explanation of Damage Codes: (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:
Species Bison
Carcass Designation lw79-7
Visit 1

Element	Damage	Associated parts	Element	Damage	Associated parts
S			R (whole) L		
S w/horns	0	unit A	R		
S w/1 horn			Teeth		
S w/antlers			Podial		
H			Bone		
M L	0	unit B	Sc L		
R	0	unit B	R		
CV 1			Hu L		
2			R		
3			Ra L		
4			R		
5			C L		
6	0	unit C	R		
7	0	unit C	Mc L		
TV 1	0	unit C	R		
2	0	unit C	Front hoof L		
3	0	unit C	R		
4	0	unit C	1 P		
5			2 P		
6			3 P		
7	0	unit C	Long bone frags		
8	0	unit C	F L	1	unit F
9	0	unit C	R		
10	0	unit C	T L	0	unit F
11	0	unit C	R		
12			Ta L		
13			R		
14			Mt L		
R segment			R		
R epi L			Calc L		
R			R		
LV 1			A L		
2			R		
3			Rear hoof		
4			Splinters		
5			CaV		
6			St		
Sa			Hide		
Pe	1	unit E	Vert (any)		
Innom L			Hyoid L		
R			R		

<u>Explanation of Damage Codes:</u> (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:

Species Bison Carcass Designation 1w79-9 Visit 1

Element	Damage	Associated parts
S		
S w/horns	0	unit A
S w/1 horn		
S w/antlers		
H		
M L	0	unit A
R	0	unit A
CV 1	0	unit A
2	0	unit A
3	1	unit A
4	1	unit A
5	1	unit A
6	10	unit A
7	10	unit A
TV 1	10	unit A
2	10	unit A
3	12	unit A
4	12	unit A
5	12	unit A
6	12	unit A
7	10	unit A
8	10	unit A
9	10	unit A
10	10	unit A
11	1	unit A
12	1	unit A
13	1	unit A
14	1	unit A
R segment	10,10...	units
R epi L	10	unit A
R	10	unit A
LV 1	10	unit A
2	10	unit A
3	10	unit A
4	10	unit A
5	10	unit A
6	10	unit A
Sa	0	unit A
Pe	0	unit A
Innom L		
R		
R (whole) L		
R		
Teeth		
Podial		
Bone		
Sc L	1	unit A
R	12	unit A
Hu L	10	unit A
R	10	unit A
Ra L	1	unit A
R	0	unit A
C L	0	unit A
R	0	unit A
Mc L	0	unit A
R	0	unit A
Front hoof L	0	unit A
R	0	unit A
1 P		
2 P		
3 P		
Long bone frags		
F L	20	unit A
R	12	unit A
T L	0	unit A
R	1	unit A
Ta L	0	unit A
R	0	unit A
Mt L	0	unit A
R	0	unit A
Calc L	0	unit A
R	0	unit A
A L	0	unit A
R	0	unit A
Rear hoof	0,0	unit A
Splinters	12	unit A
CaV	0	unit A
St		
Hide	12	unit A
Vert (any)		
Hyoid L		
R		
U L	1	unit A
R	1	unit A

Explanation of Damage Codes: (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:
Species Bison Carcass Designation 2w79-1 Visit 1

Element	Damage	Associated parts	Element	Damage	Associated parts
S			R (whole) L		
S w/horns			R		
S w/1 horn			Teeth		
S w/antlers			Podial		
H	10	unit A	Bone		
M L			Sc L		
R			R		
CV 1			Hu L		
2			R		
3			Ra L		
4			R		
5			C L		
6			R		
7			Mc L		
TV 1			R		
2			Front hoof L		
3			R		
4			1 P		
5			2 P		
6			3 P		
7			Long bone frags		
8			F L		
9			R		
10			T L		
11			R		
12			Ta L		
13			R		
14			Mt L		
R segment			R		
R epi L			Calc L		
R			R		
LV 1			A L		
2			R		
3			Rear hoof		
4			Splinters	10	units (B)
5			CaV		
6			St		
Sa			Hide		
Pe			Vert (any)		
Innom L			Hyoid L		
R			R		

Explanation of Damage Codes: (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:
Species Bison   Carcass Designation 2w79-2   Visit 1

Element	Damage	Associated parts	Element	Damage	Associated parts
S			R (whole) L		
S w/horns	10	unit A	R		
S w/1 horn			Teeth		
S w/antlers			Podial		
H			Bone		
M L			Sc L	10	unit D
R			R	10	unit E
CV 1	0	unit A	Hu L	20	unit A
2	0	unit A	R	23	unit A
3	0	unit A	Ra L	0	unit A
4	10	unit A	R	0	unit A
5	10	unit A	C L	0	unit A
6	10	unit A	R	0	unit A
7	10	unit A	Mc L	0	unit A
TV 1	10	unit A	R	0	unit A
2	10	unit A	Front hoof L	0	unit A
3	10	unit A	R	0	unit A
4			1 P		
5			2 P		
6	20	unit B	3 P		
7	20	unit B	Long bone frags		
8	20	unit B	F L		
9	20	unit B	R	30	unit C
10	20	unit B	T L	20	unit A
11	20	unit B	R	30	unit C
12	20	unit B	Ta L	0	unit A
13	20	unit B	R	0	unit C
14	20	unit B	Mt L	0	unit A
R segment	10	unit F	R	0	unit C
R epi L	10	unit G	Calc L	0	unit A
R			R	0	unit C
LV 1			A L	0	unit A
2			R	0	unit C
3			Rear hoof	0,0	units A, C
4			Splinters		
5			CaV		
6			St		
Sa	20	unit B	Hide	30	unit A
Pe	20	unit B	Vert (any)		
Innom L			Hyoid L		
R			R		
			U L	0	unit A
			R	0	unit A

<u>Explanation of Damage Codes:</u> (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:

Species Bison

Carcass Designation 2w79-3

Visit 1

Element	Damage	Associated parts
S		
S w/horns	10	unit A
S w/1 horn		
S w/antlers		
H		
M L	0	unit B
R	0	unit B
CV 1		
2		
3		
4		
5		
6		
7		
TV 1		
2		
3		
4		
5		
6		
7		
8		
9		
10		
11		
12		
13		
14		
R segment		
R epi L		
R		
LV 1		
2		
3		
4		
5		
6		
Sa		
Pe		
Innom L		
R		

Element	Damage	Associated parts
R (whole) L		
R		
Teeth		
Podial		
Bone		
Sc L		
R		
Hu L		
R		
Ra L		
R		
C L		
R		
Mc L		
R		
Front hoof L		
R		
1 P		
2 P		
3 P		
Long bone frags	10	units D,etc.
F L		
R		
T L	40	unit A
R	40	unit A
Ta L	0	unit A
R	0	unit A
Mt L	0	unit A
R	0	unit A
Calc L	0	unit A
R	0	unit A
A L	0	unit A
R	0	unit A
Rear hoof	0,0	unit A
Splinters	10	unit C
CaV		
St		
Hide		
Vert (any)		
Hyoid L		
R		

Explanation of Damage Codes: (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:

Species Bison Carcass Designation 2w79-4 Visit 1

Element	Damage	Associated parts	Element	Damage	Associated parts
S			R (whole) L		
S w/horns			R		
S w/1 horn			Teeth		
S w/antlers			Podial		
H			Bone		
M L			Sc L	30	unit A
R			R		
CV 1	0	unit C	Hu L		
2	0	unit C	R		
3	1	unit C	Ra L		
4	1	unit C	R		
5	1	unit C	C L		
6	1	unit C	R		
7	1	unit C	Mc L		
TV 1	1	unit C	R		
2	10	unit C	Front hoof L		
3	10	unit C	R		
4	1	unit C	1 P		
5	1	unit C	2 P		
6	1	unit C	3 P		
7	1	unit C	Long bone frags		
8	1	unit C	F L		
9	1	unit C	R		
10	1	unit C	T L		
11	1	unit C	R		
12	1	unit C	Ta L		
13	1	unit C	R		
14	1	unit C	Mt L		
R segment	20,10,10,10,10	units B, D-G	R		
R epi L	10,10,1,1,1,1	unit C	Calc L		
R	10,1,1,1,1,1	unit C	R		
LV 1	1	unit C	A L		
2	1	unit C	R		
3	1	unit C	Rear hoof		
4	1	unit C	Splinters		
5	1	unit C	CaV		
6	1	unit C	St		
Sa	1	unit C	Hide	40	unit C
Pe	0	unit C	Vert (any)		
Innom L			Hyoid L		
R			R		

Explanation of Damage Codes: (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:
Species Bison Carcass Designation 1w80-1 Visit 1

Element	Damage	Associated parts
S		
S w/horns	1	unit A
S w/1 horn		
S w/antlers		
H		
M L	10	unit A
R	10	unit A
CV 1	0	unit A
2	0	unit A
3	10	unit A
4	10	unit A
5	10	unit A
6	20	unit A
7	20	unit A
TV 1	23	unit A
2	23	unit A
3		
4		
5		
6	30	unit A
7	30	unit A
8	30	unit A
9	30	unit A
10	30	unit A
11	30	unit A
12	30	unit A
13	30	unit A
14	30	unit A
R segment	23,23,20,20	units C-F
R epi L		
R		
LV 1	30	unit A
2	30	unit A
3	23	unit A
4	23	unit A
5	23	unit A
6	23	unit A
Sa	34	unit A
Pe	40	unit A
Innom L		
R		
R (whole) L		
R		
Teeth		
Podial		
Bone		
Sc L		
R	23	unit B
Hu L		
R	25	unit A
Ra L	0	unit A
R	0	unit A
C L	0	unit A
R	0	unit A
Mc L	0	unit A
R	0	unit A
Front hoof L	0	unit A
R	0	unit A
1 P		
2 P		
3 P		
Long bone frags		
F L	34	unit A
R	34	unit A
T L	12	unit A
R	20	unit A
Ta L	0	unit A
R	0	unit A
Mt L	0	unit A
R	0	unit A
Calc L	0	unit A
R	0	unit A
A L	0	unit A
R	0	unit A
Rear hoof	0,0	unit A
Splinters		
CaV		
St		
Hide	20	unit A
Vert (any)		
Hyoid L	20	unit A
R		
U L	30	unit A
R	20	unit A

<u>Explanation of Damage Codes:</u> (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:

Species Bison Carcass Designation 1w80-2 Visit 1

Element	Damage	Associated parts
S		
S w/horns	0	unit A
S w/1 horn		
S w/antlers		
H		
M L	0	unit A
R	0	unit A
CV 1	20	unit A
2	20	unit A
3	20	unit A
4	20	unit A
5	12	unit A
6	12	unit A
7	12	unit A
TV 1	12	unit A
2	12	unit A
3	12	unit A
4	12	unit A
5	12	unit A
6	12	unit A
7	12	unit A
8	12	unit A
9	12	unit A
10	20	unit A
11	20	unit A
12	20	unit A
13	20	unit A
14	20	unit A
R segment		
R epi L	23,23,23,23	unit A
R	23,23,23,23	unit A
LV 1	20	unit A
2	20	unit A
3	20	unit A
4	20	unit A
5	20	unit A
6		
Sa		
Pe		
Innom L	30	unit A
R		

Element	Damage	Associated parts
R (whole) L		
R		
Teeth		
Podial		
Bone		
Sc L		
R		
Hu L	20	unit A
R	30	unit A
Ra L	0	unit A
R	1	unit A
C L	0	unit A
R	0	unit A
Mc L	0	unit A
R	0	unit A
Front hoof L	0	unit A
R	0	unit A
1 P		
2 P		
3 P		
Long bone frags		
F L	30	unit A
R	55	unit A
T L	0	unit A
R	10	unit A
Ta L	0	unit A
R	0	unit A
Mt L	0	unit A
R	0	unit A
Calc L	0	unit A
R	0	unit A
A L	0	unit A
R	0	unit A
Rear hoof	0,0	unit A
Splinters		
CaV		
St		
Hide	20	unit A
Vert (any)		
Hyoid L	999	unit A
R	999	unit A
U L	10	unit A
R	1	unit A

Explanation of Damage Codes: (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:
Species Bison Carcass Designation 1w80-3 Visit 1

Element	Damage	Associated parts	Element	Damage	Associated parts
S			R (whole) L		
S w/horns	12	unit A	R		
S w/1 horn			Teeth		
S w/antlers			Podial		
H			Bone		
M L			Sc L		
R	20	unit A	R		
CV 1	1	unit A	Hu L	999	unit A?
2	12	unit A	R	999	
3	20	unit A	Ra L	999	
4	20	unit A	R	999	
5	30	unit A	C L	999	
6	30	unit A	R	999	
7	30	unit A	Mc L	999	
TV 1	30	unit A	R	999	
2	30	unit A	Front hoof L	999	
3	30	unit A	R	999	
4	30	unit A	1 P		
5	30	unit A	2 P		
6	30	unit A	3 P		
7	30	unit A	Long bone frags		
8	30	unit A	F L	999	unit A?
9	30	unit A	R	999	
10	30	unit A	T L	999	
11	30	unit A	R	999	
12	30	unit A	Ta L	999	
13	30	unit A	R	999	
14	30	unit A	Mt L	999	
R segment			R	999	
R epi L			Calc L	999	
R			R	999	
LV 1	30	unit A	A L	999	
2	30	unit A	R	999	
3	30	unit A	Rear hoof	999,999	
4	30	unit A	Splinters		
5	30	unit A	CaV		
6	30	unit A	St		
Sa	30	unit A	Hide	29	unit A
Pe	30	unit A	Vert (any)		
Innom L			Hyoid L	20	unit A
R			R		
			U L	999	
			R	999	

Explanation of Damage Codes: (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:

Species Bison Carcass Designation 1w80-4 Visit 1

Element	Damage	Associated parts
S		
S w/horns	12	unit A
S w/1 horn		
S w/antlers		
H		
M L	20	unit A
R	20	unit A
CV 1		
2	20	unit J
3		
4		
5		
6		
7		
TV 1		
2		
3		
4		
5		
6		
7		
8		
9		
10		
11		
12		
13		
14		
R segment	34,34,34,34,23,23	E-H,J,K
R epi L		
R		
LV 1		
2		
3		
4		
5		
6		
Sa		
Pe		
Innom L		
R		

Element	Damage	Associated parts
R (whole) L		
R		
Teeth		
Podial		
Bone (unident.)	999	unit B
Sc L		
R	40	unit I
Hu L		
R		
Ra L		
R	34	unit B
C L		
R	0	unit B
Mc L		
R	0	unit B
Front hoof L		
R		
1 P		
2 P		
3 P		
Long bone frags	40	units D
F L		
R		
T L	40	unit B
R	40	unit B
Ta L	0	unit B
R	0	unit B
Mt L	0	unit B
R	0	unit B
Calc L	0	unit B
R	0	unit B
A L	0	unit B
R	0	unit B
Rear hoof	0,0	unit B
Splinters	30	units C
CaV		
St		
Hide	20	unit C
Vert (any)	999	unit B?
Hyoid L		
R		
U L		
R	34	unit B

Explanation of Damage Codes: (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7- 4

Site Inventory:
Species Bison
Carcass Designation 1w80-4
Visit 2

Element	Damage	Associated parts
S		
S w/horns	995	unit A
S w/1 horn		
S w/antlers		
H		
M L	995	unit A
R	995	unit A
CV 1		
2		
3		
4		
5		
6		
7		
TV 1		
2		
3		
4		
5		
6		
7		
8		
9		
10		
11		
12		
13		
14		
R segment		
R epi L		
R		
LV 1		
2		
3		
4		
5		
6		
Sa		
Pe		
Innom L		
R		

Element	Damage	Associated parts
R (whole) L		
R		
Teeth		
Podial		
Bone		
Sc L		
R		
Hu L		
R		
Ra L		
R		
C L		
R		
Mc L		
R		
Front hoof L		
R		
1 P		
2 P		
3 P		
Long bone frags	45	unit B
F L		
R		
T L		
R		
Ta L		
R		
Mt L		
R		
Calc L		
R		
A L		
R		
Rear hoof		
Splinters	45	unit C
CaV		
St		
Hide	40	unit D
Vert (any)		
Hyoid L		
R		

Explanation of Damage Codes: (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:
Species Bison Carcass Designation lw80-5 Visit 1

Element	Damage	Associated parts
S		
S w/horns	23	unit A
S w/1 horn		
S w/antlers		
H		
M L	10	unit A
R	0	unit A
CV 1	10	unit A
2	10	unit A
3	0	unit A
4	0	unit A
5		
6		
7		
TV 1		
2		
3		
4		
5		
6		
7		
8		
9		
10		
11		
12	1	unit A
13	1	unit A
14	1	unit A
R segment	23,30,30,30	units B,D,E,G
R epi L	1	unit A
R	1	unit A
LV 1	1	unit A
2	1	unit A
3	1	unit A
4	1	unit A
5	1	unit A
6	1	unit A
Sa	1	unit A
Pe		
Innom L	1	unit A
R	0	unit A
R (whole) L		
R		
Teeth		
Podial		
Bone		
Sc L		
R	0	unit A
Hu L		
R	5	unit A
Ra L		
R	34	unit A
C L		
R	0	unit A
Mc L		
R	0	unit A
Front hoof L		
R	0	unit A
1 P		
2 P		
3 P		
Long bone frags	45	units (A)
F L		
R	40	unit A
T L	0	unit A
R	40	unit A
Ta L	0	unit A
R	0	unit A
Mt L	0	unit A
R	0	unit A
Calc L	0	unit A
R	0	unit A
A L	0	unit A
R	0	unit A
Rear hoof	0,0	unit A
Splinters	30	units C,F
CaV	0(all)	unit A
St	40	unit A
Hide	10	unit A
Vert (any)		
Hyoid L		
R		
U L		
R	30	unit A

Explanation of Damage Codes: (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:
Species Bison
Carcass Designation 10 (skeleton) Visit 1 and 2

Element	Damage	Associated parts
S	1	unit A
S w/horns		
S w/1 horn		
S w/antlers		
H	0,0	units
M L		
R		
CV 1		
2	0	units
3	0	
4	0	
5		
6	0	
7		
TV 1	1	
2	1	
3	12	
4	12	
5		
6		
7	10	
8	10	
9	10	
10	10	
11		
12		
13		
14		
R segment	10	
R epi L	10	
R	10	
LV 1		
2	10	
3	10	
4	10	
5		
6		
Sa	12	
Pe	51	
Innom L		
R		
R (whole) L		
R		
Teeth		
Podial		
Bone		
Sc L	10	units
R	10	
Hu L	10	
R	50	
Ra L	0	
R	0	
C L	0	
R		
Mc L	0	
R		
Front hoof L		
R		
1 P	0,0	
2 P		
3 P		
Long bone frags		
F L	1	
R		
T L	1	
R	1	
Ta L		
R		
Mt L		
R	0	
Calc L		
R		
A L		
R		
Rear hoof		
Splinters		
CaV		
St		
Hide		
Vert (any)		
Hyoid L		
R		
U L	50	
R	0	

Explanation of Damage Codes: (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:
Species Bison   Carcass Designation 11 (skeleton) Visit 1

Element	Damage	Associated parts	Element	Damage	Associated parts
S	0	unit A	R (whole) L		
S w/horns			R		
S w/1 horn			Teeth		
S w/antlers			Podial		
H			Bone		
M L			Sc L	999	units
R			R	0	
CV 1	0	units	Hu L		
2			R		
3			Ra L		
4			R		
5			C L		
6			R		
7			Mc L		
TV 1			R		
2			Front hoof L		
3			R		
4			1 P		
5			2 P		
6			3 P		
7			Long bone frags		
8			F L	999	
9			R	0	
10			T L		
11			R		
12			Ta L		
13			R		
14			Mt L		
R segment			R		
R epi L			Calc L		
R			R		
LV 1			A L		
2			R		
3			Rear hoof		
4			Splinters		
5			CaV		
6			St		
Sa			Hide		
Pe	0		Vert (any)(unident.)0(numerous)		
Innom L			Hyoid L		
R			R		

Explanation of Damage Codes: (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:
Species Bison Carcass Designation 12 (skeleton) Visit 1

Element	Damage	Associated parts
S		
S w/horns	20	unit A
S w/1 horn		
S w/antlers		
H		
M L	5	units
R	0	
CV 1		
2		
3		
4		
5		
6		
7		
TV 1		
2		
3		
4		
5		
6		
7		
8		
9		
10		
11		
12		
13		
14		
R segment	30	
R epi L		
R	30	
LV 1		
2		
3		
4		
5		
6		
Sa	10	
Pe		
Innom L	999	
R	999	

Element	Damage	Associated parts
R (whole) L		
R		
Teeth	5	units
Podial		
Bone		
Sc L	5	
R	5	
Hu L	30	
R	1	
Ra L	0	
R	0	
C L		
R	0	
Mc L		
R	0	
Front hoof L		
R		
1 P	0,0	
2 P	5,0	
3 P		
Long bone frags		
F L		
R		
T L	20	
R		
Ta L		
R		
Mt L ?	0	
R		
Calc L		
R	0	
A L		
R		
Rear hoof		
Splinters	30,5	
CaV		
St	5	
Hide		
Vert (any)	23,23,23,23,23	
Hyoid L		
R		
U L	0	
R	0	

Explanation of Damage Codes: (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:
Species Bison Carcass Designation 13 (skeleton) Visit 1

Element	Damage	Associated parts
S		
S w/horns		
S w/1 horn		
S w/antlers		
H		
M L		
R		
CV 1		
2		
3		
4		
5		
6		
7		
TV 1		
2		
3		
4		
5		
6		
7		
8		
9	10	unit G
10	10	unit G
11	10	unit G
12	10	unit G
13	10	unit G
14	10	unit G
R segment	10(numerous units)	
R epi L		
R		
LV 1	10	unit G
2	10	unit G
3	10	unit G
4	10	unit G
5	10	unit G
6	10	unit G
Sa	0	unit G
Pe	10	unit G
Innom L		
R		

Element	Damage	Associated parts
R (whole) L		
R		
Teeth		
Podial		
Bone		
Sc L	0	unit A
R	0	unit B
Hu L	10	unit D
R	10	unit C
Ra L	0	unit D
R	0	unit E
C L		
R		
Mc L		
R		
Front hoof L		
R		
1 P		
2 P		
3 P		
Long bone frags		
F L	12	init I
R		
T L	10	unit I
R	1	unit H
Ta L	0	unit I
R		
Mt L	0	unit I
R		
Calc L	0	unit I
R		
A L	0	unit I
R		
Rear hoof L	0	unit I
Splinters		
CaV		
St		
Hide		
Vert (any)		
Hyoid L		
R		
U L	0	unit D
R	0	unit F

Explanation of Damage Codes: (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:

Species Bison Carcass Designation 14 (skeleton) Visit 1

Element	Damage	Associated parts	Element	Damage	Associated parts
S			R (whole) L	0	numerous
S w/horns			R	0	numerous
S w/1 horn			Teeth		
S w/antlers			Podial		
H			Bone		
M L			Sc L		
R			R	0	units
CV 1			Hu L		
2			R	0	
3			Ra L		
4			R	0	
5			C L		
6			R		
7			Mc L		
TV 1			R		
2			Front hoof L		
3			R		
4			1 P		
5			2 P		
6			3 P		
7			Long bone frags		
8			F L	0	
9			R		
10			T L	0	
11			R		
12			Ta L		
13			R		
14			Mt L		
R segment			R		
R epi L			Calc L		
R			R		
LV 1			A L		
2			R		
3			Rear hoof		
4			Splinters		
5			CaV		
6			St		
Sa			Hide		
Pe			Vert (any)	0	numerous
Innom L			Hyoid L		
R			R		
			U L		
			R	0	

Explanation of Damage Codes: (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:

Species Bison Carcass Designation 15 (skeleton) Visit 1

Element	Damage	Associated parts
S	0	unit A
S w/horns		
S w/1 horn		
S w/antlers		
H		
M L	0	units
R	0	
CV 1	0	
2	0	
3	0	
4	0	
5	0	
6	0	
7	0	
TV 1	0	
2	0	
3	0	
4	0	
5	0	
6	0	
7	0	
8	0	
9	0	
10	0	
11	0	
12	0	
13	0	
14	0	
R segment		
R epi L		
R		
LV 1	0	
2	0	
3	0	
4	0	
5	0	
6	0	
Sa	0	
Pe	0	
Innom L		
R		

Element	Damage	Associated parts
R (whole) L		
R		
Teeth		
Podial		
Bone		
Sc L	0	units
R	0	
Hu L	0	
R	0	
Ra L	0	
R	0	
C L	0	
R	0	
Mc L	0	
R	0	
Front hoof L	0	
R	0	
1 P		
2 P		
3 P		
Long bone frags		
F L	0	
R	0	
T L	0	
R	0	
Ta L	0	
R	0	
Mt L		
R	0	
Calc L	0	
R	0	
A L	0	
R	0	
Rear hoof	0,0	
Splinters		
CaV		
St		
Hide		
Vert (any)		
Hyoid L		
R		
U L	0	
R	0	

Explanation of Damage Codes: (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:
Species Bison Carcass Designation 16 (skeleton) Visit 1

Element	Damage	Associated parts	Element	Damage	Associated parts
S			R (whole) L		
S w/horns	0	unit A	R		
S w/1 horn			Teeth		
S w/antlers			Podial		
H			Bone		
M L	5	unit B	Sc L ?	20	unit J
R	0	unit C	R		
CV 1	0	unit D	Hu L		
2	0	unit E	R		
3	0	unit F	Ra L		
4	0	unit G	R		
5			C L		
6			R		
7			Mc L		
TV 1			R		
2			Front hoof L		
3			R		
4			1 P		
5			2 P		
6			3 P		
7			Long bone frags		
8			F L		
9			R		
10			T L		
11			R		
12			Ta L		
13			R		
14	23	unit H	Mt L		
R segment	23,23	units K,-L	R		
R epi L			Calc L		
R			R		
LV 1	23	unit H	A L		
2	23	unit H	R		
3	23	unit H	Rear hoof L?	0	unit I
4	23	unit H	Splinters		
5	23	unit H	CaV		
6	23	unit H	St		
Sa	1	unit H	Hide		
Pe	20	unit H	Vert (any)		
Innom L			Hyoid L		
R			R		

<u>Explanation of Damage Codes:</u> (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:
Species Bison Carcass Designation 17 (skeleton) Visit 1

Element	Damage	Associated parts
S	0	unit A
S w/horns		
S w/1 horn		
S w/antlers		
H		
M L		
R		
CV 1		
2		
3		
4		
5		
6		
7		
TV 1		
2		
3		
4		
5		
6		
7		
8		
9		
10		
11		
12		
13		
14		
R segment		
R epi L		
R		
LV 1		
2		
3		
4		
5		
6		
Sa		
Pe		
Innom L	0	units
R	0	

Element	Damage	Associated parts
R (whole) L		
R		
Teeth		
Podial		
Bone		
Sc L	0	units
R	0	
Hu L	0(head and distal)	
R		
Ra L	0	
R	0	
C L		
R		
Mc L		
R	0	
Front hoof L		
R		
1 P		
2 P		
3 P		
Long bone frags		
F L		
R		
T L	0	
R	0(proximal and shaft)	
Ta L		
R		
Mt L		
R		
Calc L		
R		
A L		
R		
Rear hoof		
Splinters		
CaV		
St		
Hide		
Vert (any) (unident.)	1	units
Hyoid L		
R		
U L	0	
R	0	

Explanation of Damage Codes: (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:
Species Bison Carcass Designation 18 (skeleton) Visit 1

Element	Damage	Associated parts
S	0	unit A
S w/horns		
S w/1 horn		
S w/antlers		
H		
M L		
R		
CV 1		
2		
3		
4		
5		
6		
7		
TV 1		
2		
3		
4		
5		
6		
7		
8		
9		
10		
11		
12		
13		
14		
R segment	12	numerous
R epi L		
R		
LV 1		
2		
3		
4		
5		
6		
Sa	12	units
Pe	12	
Innom L		
R		

Element	Damage	Associated parts
R (whole) L		
R		
Teeth		
Podial		
Bone		
Sc L	0	units
R	0	
Hu L		
R	0	
Ra L	0	
R	0	
C L		
R		
Mc L	0	
R		
Front hoof L		
R		
1 P	0	
2 P		
3 P		
Long bone frags		
F L		
R		
T L		
R		
Ta L		
R		
Mt L		
R		
Calc L		
R		
A L		
R		
Rear hoof		
Splinters		
CaV		
St		
Hide		
Vert (any)(undifferentiated)		10
Hyoid L		
R		
U L	0	
R		

Explanation of Damage Codes: (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:
Species Bison Carcass Designation 19(skeleton) Visit 1

Element	Damage	Associated parts
S	0	unit A
S w/horns		
S w/1 horn		
S w/antlers		
H		
M L		
R		
CV 1		
2		
3		
4		
5		
6		
7		
TV 1		
2		
3		
4		
5		
6		
7		
8		
9		
10		
11		
12		
13		
14		
R segment		
R epi L		
R		
LV 1		
2		
3		
4		
5		
6		
Sa		
Pe		
Innom L		
R		
R (whole) L		
R		
Teeth		
Podial		
Bone (unident.)	999,999,999...	units C-G
Sc L		
R		
Hu L		
R		
Ra L		
R		
C L		
R		
Mc L		
R		
Front hoof L		
R		
1 P		
2 P		
3 P		
Long bone frags		
F L		
R		
T L		
R		
Ta L		
R		
Mt L		
R		
Calc L		
R		
A L		
R		
Rear hoof		
Splinters		
CaV		
St		
Hide		
Vert (any)	0,0,0	unit B
Hyoid L		
R		

Explanation of Damage Codes: (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:
Species Bison   Carcass Designation 21   Visit 1

Element	Damage	Associated parts	Element	Damage	Associated parts
S			R (whole) L		
S w/horns			R		
S w/1 horn	50	unit A	Teeth		
S w/antlers			Podial		
H			Bone		
M L	0	unit C	Sc L	51	unit F
R	0	unit B	R	0	unit E
CV 1	0	unit A	Hu L		
2	0	unit A	R		
3			Ra L		
4			R		
5			C L		
6			R		
7			Mc L		
TV 1			R		
2			Front hoof L		
3			R		
4			1 P		
5	0	unit A	2 P		
6	0	unit A	3 P		
7	0	unit A	Long bone frags	50	unit F
8			F L		
9			R	50	unit L
10			T L		
11			R		
12			Ta L		
13			R		
14			Mt L		
R segment	0,0,0,0	units G-J	R		
R epi L	50,0,0	unit A	Calc L		
R	0,0,0	unit A	R		
LV 1			A L		
2			R		
3			Rear hoof		
4			Splinters		
5			CaV		
6			St		
Sa			Hide	51	unit A
Pe			Vert (any)		
Innom L	0	unit A	Hyoid L		
R	0	unit A	R		

<u>Explanation of Damage Codes:</u> (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:

Species Bison

Carcass Designation 22 (skeleton) Visit 1

Element	Damage	Associated parts
S		
S w/horns	0	units
S w/1 horn		
S w/antlers		
H		
M L	0	
R	0	
CV 1		
2		
3		
4		
5		
6		
7		
TV 1		
2		
3		
4		
5		
6		
7		
8		
9		
10		
11		
12		
13		
14		
R segment		
R epi L		
R		
LV 1		
2		
3		
4		
5		
6		
Sa	10	
Pe	10	
Innom L		
R		

Element	Damage	Associated parts
R (whole) L		
R		
Teeth		
Podial		
Bone		
Sc L		
R	1	units
Hu L	0	
R		
Ra L		
R	0	
C L		
R		
Mc L		
R	0	
Front hoof L		
R		
1 P		
2 P		
3 P		
Long bone frags		
F L		
R	12	
T L		
R		
Ta L		
R		
Mt L		
R	0	
Calc L		
R		
A L		
R		
Rear hoof		
Splinters		
CaV		
St		
Hide		
Vert (any)		
Hyoid L		
R		
U L		
R	0	

Explanation of Damage Codes: (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:
Species Bison Carcass Designation 23 (skeleton) Visit 1

Element	Damage	Associated parts	Element	Damage	Associated parts
S			R (whole) L		
S w/horns			R		
S w/1 horn			Teeth		
S w/antlers			Podial		
H			Bone		
M L	0	units	Sc L		
R	0		R ?	10	units
CV 1			Hu L		
2			R	20(distal)	
3			Ra L		
4			R		
5			C L		
6			R		
7			Mc L	0	
TV 1			R	0	
2			Front hoof L		
3			R		
4			1 P		
5			2 P		
6			3 P		
7			Long bone frags		
8			F L	23	
9			R	20	
10			T L		
11			R ?	0	
12			Ta L		
13			R		
14			Mt L	0	
R segment	10	numerous	R	0	
R epi L			Calc L		
R			R		
LV 1			A L		
2			R		
3			Rear hoof		
4			Splinters		
5			CaV		
6			St		
Sa	12		Hide		
Pe	1		Vert (any)	12	numerous
Innom L			Hyoid L		
R			R		

Explanation of Damage Codes: (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:
Species Bison Carcass Designation 24 (skeleton) Visit 1

Element	Damage	Associated parts	Element	Damage	Associated parts
S	0	units	R (whole) L		
S w/horns			R		
S w/1 horn			Teeth		
S w/antlers			Podial		
H			Bone		
M L	0		Sc L		
R	0		R		
CV 1			Hu L	30	
2			R	23	
3			Ra L		
4			R		
5			C L		
6			R		
7			Mc L		
TV 1			R		
2			Front hoof L		
3			R		
4			1 P		
5			2 P		
6			3 P		
7			Long bone frags		
8			F L		
9			R		
10			T L		
11			R		
12			Ta L		
13			R		
14			Mt L		
R segment	12	numerous	R		
R epi L			Calc L		
R			R		
LV 1			A L		
2			R		
3			Rear hoof		
4			Splinters		
5			CaV		
6			St		
Sa	12		Hide		
Pe	12		Vert (any)(undifferentiated)	12	(many)
Innom L			Hyoid L		
R			R		

Explanation of Damage Codes: (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:
Species Bison Carcass Designation 25 (skeleton) Visit 1

Element	Damage	Associated parts	Element	Damage	Associated parts
S			R (whole) L		
S w/horns	0	cluster A	R		
S w/1 horn			Teeth		
S w/antlers			Podial		
H			Bone		
M L	0	cluster C	Sc L	1	cluster B
R	0	cluster C	R	0	cluster B
CV 1	0	cluster C	Hu L	0	cluster B
2	0	cluster C	R	0	cluster A
3			Ra L	0	
4	0		R	0	cluster A
5	0		C L		
6			R		
7			Mc L		
TV 1			R		
2			Front hoof L		
3			R		
4			1 P		
5			2 P		
6			3 P		
7			Long bone frags		
8			F L	10	
9			R	10	cluster D
10			T L	0	cluster B
11			R	10	cluster D
12			Ta L		
13			R		
14			Mt L		
R segment			R		
R epi L			Calc L		
R			R		
LV 1			A L		
2			R		
3			Rear hoof		
4			Splinters		
5			CaV		
6			St	0	
Sa	0		Hide		
Pe	50		Vert (any)	0	many
Innom L			Hyoid L		
R			R		
			U L	0	
			R	0	cluster A

Explanation of Damage Codes: (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:
Species Bison Carcass Designation 26 (skeleton) Visit 1

Element	Damage	Associated parts	Element	Damage	Associated parts
S			R (whole) L		
S w/horns	0	units	R		
S w/1 horn			Teeth		
S w/antlers			Podial		
H			Bone		
M L			Sc L		
R			R		
CV 1			Hu L	23	units
2			R	23	
3			Ra L		
4			R ?	0	
5			C L		
6			R		
7			Mc L ?	0	
TV 1			R		
2			Front hoof L		
3			R		
4			1 P		
5			2 P		
6			3 P		
7			Long bone frags		
8			F L		
9			R		
10			T L	23	
11			R		
12			Ta L		
13			R		
14			Mt L ?	0	
R segment			R		
R epi L			Calc L		
R			R		
LV 1			A L		
2			R		
3			Rear hoof		
4			Splinters	12	numerous
5			CaV		
6			St		
Sa			Hide		
Pe	12		Vert (any)	12	numerous
Innom L			Hyoid L		
R			R		

Explanation of Damage Codes: (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:
Species Bison Carcass Designation 27 (skeleton) Visit 1

Element	Damage	Associated parts
S		
S w/horns		
S w/1 horn		
S w/antlers		
H	0,0	separated
M L	0	unit A
R	0	unit A
CV 1		
2		
3		
4		
5		
6		
7		
TV 1		
2		
3		
4		
5		
6		
7		
8		
9		
10		
11		
12		
13		
14		
R segment	10	numerous
R epi L	12	numerous
R	12	
LV 1		
2		
3		
4		
5		
6		
Sa		
Pe		
Innom L		
R		
R (whole) L		
R		
Teeth		
Podial		
Bone		
Sc L ?	45	
R		
Hu L		
R		
Ra L		
R		
C L		
R		
Mc L ?	0	
R		
Front hoof L		
R		
1 P		
2 P		
3 P		
Long bone frags		
F L		
R		
T L		
R		
Ta L		
R		
Mt L		
R		
Calc L		
R		
A L		
R		
Rear hoof		
Splinters		
CaV		
St		
Hide		
Vert (any)		
Hyoid L		
R		

Explanation of Damage Codes: (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:
Species Alces Carcass Designation 79-9 Visit 1

Element	Damage	Associated parts
S		
S w/horns		
S w/1 horn		
S w/antlers		
H		
M L		
R		
CV 1		
2		
3		
4		
5		
6		
7		
TV 1		
2		
3		
4		
5		
6		
7		
8		
9		
10		
11		
12		
13		
14		
R segment		
R epi L		
R		
LV 1		
2		
3		
4		
5		
6		
Sa		
Pe		
Innom L		
R		

Element	Damage	Associated parts
R (whole) L		
R		
Teeth		
Podial		
Bone		
Sc L		
R		
Hu L		
R (distal)	56	unit B
Ra L		
R		
C L		
R		
Mc L		
R		
Front hoof L		
R		
1 P		
2 P		
3 P		
Long bone frags		
F L		
R		
T L		
R		
Ta L		
R		
Mt L		
R		
Calc L		
R		
A L		
R		
Rear hoof		
Splinters	5	unit A
CaV		
St		
Hide		
Vert (any)		
Hyoid L		
R		

Explanation of Damage Codes: (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:

Species Alces Carcass Designation 79-18 Visit 1

Element	Damage	Associated parts	Element	Damage	Associated parts.
S	0	unit A	R (whole) L		
S w/horns			R		
S w/1 horn			Teeth		
S w/antlers			Podial		
H			Bone		
M L	10	unit A	Sc L	10	unit C
R	10	unit A	R		
CV 1	1	unit A	Hu L	23	unit D
2	1	unit A	R		
3	1	unit A	Ra L	1	unit D
4	10	unit A	R		
5	10	unit A	C L	0	unit D
6	10	unit A	R		
7	10	unit A	Mc L	0	unit D
TV 1	20	unit A	R		
2	20	unit A	Front hoof L	20	unit D
3	20	unit A	R		
4	20	unit A	1 P		
5	20	unit A	2 P		
6	20	unit A	3 P		
7			Long bone frags		
8			F L	30	unit F
9	23	unit B	R	5	unit E
10	23	unit B	T L	12	unit F
11	23	unit B	R		
12	23	unit B	Ta L	0	unit F
13	23	unit B	R		
14	23	unit B	Mt L	1	unit F
R segment	30,30,30 etc.	units	R		
R epi L			Calc L	30	unit F
R			R		
LV 1	23	unit B	A L		
2	23	unit B	R		
3	23	unit B	Rear hoof L	20	unit F
4	23	unit B	Splinters		
5	23	unit B	CaV		
6	23	unit B	St		
Sa	30	unit B	Hide		
Pe	30	unit B	Vert (any)		
Innom L			Hyoid L		
R			R		
			U L	10	unit D
			R		

Explanation of Damage Codes: (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:
Species Alces Carcass Designation 79-19 Visit 1

Element	Damage	Associated parts	Element	Damage	Associated parts
S	10	unit A	R (whole) L		
S w/horns			R		
S w/1 horn			Teeth		
S w/antlers			Podial		
H			Bone		
M L	10	unit A	Sc L ?	30	unit C
R	10	unit A	R		
CV 1	1	unit A	Hu L	20	unit D
2	1	unit A	R		
3	10	unit A	Ra L	0	unit D
4	10	unit A	R		
5	12	unit A	C L	0	unit D
6	12	unit A	R		
7	12	unit A	Mc L	0	unit D
TV 1			R		
2 ?			Front hoof L	23	unit D
3 ?			R		
4 ?			1 P		
5 ?			2 P		
6 ?			3 P		
7	12	unit B	Long bone frags		
8	12	unit B	F L		
9	12	unit B	R (head)	23	unit E
10	12	unit B	T L		
11	12	unit B	R	12	unit E
12	12	unit B	Ta L		
13	12	unit B	R	0	unit E
14	12	unit B	Mt L		
R segment	10,10,10, etc.	units	R	0	unit E
R epi L	1,0	unit B	Calc L		
R	0,1	unit B	R	0	unit E
LV 1	20	unit B	A L		
2	20	unit B	R	0	unit E
3	20	unit B	Rear hoof R	10	unit E
4	20	unit B	Splinters		
5	20	unit B	CaV		
6	20	unit B	St		
Sa	20	unit B	Hide		
Pe	20	unit B	Vert (any)		
Innom L			Hyoid L		
R			R		
			U L	12	unit D

Explanation of Damage Codes: (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:

Species Alces Carcass Designation 79-27 Visit 1

Element	Damage	Associated parts
S	10	unit A
S w/horns		
S w/1 horn		
S w/antlers		
H		
M L ?	10	unit B
R		
CV 1		
2		
3		
4		
5		
6		
7		
TV 1		
2		
3		
4		
5		
6		
7		
8		
9		
10		
11		
12		
13		
14		
R segment		
R epi L		
R		
LV 1		
2		
3		
4		
5		
6		
Sa		
Pe		
Innom L		
R		
R (whole) L		
R		
Teeth		
Podial		
Bone		
Sc L		
R		
Hu L	23	unit C
R	23	unit D
Ra L		
R	0	unit E
C L		
R		
Mc L	0	unit F
R	0	unit F
Front hoof L ?	0	unit G
R		
1 P		
2 P		
3 P		
Long bone frags		
F L ?	23	unit H
R		
T L ?	30	unit I
R	30	unit J
Ta L	0	unit K
R		
Mt L	0	unit K
R		
Calc L		
R		
A L		
R		
Rear hoof		
Splinters		
CaV		
St		
Hide		
Vert (any)		
Hyoid L		
R		
U L		
R	23	unit E

Explanation of Damage Codes: (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:

Species Alces

Carcass Designation 79-28

Visit 1

Element	Damage	Associated parts
S	45	unit A
S w/horns		
S w/1 horn		
S w/antlers		
H		
M L	45	unit A
R	30	unit A
CV 1	20	unit A
2	20	unit A
3		
4		
5		
6		
7		
TV 1		
2		
3		
4		
5		
6		
7		
8		
9		
10		
11		
12		
13		
14		
R segment	30,30,30,etc.	units
R epi L		
R		
LV 1		
2		
3		
4		
5		
6		
Sa		
Pe		
Innom L		
R		

Element	Damage	Associated parts
R (whole) L		
R		
Teeth		
Podial		
Bone		
Sc L	30	unit B
R	30	unit C
Hu L		
R	45	unit D
Ra L		
R	0	unit D
C L		
R	0	unit D
Mc L		
R	0	unit D
Front hoof L		
R	0	unit D
1 P		
2 P		
3 P		
Long bone frags		
F L		
R	45	unit E
T L		
R	34	unit E
Ta L		
R	0	unit E
Mt L		
R	55	unit E
Calc L		
R	20	unit E
A L		
R	0	unit E
Rear hoof R	30	unit E
Splinters		
CaV		
St		
Hide		
Vert (any)		
Hyoid L		
R		
U L		
R	23	unit D

Explanation of Damage Codes: (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:
Species Alces   Carcass Designation 79-31   Visit 1

Element	Damage	Associated parts
S	0	unit A
S w/horns		
S w/1 horn		
S w/antlers		
H		
M L	0	unit A
R	0	unit A
CV 1	0	unit A
2	0	unit B
3	1	unit B
4	10	unit B
5	10	unit B
6	10	unit B
7	45	unit B
TV 1		
2		
3		
4		
5		
6		
7		
8		
9		
10		
11		
12		
13		
14		
R segment	30,30,30, etc.	units -
R epi L		
R		
LV 1		
2		
3		
4		
5		
6		
Sa		
Pe		
Innom L		
R		

Element	Damage	Associated parts
R (whole) L		
R		
Teeth		
Podial		
Bone		
Sc L		
R		
Hu L	40	unit C
R	30	unit D
Ra L	0	unit C
R	0	unit D
C L	0	unit C
R	0	unit D
Mc L	0	unit C
R	0	unit D
Front hoof L	0	unit C
R	0	unit D
1 P		
2 P		
3 P		
Long bone frags		
F L	34	unit F
R	20	unit E
T L	20	unit F
R	30	unit E
Ta L	0	unit F
R	0	unit E
Mt L	20	unit F
R	0	unit E
Calc L	12	unit F
R	12	unit E
A L	0	unit F
R	0	unit E
Rear hoof	12,0	unit F, E
Splinters(vertebral)	45	units
CaV		
St		
Hide		
Vert (any)		
Hyoid L		
R		
U L	12	unit C
R	20	unit D
Splinters	40	units

Explanation of Damage Codes: (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:
Species Alces Carcass Designation 79-48 Visit 1

Element	Damage	Associated parts	Element	Damage	Associated parts
S	0	unit A	R (whole) L		
S w/horns			R		
S w/1 horn			Teeth		
S w/antlers			Podial		
H			Bone		
M L	0	unit A	Sc L	1	unit C
R	0	unit A	R	12	unit D
CV 1	0	unit A	Hu L	10	unit C
2	0	unit A	R	10	unit D
3	0	unit A	Ra L	0	unit C
4	0	unit A	R	0	unit D
5	0	unit A	C L	0	unit C
6	0	unit A	R	0	unit D
7	0	unit A	Mc L	0	unit C
TV 1	1	unit A	R	0	unit D
2	1	unit A	Front hoof L	0	unit C
3	1	unit A	R	0	unit D
4	1	unit A	1 P		
5	1	unit A	2 P		
6	1	unit A	3 P		
7			Long bone frags		
8			F L	10	unit F
9			R	10	unit E
10	1	unit B	T L	0	unit F
11	1	unit B	R	0	unit E
12	1	unit B	Ta L	0	unit F
13	1	unit B	R	0	unit E
14	1	unit B	Mt L	0	unit F
R segment			R	0	unit E
R epi L	1	unit B (5)	Calc L	0	unit F
R	1	unit B (9)	R	0	unit E
LV 1	1	unit B	A L	0	unit F
2	1	unit B	R	0	unit E
3	0	unit B	Rear hoof	0,0	unit F, E
4	0	unit B	Splinters		
5	0	unit B	CaV		
6	0	unit B	St	1	unit A
Sa	1	unit B	Hide		
Pe	1	unit B	Vert (any)		
Innom L			Hyoid L		
R			R		
			U L	10	unit C
			R	0	unit D

Explanation of Damage Codes: (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:
Species Alces Carcass Designation 79-56 Visit 1

Element	Damage	Associated parts
S	0	unit A
S w/horns		
S w/1 horn		
S w/antlers		
H		
M L	0	unit E
R	0	unit E
CV 1	0	unit A
2	1	unit B
3	1	unit B
4	1	unit B
5	1	unit B
6	1	unit B
7	1	unit B
TV 1	1	unit B
2	1	unit B
3	1	unit B
4	1	unit B
5	1	unit B
6		
7		
8		
9	1	unit C
10	1	unit C
11	1	unit C
12	1	unit C
13	1	unit C
14	1	unit C
R segment		
R epi L		
R		
LV 1		
2		
3		
4		
5		
6		
Sa	0	unit F
Pe	10	unit G
Innom L		
R		
Antler	1	unit A
R (whole) L	0 (x 12)	units
R	0 (x 12)	units
Teeth		
Podial(unident.)	0	unit H
Bone		
Sc L		
R	0	unit J
Hu L	1	unit M
R	10	unit N
Ra L		
R	0	unit O
C L		
R		
Mc L ?	0	unit L
R		
Front hoof L		
R		
1 P	0	unit L
2 P	0	unit L
3 P	0	unit L
Long bone frags		
F L	0	unit K
R		
T L		
R		
Ta L		
R		
Mt L		
R		
Calc L		
R		
A L		
R		
Rear hoof		
Splinters		
CaV		
St	0	unit I
Hide		
Vert (any)	0	unit D
Hyoid L		
R		
U L		
R	0	unit O

Explanation of Damage Codes: (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:

Species Alces Carcass Designation 79-58 Visit 1

Element	Damage	Associated parts
S	30	unit A
S w/horns		
S w/1 horn		
S w/antlers		
H		
M L	0	unit B
R	0	unit B
CV 1	0	unit A
2	0	unit A
3	0	unit A
4	0	unit A
5	10	unit A
6	20	unit A
7	30	unit A
TV 1	30	unit A
2	30	unit A
3	30	unit A
4	30	unit A
5	30	unit A
6	30	unit A
7	30	unit A
8	30	unit A
9	30	unit A
10	30	unit A
11	30	unit A
12	30	unit A
13		
14		
R segment		
R epi L		
R		
LV 1	30	unit A
2	30	unit A
3	30	unit A
4	30	unit A
5	30	unit A
6	30	unit A
Sa		
Pe	23	unit A
Innom L		
R		
R (whole) L		
R		
Teeth		
Podial		
Bone		
Sc L	23	unit C
R		
Hu L	10	unit E
R	23	unit D
Ra L	0	unit E
R	0	unit D
C L	0	unit E
R		
Mc L	0	unit E
R	0	unit D
Front hoof L	0	unit E
R	0	unit D
1 P		
2 P		
3 P		
Long bone frags		
F L	23	unit G
R	23	unit F
T L	23	unit G
R	30	unit F
Ta L	0	unit G
R	0	unit F
Mt L	0	unit G
R	0	unit F
Calc L	1	unit G
R	10	unit F
A L	0	unit G
R	0	unit F
Rear hoof	0,1	unit G, F
Splinters		
CaV		
St		
Hide		
Vert (any)		
Hyoid L		
R		
U L	0	unit E
R	23	unit D

Explanation of Damage Codes: (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

Table 7-4

Site Inventory:

Species Alces Carcass Designation Moose Lake Visit 1

Element	Damage	Associated parts
S		
S w/horns		
S w/1 horn		
S w/antlers		
H		
M L		
R		
CV 1		
2		
3		
4		
5		
6		
7		
TV 1		
2		
3		
4		
5		
6		
7		
8		
9		
10		
11		
12		
13		
14		
R segment		
R epi L		
R		
LV 1		
2		
3		
4		
5		
6		
Sa		
Pe	34	unit A
Innom L		
R		

Element	Damage	Associated parts
R (whole) L		
R		
Teeth		
Podial		
Bone		
Sc L ?	45	unit B
R		
Hu L		
R		
Ra L		
R		
C L		
R		
Mc L		
R		
Front hoof L		
R		
1 P		
2 P		
3 P		
Long bone frags		
F L		
R	40	unit C
T L		
R	23	unit C
Ta L		
R	0	unit C
Mt L		
R	0	unit C
Calc L		
R	30	unit C
A L		
R	0	unit C
Rear hoof		
Splinters		
CaV		
St		
Hide		
Vert (any)		
Hyoid L		
R		

Explanation of Damage Codes: (999= not examined)

No Damage	0	Stage 2	20	Stage 4	40
Barely Touched	1	Stage 2, nearly 3	23	Scavenge	50
Stage 1	10	Stage 3	30	Artificial	6
Stage 1, nearly 2	12	Stage 3, nearly 4	34	Unusual gnaw	5

VIII. Descriptive and Comparative Data on Carcass and Bone Modification

OBSERVATIONS OF CARCASS DISMEMBERMENT AND BONE DAMAGE BY CARNIVORES AND OTHER NATURAL AGENCIES IN THE CASE STUDY AREAS

Bone Damage and Body Dismemberment

A pack of 10-15 wolves, when feeding on the carcass of an adult bison or moose that it has freshly killed, can consume nearly all meat and about one half the hide within two or three days of bringing down the animal. In late winter when prey are feeling the effects of deepening snow and continued cold, wolves can usually kill more easily than in the other seasons. Packs will consequently take longer to fully utilize carcasses in February and March than they did in November and December, since later in the season there are at any one time more available carcasses to feed from. Most fresh carcasses are returned to over the following days until quite well cleaned. Living bison, moose, deer, and elk do not generally move far out of central wintering ranges, and wolves can thus travel their core hunting areas repeatedly over wintertime without going far from dependable prey resources. This increases the potential number of times wolves will encounter known carcasses, although snowfall might effectively remove many carcasses from the landscape. However, wolves may in effect memorize the locations of landmarks such as carcasses in their territories (Peters 1978). Scavenged carcasses (that is, bodies found by wolves after the animals have already died of disease, starvation, or other causes) are typically not well utilized during wintertime, unless consistently re-encountered, although these carcasses are often more utilized in the spring, following the thaw. Occasionally there may be more kills made than can be even moderately utilized, especially in severe winters that tax the health of prey animals (see Mech and Frenzel 1971). Such circumstances are most likely the exception, not the rule, except perhaps in times of unidirectional climatic change. Domestic livestock, except horses in mixed herds (L. Carbyn 1980 pers. comm.), are usually easy to kill, and their carcasses are often poorly utilized (see Young 1944). The stallions in mixed horse herds usually defend their mares and foals as a group, creating a defensive block that wolves do not easily penetrate.

During the main predation season in the north, skeletons of adult moose are usually sectioned by feeding wolves into the following articulated or isolated parts (not necessarily sequentially):

(1) Skull, often with articulated mandibles, and usually one or more cervical vertebrae. Often the head remains attached to all cervical vertebrae which are articulated with some thoracic vertebrae, on which ribs or articular ends of ribs may still be attached. The sternal bones are usually eaten.

(2) The rest of the vertebrae, still in articulation, attached to the sacrum and pelvis. Sometimes the spinal column is sectioned further into an articulated cervical group, the head with a few cervical vertebrae attached, and a thoracic/lumbar group. For moose which are less than eight years old, the pelvis may oftentimes be detached from the sacrum and lumbar vertebrae.

(3) The scapulae, most often free or unattached to any body part.

(4) The legs, from proximal end of the humeri through hooves, and from proximal end of femora through hooves, in articulation. One or two legs may be removed from the immediate killsite, if larger packs feed.

(5) Isolated medial segments of ribs, generally from 15 cm. to 35 cm. long.

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

For well-utilized early winter kills of bison, the skeletal units would be sectioned as follows:

(1) Skull and mandibles with all cervical vertebrae attached and a few thoracic vertebrae, with some rib fragments articulated. The spinous processes of thoracic vertebrae would be about one half removed.

(2) A thoracic/lumbar vertebrae segment, containing the sacrum and the pelvis.

(3) The individual legs, one of which may be removed from the main skeletal locus.

(4) The scapulae, both of which are free, and one of which may be far removed.

(5) Segments of ribs, 15 cm. to 45 cm. long, scattered about.

(6) Bone splinters and chips.

For well-utilized late winter kills of bison, the units would be:

(1) Skull-mandibles-vertebral column-sacrum-pelvis, articulated with three legs.

(2) At least one disarticulated leg, held in anatomical order with the trunk by strips of uneaten hide.

(3) One or both free scapulae.

(4) Rib segments.

(5) Splinters and chips.

Uneaten hide often keeps all the limbs in anatomical order or near to it, although the humeral and femoral heads may be disconnected from the axial skeleton. A hungry wolf pack will fully separate at least one entire leg from the carcass.

For adult bison and moose, lower legs (from the tibia's proximal epiphysis or proximal one-third of the shaft, and from the radius-ulna's proximal epiphysis, down to the hooves) are very rarely even stripped of hide during the first feedings. Later feedings, such as springtime bear scavenging on winter wolf kills, or scavenging by a second wolf pack after the killing pack departs, may leave the lower legs stripped of hide, but still usually articulated from the distal end of the tibia or the distal end of the radius through the hooves, the horny sheaths of which may be partly destroyed by crunching in the jaws. By the middle of the first summer following death, if scavenging has not been unusually light, the bones and legs are separating. Bones lying in warm, moist areas (such as shaded woods) will separate first.

On fully utilized adult bison or moose carcasses abandoned in the main killing season (usually winter), long bones are rarely fractured, although the entire articulating ends of many may be wholly gnawed and broken off (Figure 38). The proximal end of the humerus, the greater trochanter and distal end of the femur, the proximal end of the tibia are most frequently the parts completely removed by wolves. The removal of about one half the proximal end of one or both humeri has been recorded at every bison and moose carcass killed in winter by wolves (in this sample). It is characteristic of <u>kills</u> that one or both humeri are modified into partly or fully open-ended tubes or cylinders, that greater torchanters of femora are removed, and that some or all ribs are broken off below their articulating ends. Nasal bones of bison are often gnawed at fresh kills. When old skeletons are found, the remaining bones, especially the humeral shafts, will usually (but not always) have tooth scorings and pittings on the upper part of the bone near where the articulating end was removed.

The first bones are to be damaged by the teeth of feeding wolves are probably the pelvis, the femora, and the ribs and vertebrae. Some (or all) ribs are snapped off in segments close to 30 cm. long, the break occurring most often within a few centimeters of the articular ends, which usually remain in articulation with vertebrae. On most thoracic vertebrae the spinous processes are often one half or more removed by being broken off, as opposed to being ground off by sustaining gnawing. The vertebral border of one or both disarticulated scapulae may be ragged in outline, and the distal part of the blade may show a few (or no) puncture holes from teeth.

There are definable stages of utilization of bison, deer, and moose carcasses, each stage characterized by specific damage done to certain elements (See Tables 8-1 and 8-2).

Killsite Bone Distribution

The first bone disturbed out of anatomical order when wolves feed on carcasses of animals that they themselves have killed (as opposed to those they have merely scavenged) are ribs and one scapula (the one on the uppermost side of the carcass). The scapula(e) may be within a few meters of the carcass, or may be far removed (over 30 meters away). One scapula may often be carried entirely away.

If the legs of moose carcasses are disarticulated from the trunk, they most often are lying within 15 meters of it and each other. They will be complete and articulated. Occasionally a femur may be completely disconnected and carried far from the carcass, to be gnawed on or to be dropped when the pack begins to move in earnest on another hunt. If a femur is successfully disarticulated, the remainder of the lower leg, from proximal tibia through hoof, may also be carried away from the carcass site, especially by members of small groups of scavenging wolves. The lower legs of adult bison are quite heavy, yet I have seen where a wolf ran 200 meters through 60 cm. deep snow with an articulated bull's leg in its mouth before dropping it.

Splinters of ribs and vertebrae commonly mark the original death site of the prey animal, and are usually surrounded by bits of hair and rumen and gut contents. The rest of the skeleton may be dragged, partially articulated, many meters away (except in the case of adult bison bulls, whose carcasses are seldom moved). The spinal column of adult moose and of female adult bison is often broken into two segments, one of which contains the pelvis and which may be dragged or carried a few meters from the head/spinal column unit (See Figure 35, top and bottom left).

Bone Representation: Element Survival

For adult moose and for female or smaller male bison, one entire leg is often missing or difficult to find at killsites. The skull and the mandible almost always remain, as do at least two lower legs or complete legs. Thus, phalanges, metapodials, and teeth are characteristic elements at killsites, even for calves and yearlings, whose skeletons may be otherwise nearly completely consumed. Crania of calves and yearlings may be partly devoured or carried off, while mandibles or sections of mandibles more often remain at or near the original kill and feeding sites. There are usually a few medial rib fragments about too, even when all else has been eaten or removed, but seldom more than a dozen or so. There may also be fragments of long bone shafts at killsite of calf and yearling bison and moose.

Even a few months after kills are abandoned on dry, subhumid grasslands, woodlands, or forests, the bones retain some appeal to carnivorous scavengers; the marrow as a shrunken lump usually survives one spring and summer and part of the fall, if in occasionally shady and moist locations, but greasiness may be gone by the second spring except at epiphyseal ends that were not opened up by gnawing. Scavengers may carry off lower legs and may try to drag skulls away from old bison kills, these being the parts protected longest by uneaten, unpeeled hide, and hence still greasy and fetid for the longest time.

On bison ranges where humans have not collected bones for years, occasionally single elements are found many hundreds of meters from the nearest known carcass or skeletal site. So far my collected sample is quite small, but the most common bones found individually are metapodials, rib segments, calf skulls, and long bones of the rear leg. I have also found separate first and second phalanges, parts of pelves, and many sets of articulated vertebrae (two or more, seldom more than five together). As of yet, den and lair accumulations have not been adequately inventoried, but it is known that in the study areas many times several prey animals (of different ages and sexes) may be represented at single wolf dens or den complexes.

The skulls of adult bison always occur at or within a few dozen meters of the original carcass site, even when all but a very few other bones remain.

Moose skulls are usually cleaned of flesh by the spring, unlike bison skulls which retain a covering of long hair and thick skin well into the first summer following death. The brains in bison skulls may decay more slowly than moose brains, and maintain the appeal of the skull to scavengers for months after original feeding by wolves. Cervical vertebrae that remain articulated to bison or moose skulls may eventually detach from the skull and from each other by midsummer. However, I have recorded instances in wooded habitats where bison skulls with all cervical and some thoracic vertebrae remain in an articulated unit for over a year after the animal's death.

Scavenging bears will eat the hide from lower legs of bison or moose carcasses (M. Meagher 1980 pers. comm.; Haynes unpublished data), and will gnaw greasy bones, oftentimes disarticulating them and breaking them up (R.O. Peterson 1980 pers. comm.; J. Woolington 1980 pers. comm.). Bears may remove elements from carcass sites, but usually remain at the site feeding on soft tissue even for several days (see Magoun 1976). Wolverines habitually remove bones and body parts to cache them elsewhere, in places that are nearly impossible to find (and which would make poor potential fossil locales). Wolverines will return over and over to carcasses until there is nothing left that can be carried away. I have also watched a tiny ermine removing 10 cm. long rib segments and part of a pelvis from a fresh (but frozen) bison carcass even as I stood over the bones photographing them.

It is not known to what use wolverines and other bone-removing scavengers put most of their cached bones; wolverines are capable of breaking up the long bones of subadult moose (see Haglund 1966), but probably do so infrequently at killsites or caches.

In habitats where summer prey densities are relatively low, prey carcasses may be quite fully utilized by a large number of carnivorous species, including foxes, bears, wolverines, wolves, eagles, ravens, and mustelids. Many sites of caribou, deer, moose, or elk would contain a very few bones, perhaps only one or two (see Magoun 1976 for a valuable study of carcas utilization in northeastern Alaska).

Table 8-2 summarizes the observed sequence of bone damage and disarticulation by larger wolf packs feeding on kills they have themselves made. Damage beyond the kinds described (such as, for example, heavy gnawing damage to the distal condyles of an adult bison humerus) more likely is due to scavenging animals, not killing animals. Damage or disarticulation of bones out of sequence or the absence of one or two normal sequential stages most often signifies feeding on an already dead prey carcass, and not on a true kill. The potential importance of this distinction can be illustrated with the example of a single element: A gnawed, spirally fractured bison femur that still possesses most or all of its greater trochanter or its larger trochlear rim was almost surely broken by an agency other than the gnawing animal, either before or after the gnawing. The bone may have been artifactually broken by humans extracting marrow. When previously-broken bones are gnawed, there may be some small or hard to recognize tooth marks on fracture edges; fracture edges may also be slightly chipped by teeth in small spots. Some fracture edges may also become rounded.

Some bears are clever enough to learn how to cleanly break long bones to get at the marrow, especially in stony areas (Haynes unpublished data). Some extinct larger bears, such as *Arctodus*, may have been capable of using their teeth and jaw power to break bison long bones without producing a recognizable gnaw damage on compact bone surfaces. However, in my opinion such habitual activity by large bears has not been demonstrated yet, although I have clearly seen the potential for it in captive and wild large bears.

Proboscidean Carcass Disintegration: Speculation

Beard (1977) presents over 150 photographs of elephant carcasses and skeletons, the remains of animals that died in severe drought years (presumably 1964-1965, but possibly later years) in Tsavo National Park, Kenya. There may be duplications of carcasses in some photos; most of the photographs are aerials taken from fixed-wing aircraft making low passes, and so the relatively low clarity and resolution do not allow detailed study of bone modifications due to weathering or scavenger activity. However, because of the temporary abundance of carrion in the region (thousands of elephants perished in the drought), scavenging activity at each carcass was probably very minimal (see Coe 1978). Vultures and hyenas probably visited each carcass, but may not have lingered at any one.

Over 80 of the photos depict carcasses with skin still draped over much of the skeleton, but lacking tusks, which were probably removed by humans. Skulls and lower jaws may have been somewhat disturbed or damaged by chopping or prying tusks loose, but for the most part the carcasses appear undisturbed. Much of the time the tusks slide easily out of alveoli upon some drying of the bone and flesh of a carcass (Deraniyagala 1955; Douglas-Hamilton 1978), so chopping or other actions may not have been necessary.

More than 20 photos depict carcasses with a large part of the skin remaining over the bones and with tusks still within the skull alveoli. Over 30 photos depict skeletons or bones without noticeable skin remaining, and also without tusks. There are less than 10 photos depicting skeletons or bones without noticeable hide but with tusks visible in alveoli.

Of this latter category, which might be the only set of carcasses entirely unvisited and undisturbed by humans, most skeletons lie in anatomical order on one side or the other, with axial elements mostly articulated and with lower leg elements tending to be scattered away from the axial elements. Foot bones in all photos appear well scattered, and perhaps a few of them are missing.

Most carcasses (of all categories) clearly lie on one side or the other, although less than a half dozen lie on brisket, belly, and their lower jaws. In most cases the scatter of long bones, foot bones, and ribs is in one direction, either the direction the feet point or in the direction the head and tail run. Some sites are very neat and most bones are tightly articulated even after all hide has disappeared, while other skeletons are scattered even while most of the up-side hide is still visible over the bones. In some photos, whole leg units (semi-articulated) are separated a few meters from the rest of the carcass.

It appears that the foot bones separate and scatter early, even while most other bones are covered with hide; the up-side scapula and the head/cervical vertebrae area are also exposed quite early in the decay process; meanwhile the tail is still in place and encased in skin. The order of bone exposure may be (1) head, (2) feet bones, which scatter quickly due to scavenging, (3) neck and scapula. Stomach contents may remain in place after all skin is gone. Vertebrae may remain in articulated subunits even after tibs separate and fall away.

Bones of course drop to the ground when soft tissue is sufficiently decayed. The up-side long bones, ribs, and half pelvis will not balance atop the down-side bones, but will settle next to them, partly overlapping them, or in a mixed-up pile. In some photos it appears that the up-side scapula has slipped to the ground next to the skull or lies atop the lower jaw.

All of the photos show remains of individual animals lying alone, some of them lying on edges of shallow depressions(probably dry waterholes) which are not much larger in diameter than the elephants are long. Many carcasses are surrounded by trampled heavy traffic areas forming a ring around them, possibly due to scavengers or human visitors.

Table 8-1

Utilization (feeding) flow for carcasses of adult prey fed on in winter by wolves (see Haynes 1981 in press and Chapter 6 for similar data on deer):

MOOSE

Rump: anus, hip flesh eaten. Belly entered, viscera and blood devoured. Rumen exposed.
Ribs: broken off on one side.
↓
Shoulder: flesh eaten on one side.
↓
Pelvis: cleaned, light damage.
Femur: trochanter partly removed. Lateral condyle damaged.
↓
Vertebrae: processes broken.
↓
Humerus: lateral tuberosity eaten off.
↓
Scapula: cleaned, disarticulated, damaged. Nasal bones and head flesh cleaned.
Femur: distal end damaged.
Tibia: proximal end damaged.
↓
Legs: one or both rear legs disarticulated, scattered a bit.
↓
Spine: broken into two parts.
↓
Mandibles: sometimes disarticulated.
↓
Humerus: head gone on one or both.
↓
Femur: trochlea well gouged.
↓
Tibia: crest gouged.
↓
Tibia: proximal gone.
↓
SCAVENGE STAGES

BISON

Rump: tail gone, hip flesh eaten. Belly opened.
Ribs: broken off on one side.
Shoulder: flesh opened.
↓
Pelvis: cleaned and damaged.
↓
Femur: trochanter partly removed, lateral condyle damaged.
Vertebrae: processes broken.
↓
Humerus: one or both tuberosities removed.
↓
Scapula: one removed.
↓
Skull: nasal bones damaged. Ear eaten.
Spine: cleaned.
↓
Mandibles: removed.
↓
Humerus: head gone.
↓
Femur: distal end gouged.
Tibia: proximal end gouged.
↓
Rear leg: one or both disarticulated from trunk.
↓
Tibia: "crest" opened up.
↓
Tibia: proximal end gone.
↓
SCAVENGE STAGES

Table 8-2

Damage to bones of adult Bison fed on by packs of wolves (10-15 animals) at different stages of carcass utilization:

NOTE: Unusual or irregular sequencing may be due to scavenging by non-killing animals, freezing of part of carcasses into snow or ice, removal of parts by bears, presence of disease, or similar factors.

Element	Utilization (Cumulative: That is, all damage accumulates as you read from left to right) Light to moderate	Full	Heavy
Femur	Trochanter stump left (2 cm. high). Greater trochlear rim scored at right angle to axis, 1.2 cm. deep. Minor to unnoticeable damage to medial condyle. STAGE 1, STAGE 1-2.	Medial condyle gouged. Lateral condyle surface gone. Trochlea well opened (5 x 7 cm. area). Trochanter stump gone. Tooth marks undercut head. STAGE 2, STAGE 2-3	Distal end gone. Head nearly gone. Shaft being broken up. STAGE 4
Tibia	Lateral proximal edge grooved or beveled. Some furrowing or gouging also. STAGE 1	Crest opened up or gone. Medullary tissue exposed at lateral proximal end. Medial edges furrowed. Still articulated to femur. STAGE 2-3	Proximal end gone. Most fracture edges sharp. Some localized edge-rounding. Still articulated to ankle bones. STAGE 4(a) (STAGE 4b shows more edge-rounding. STAGE 5 = shaft being broken up.)
Humerus	Greater tuberosities gone or furrowed. STAGE 1	Tuberosities gone. Head open. Tooth scoring on shaft compacta. STAGE 2-3	Proximal end gone, about 1/3 proximal shaft gone. Condyles gnawed a bit in scavenging. STAGE 3-4

Table 8-2
continued

Damage to bones of adult Bison Fed on by packs of wolves (10-15 animals) at different stages of carcass utilization:

NOTE: Unusual or irregular sequencing may be due to scavenging by non-killing animals, freezing of part of carcasses into snow or ice, removal of parts by bears, presence of disease, or similar factors.

Element	Utilization (Cumulative: That is, all damage accumulates as you read from left to right) Light to moderate	 Full	 Heavy
Pelvis	Edges of ilium and ischium gnawed. Cancellous tissue exposed. STAGE 1	Fully cleaned of soft tissue. Ilium and ischium partly gone. STAGE 2-3	Broken, only stumps left of ilium and ischium. STAGE 4
Scapula	Vertebral border cartilage and bone ragged. Still attached to foreleg. STAGE 1	No cartilage left on vertebral border, bone edge splintered and jagged. Disarticulated from humerus. STAGE 2-3	Blade crunched and splintered at vertebral end. Some of spinous process 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. Horns scratched. STAGE 2-3	Nasal bones ragged at ends. Anterior premaxillaries broken. In scavenging, horns pulled off cores. STAGE 4
Mandibles	Partly cleaned of tissue. Articulated. STAGE 1	Cleaned. One hyoid remains. STAGE 2-3	Inner surfaces scratched. In scavenging, disarticulated. STAGE 4

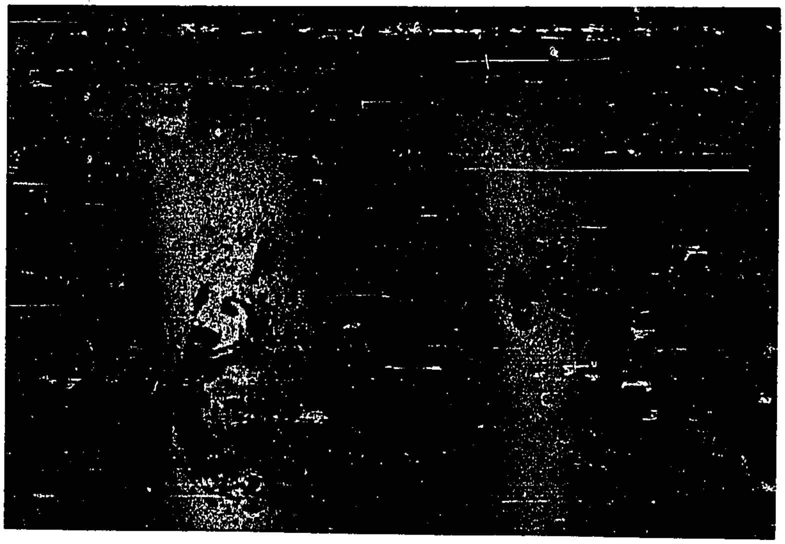


Figure 38. Bison humeri, both from adult males, with entire proximal ends gnawed off by wild wolves.

Figure 39. Caribou antler beam from adult male killed by wolves in central Alaska, 1978.

REVIEW OF SOME OTHER STUDIES OF NATURAL CARCASS DISINTEGRATION

The sequence of animal carcass disarticulation and damage when humans are not involved has been studied by a small number of researchers (see below). Many of these kinds of observations are concerned with soft tissue decay. Akopyan (1953) observed the carcasses of 296 ground squirrels in the southeastern steppes of the USSR over a three year period, finding that carrion insects can bury some bodies up to 40 cm. deep. Payne (1965) found that baby pig carcasses, when subject to decay in a South Carolina woodlot, passed through six stages of decomposition if insects were present: fresh; bloated; active decay; advanced decay; dry; and enduring remains. The final stages were reached in six days. When insects were not present, the stage conditions were: fresh; bloating and decomposing; flaccid and dehydrated; mummified; dessicated; and disintegrating. This latter sequence could take months. Similarly, Pierce (1949) proposed a series of stages of mammalian carcass decomposition in California asphalt pits when insects were present, but Miller and Peck (1979) have re-examined this work and found it to be full or errors.

Rolfe and Brett (1969) reviewed the literature on soft tissue decay and disarticulation. They summarize some German literature and present the following general sequence:

(1) Lower jaws detach.

(2) Skull and limbs disconnect from trunk.

(3) Ribs loosen and detach.

(4) Limbs disarticulate into subunits.

(5) Vertebral column disarticulates.

(6) Bones disintegrate.

Angel (1978) emphasizes a notorious variability in rates of soft tissue and bone decay (in regards to human material). He summarizes human carcass deterioration in temperate zones in the following sequence:

(1) Viscera consumed by fly larvae, one to four weeks. Stink diminishes by one month. Muscle consumed by fly and dermestid larvae, one to two months. Odors clearly notable for two to three months. Brain remnants may persist three to four months.

(2) Ligaments, tendons, periosteum hold vertebrae and other bones together up to three to four months, may persist on bones seven to nine months. Odor only slight at six months. Bones slightly greasy four to five months. Only traces of bone grease remain by nine months.

(3) Cartilage black and dried by four months, persists up to 12-15 months. No bone grease left after 12 months. Rodents begin to gnaw.

(4) Fats (as adipocere) may persist up to 12-15 months. Skin lasts in patches six months.

(5) Empty insect pupae cases last one year.

(6) Bone surfaces crack at three to five years. Spongiosa decays, starting at five years. Cortex decay starts at 20-30 years.

Toots (1965) observed the following sequence of disarticulation of coyote, sheep, and antelope carcasses in semiarid to near-arid desert habitats in Wyoming:

(1) Most of the soft parts decompose, although hide, hair, and ligaments remain. The limbs are displaced from the trunk, but are still in articulation. The skull, mandibles, and one or a few cervical vertebrae separate as a unit from the trunk.

(2) Some hide and ligaments remain on limbs, which are displaced as units. Upper side of ribs are disconnected, but lie near original anatomical order. The skull is disconnected but nearly in place. Vertebral column shows only a single break.

(3) Most ligaments are gone. Limbs are disconnected and mostly disjointed, although some elements may remain articulated. Lower jaws are disconnected from each other and from the skull. Most ribs are in contact with vertebrae, but are disconnected. The vertebral column is still articulated through part of the cervical vertebrae and through the sacrum and pelvis. Some scattering is occurring, especially of the skull and upper cervical vertebral. Weathering and breakage are occurring.

(4) Vertebrae gradually separate into smaller articulated units. Bones crack and slowly disintegrate.

Most scatter of disconnected bones is not due to carrion feeding by scavengers, but instead occurs long after soft tissue has disappeared.

Hill (1975,1979) observed topi carcasses on the delta flats of the Laga Tulu Bor in an arid African region, and found the following patterned sequence of disarticulation, with carnivores most likely being the principal dispersal agent:

(1) Foreleg detaches.

(2) Caudal vertebrae detach.

(3) Scapula disarticulated from humerus.

(4) Mandible detaches.

(5) Humerus-radius/ulna detaches from lower foreleg elements.

(6) Atlas and cranium separate together from rest of vertebral column.

(7) Carpals freed, the metacarpal is freed from hoof.

(8) Phalanges separate from each other, humerus separates from radius/ulna. Rear leg separates from pelvis.

(9) Second and third phalanges of forefoot separate.

(10) Ulna and radius separating.

(11) Rear limb tarsals through hoof freed as a unit. Phalanges begin to separate.

(12) Tibia and femur disconnect.

(13) Cranium separates from atlas.

(14) Tarsals and metatarsals disconnect.

(15) Ribs separate from vertebrae.

(16) Vertebrae begin disconnecting.

(17) Innominate separates from sacrum.

(18) Vertebrae separating, axis disconnects.

(19) Sacrum separates from lumbars.

(20) Cervical vertebrae disconnect.

These carcasses were fed upon by insects as well as by birds and mammalian scavengers, so soft tissue decay may not even have had time to occur in some cases. Thus, the timing of bone exposure and subsequent joint disarticulation may vary within identical environments; the sequence may be consistent, however, which is Hill's and Toots' major point.

OBSERVATIONS OF FOSSIL ELEMENT DAMAGE DUE TO GNAWING ANIMALS: THE GEIST COLLECTIONS AND THE SMITHSONIAN COLLECTIONS

Introductory Notes

Some of the damage types observed in modern wolf-kill assemblages and bear-scavenged assemblages were sought in an accumulation of several thousand Alaskan and Yukon Quaternary mammalian remains collected by Otto W. Geist on behalf of the University of Alaska Museum (see Chapter 3) and in collections of Pleistocene mammalian bones at the Smithsonian Institution, Department of Paleobiology. Many Pleistocene specimens in both museums lack detailed provenance, but most from Alaska are thought to be derived from sediments of Wisconsin age (Pewe 1975:95).

The fauna represented in the museum collections include *Bison* spp., *Alces*, *Cervus*, *Odocoileus*, *Rangifer*, *Mammuthus*, and *Equus* spp. No effort was made to count specimens, but all were examined.

It is unfortunate that fossil bone collections have been made so selectively, and that many fractured, gnawed, or otherwise damaged specimens are oftentimes discarded after too few are identified and measured. Many fragments of bone that could have been collected from central Alaska (but were discarded) might have contained valuable evidence regarding proportions of heavily utilized carcasses and lightly utilized carcasses; this kind of information is oftentimes a reflection of predator abilities to acquire prey in the past.

In modern assemblages and natural death accumulations of recent bones, the proportion of bones showing gnawing damage would vary with prey species and would also vary according to relative prey vulnerability. Weathering destruction and dispersal of elements by scavengers would further alter the proportions. At the present time attempts are being made to define how the proportions of prey taken by wolves in several modern communities, such as those containing wolf and bison, wolf and moose, and wolf and deer, relate to surviving numbers of bones.

The museum research was not intended to determine the relative abundance or scarcity of damaged bone in the museum collections, but to note the presence of certain types of damage in fossil bone collections. Geist himself ([1953?]:42) reported fewer instances of carnivore gnawing damage on the specimens he collected than I saw on those specimens.

It is possible that bones in the museum collections had suffered gnawing damage not at all similar to the modern types of damage, and therefore were unnoticed during the examinations. In addition, possible signs of gnawing by small scavengers and carnivores such as coyotes and wolverines were observed, but are not discussed here.

Observations (also see Haynes 1980a)

Fossilized antler that had not been cast (and was in velvet) at the time of its deposition in many cases showed probable wolf gnawing damage. Rodents may gnaw polished or cast antlers, but apparently wolves never do. Many antlers had also been gnawed by artiodactyls before fossilization. The wolf-gnawed pieces showed furrows transverse to the long axis of the beam, each furrow being

2-4 cm. long and about 4 mm. wide (Figure 39; also see Haynes 1980a: figures 1 and 2). Palmate tines has probably been eaten away first, and main beams were broken. Many caribou and moose antlers in the museum collections lack most or all of the brow or first tine as well as the bez or second tine and higher tines, probably due to a combination of factors such as rodent gnawing, stream abrasion, and weathering erosion. Edge rounding and surface smoothing were commonly seen on antlers, many bases were naturally bevelled, and burrs usually had been removed, probably due to abrasion in seasonally frost-heaved soils.

These kinds of modification are similar to what might be expected from cultural alterations in the manufacture of antler hammers, hafts, or other artifacts. In most cases where contextual data are poorly known, I do not think there is any better reason to assign the modifications to human behavior than there is to explain the alterations by actions of natural processes.

Very few out of hundreds of vertebrae in the University of Alaska and Smithsonian Collections are complete and undamaged. The spinous processes on all vertebrae of bison, proboscidean, and other large species at the University of Alaska Museum were damaged. Some had most likely been broken after fossilization, but damage patterns on many specimens were similar to the modern patterns which result from carnivore gnawing during medium carcass utilization.

Gnawing damage on the vertebrae of extremely large prey may even allow one to suggest the possible attitude of the carcass at death, on the basis of asymmetrical damage to elements or processes of each side. In the Geist materials at the University of Alaska, for example, there is a partial set of thoracic vertebrae from a single proboscidean, collected from an unidentified locale in central Alaska. These bones exhibit heavy gnawing only on transverse processes of the right side, prompting judgement that the carcass was lying on one side (most likely the left) throughout its early decay period, and the axial elements were not disarticulated or rolled. Such observations may be rare, but they might contribute to more complete understanding of possible disturbances to carcasses after death. Some long bones of adult and juvenile proboscideans show probably carnivore gnawing damage across articular surfaces, so it appears that certain carnivores may have been capable of dismembering the limbs of mammoth-sized prey. It is also possible that carnivores were scavenging the remains of freshly butchered mammoths from human sites.

In the museum collections fossil humeri often showed loss of only external tuberosities, damage associated with moderate to light carcass utilization (see Haynes 1950a:figure 3;Figure 40,bottom left). Many specimens lacked proximal ends, probably as a result of gnawing damage combined with post-depositional breakage of the weakened element.

Probable gnawing damage on fossil femora (of _Bison_, _Equus_, or _Alces_) was often typical of light to moderate utilization, and indicated predation rather than scavenging by wolves in optimally-sized packs during wintertime, probably in rather harsh winter seasons (see Haynes 1980a:figure 7).

Damage seen on fossil tibiae was sometimes typical of predation gnawing-_cum_ trampling-_cum_ scavenge gnawing patterns, in which the entire proximal end is broken off shafts and distal ends (Figure

40,top left;see Haynes 1980a:figure 10). Both Equus and Bison specimens showed such damage, indicating high density of carnivores and a tendency of bones to lay unprotected in ungulate feeding areas for a short time (less than five years) before burial or redeposition in protected environments. Most of the examined tibiae, however, are gnaw-damaged in patterns more typical of moderate to light utilization, indicating high availability or vulnerability of prey animals relative to predator numbers (see Haynes 1980a:figure 11).

Many ungulate metapodials in the museum collections were split lengthwise, such that anterior halves were separating from the posterior halves (see Haynes 1980a:figure 12). This break is sometimes called a coronal fracture when it initiates at the proximal surface of the element. Fossil bone collections may contain specimens in all stages of the development of this break, which is not necessarily due to cultural activity or animal activity. This break is a common example of a weathering crack or a longitudinal split that results from shrinkage of the bone tissue upon drying.

Metapodials were found in the collections that showed pitting and scratching on distal ends above and on condyles. Such damage has been seen on fossil Alces and Bison bones in Alaskan and Yukon collections, and on fossil Camelops and Bison bones from Colorado.

Even on very well utilized modern wolf kills, metapodials are rarely gnawed distal to the proximal epiphysis. Scavenging bears will peel hide from the remaining lower legs of dead animals such as bison (M. Meagher 1980 pers. comm.) and will clean up killsites abandoned by wolves; however, the shape of the pits on the museum bones does not appear to conform to the shape of bear teeth crowns. Instead, these pits and gouges seen to have been made by animals whose jaws were the size of those of a hugh wolf or a brown bear, but which possessed relatively blunt cone-shaped teeth (see Haynes 1980a:figure 13; also see Morlan 1980:plate 3[page 63]). This damage might be assignable to scavenging canids with hyena-like habits (perhaps Canis dirus), or unusually hungry large cats with worn cheek teeth. The scavenging probably took place in the spring or summer following predation, or within three months of the prey animal's death, whatever the season, when the bones were still greasy and covered by some hide. This is the most common timing of lower-leg scavenging in modern wilderness areas of North America, when the rest of the carcass' soft tissue is virtually gone, and only the lower legs are still encased in hide. Most wolf kills or winter related deaths occur late in winter or very early in spring, and these carcasses are scavenged by bears emerging from their cold season torpor and by wolves in small, denning-season groups through the summer and fall.

Innominates with broken edges suffer weathering erosion more easily than ungnawed bones. In many fossil collections only the acetabulum and surrounding denser bone survived. Again, this may be due to a combination of gnawing damage and post-depositional breakage and erosion(Figure 40, top right).

In the museum collections several localities produces spirally fractured bones (Figure 40, bottom right; also see Haynes 1980a:figure 14), but it should be noted that the absence from collections of such broken bones from other localities may be due to the biases of collectors against damaged specimens rather than to their absence from fossil deposits. Wolves will not often break up long bones of adult bison or moose unless the carcasses are being heavily scavenged. In such cases, the bones will usually have developed longitudinal drying cracks and so will be fractured by the carnivore in spiral and linear configurations. Such fracture types can occur months after the prey animal's death. Scavenging bears and wolves that arrive at a very fresh carcass already fed upon by killing predators may break long bones in spiral configurations without any linear breakage, but unless the proportion of scavengers and predators to prey is extremely high this latter situation would be uncommon.

Gnaw damage from a large felid, large canids, and large bears is detectable on many specimens in central Alaskan and other collections of fossil bone at the University of Alaska Museum and at the Smithsonian Institution. On the other hand, the bones of the carnivores themselves are virtually or actually lacking from most collecting locales. Thus, there is available only on prey bones the data which could indicate species members of local animal communities. In connection with this, Guthrie (1980) speculates that _Panthera leo atrox_ and _Arctodus_ were the main predators of _Bison priscus_ during the late Pleistocene. Tangible evidence to support this proposition may be found from an extensive examination of Pleistocene bones.

Probable gnaw damage by a lion is seen most clearly on one bone specimen, an _Alces_ femur (no. 7627) collected in the Yukon or Alaska by Copley Amory and now in S.I. vertebrate paleontology collections. The trochlear rims are lightly gnawed, the lateral condyle is gnawed, and the neck of the head is scored by tooth marks.

Canid gnaw damage was common on many specimens in all collections, including _Bison_ femora from the Lindemeier site in Colorado.

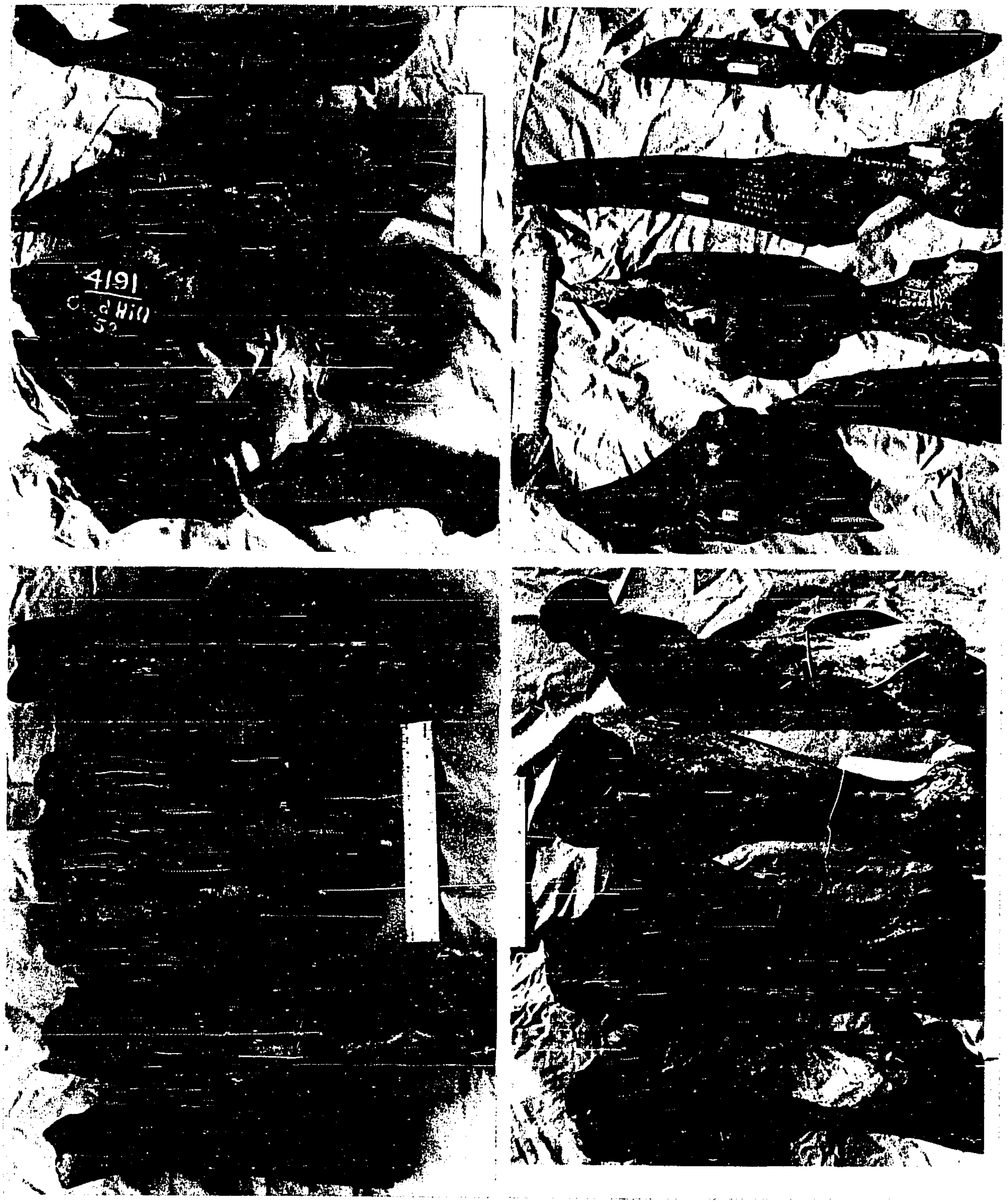
Figure 40. Selected bones from the Geist collections at the University of Alaska Museum, Fairbanks.

TOP LEFT: *Equus* and *Bison* tibiae with proximal ends broken off.

BOTTOM LEFT: *Equus*, *Bison*, and *Alces* humeri with greater tuberosities gnawed off.

TOP RIGHT: *Bison* innominate fragments with evidence of gnawing by canids.

BOTTOM RIGHT: Spirally fractured bone fragments collected along the Old Crow River.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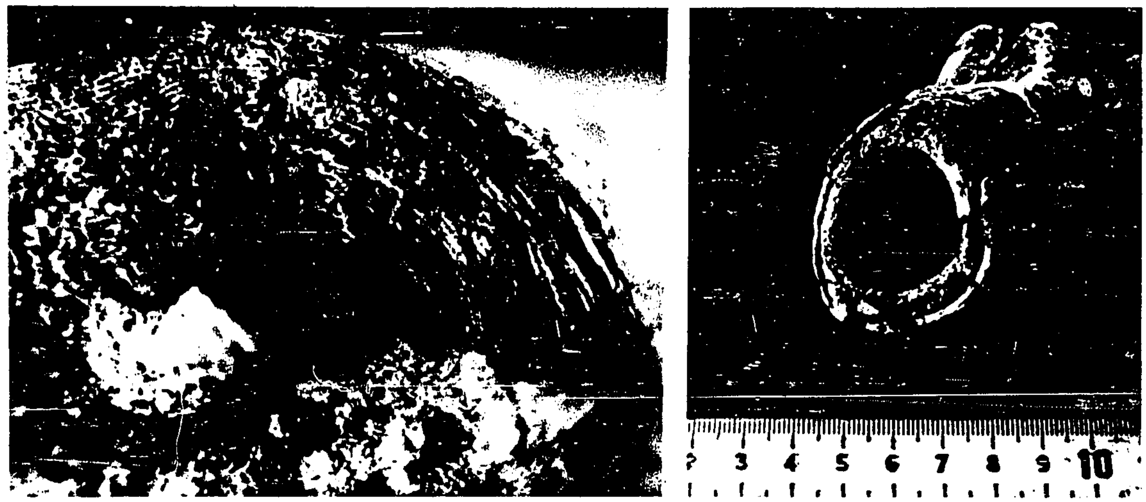


Figure 41. Exfoliation of bone.
TOP LEFT: Section view of neonate Equus' broken radius showing layering of tissue.
TOP RIGHT: Section view of sawn Bos femur showing severe exfoliation of outer circumferential layers.
BOTTOM: Weathered, gnawed, Pleistocene age Bison radius distal end, from the Geist collections.

Probable bear gnaw damage was seen on specimens from the Lindenmeier site; several Bison tibiae appeared to have been gnawed by an animal with a large mouth and flat teeth, such as a bear or a large pig.

Probable bear gnawing was also seen on an Equus tibia from Pleistocene Idaho collections in the S.I. vertebrate paleontology division. The proximal end of this specimen (drawer 3 from top, case no. 27676) shows unmistakeable gnaw damage, with a single deep and thick tooth impression in the cancellous tissue of the crest.

The proximal end of one Alces tibia from Pleistocene Alaska (collected by the University of California, now in S.I. Vertebrate Paleontology, case 27467, drawer 4 from top) may have been gnawed by a bear.

A Mammuthus pelvis fragment collected near Lost Chicken Creek, Alaska, specimen no. 21510 in S.I. collections, shows large tooth marks on compact bone, and tooth impressions in cancellous bone, possibly from bear gnawing.

In none of the collections mentioned above are there found bones of canids, felids, or bears.

During weathering of bones, the outermost lamellar tissue may actually shrink and peel off (Figure 41). The loss of these outermost layers may remove the shallower traces of carnivore tooth marks or butchering cuts made by tool-using humans. It is very difficult to detect the loss of circumferential lamellae if the exfoliation is complete, as it often is on bones of subadult animals. Many of the museum specimens appeared to have lost thin layers of compact bone tissue from much of their surfaces but retained enough patches of original layers to make their exfoliation apparent. These specimens probably were deposited on poorly-drained open ground surfaces, subjected to unimpeded sunlight part of the year, and later redeposited or buried in more protected environments.

Even without serious exfoliation, many surface marks such as teeth scratches may be softened by weathering erosion, stream abrasion, or abrasion during frost-heave or other geomorphic processes. Root acids may create dense networks of fine etch marks, especially on the surfaces of bones that have lain in wet grasslands, sedge fans, or tundras. It would be practically impossible to discriminate some carnivore gnawing from etching without some idea of the general shape characteristics of typical carnivore modification, such as the sequential removal of processes and tuberosities.

Several localities in Alaska have yielded articulated ungulate body parts or nearly-whole carcasses (See Péwé 1975). If these animals died in winters, then the articulated and mummified remains were buried or permanently protected by freezing before a full year had passed (see Table 9-1 for sequence and timing of carcass disintegration).

I would guess that autumn floods may have washed summer death carcass parts into mucks that froze and stayed frozen for millenia, or that spring floods redeposited winter deaths (or carnivore kills) into sediments that remained wet or perennially cold for millenia. The larger carcasses may have been only minimally scavenged, and were probably deposited in their final environment of preservation during cold seasons, although soft tissue decay may have occurred before then. I would guess that these carcasses are from late summer or fall deaths that soon froze or were buried.

Microbial decay begins almost immediately after death, unless inhibited by rapid burial, dessication, or natural antibiotics (Rolfe and Brett 1969). Moisture speeds the decomposition of carcasses by encouraging growth of bacteria (which are already normally present in living bodies). The optimum temperature range for decay is 21-38°C. Diseased subjects decay faster than healthy ones, fat subjects decay faster than lean ones, and old subjects decay faster than young ones. A mummified carcass does not disarticulate, whereas a quickly-macerated body may come apart within days. The Alaskan "mummies" may have been subject to extreme drying in bright sunlight, with a minimum of scavenging by larger carnivores.

(Also see Figures 42 and 43 for other examples of modified bones from northern locales.)

Figure 42. Geist collections materials.
TOP two: Reverse and obverse of proboscidean long bone fragment displaying gouge marks, scratches, and edge-rounding.
BOTTOM far left: Coronal fracture on metapodial.
BOTTOM left: Gnawed *Bison* tibia proximal end.
BOTTOM right: Gnaw marks on *Bison* rib.
BOTTOM far right: Gnaw marks on proboscidean rib fragment.

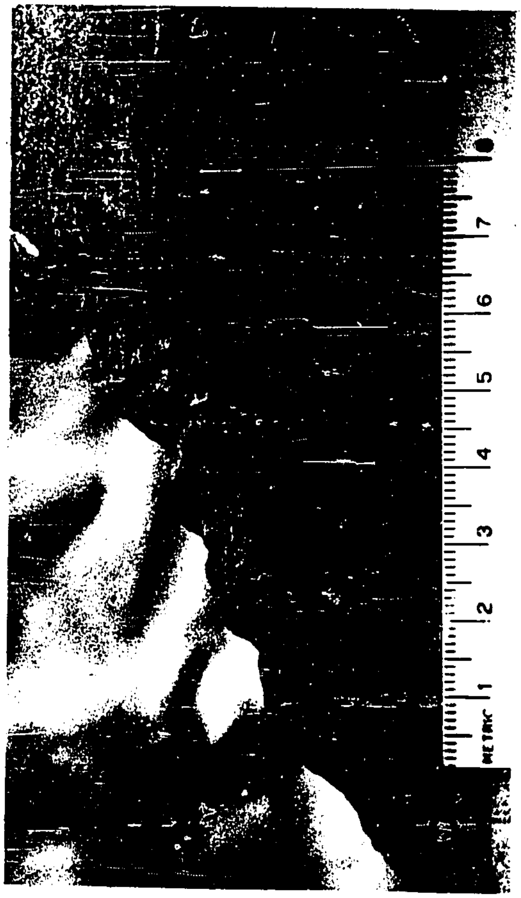

METRIC 1 2 3 4 5 6 7 8 9 10 11 12 13
METRIC 1 2
METRIC 1 2

Figure 43. Geist collections materials.

LEFT: Proboscidean long bones. Specimen to left is a tibia with gnaw damage on upper (proximal) end and a spiral fracture on the lower part of the shaft.

TOP RIGHT: Close-up of fracture edge on tibia, showing tooth marks near edge.

BOTTOM RIGHT: Same edge viewed from above, showing edge-rounding.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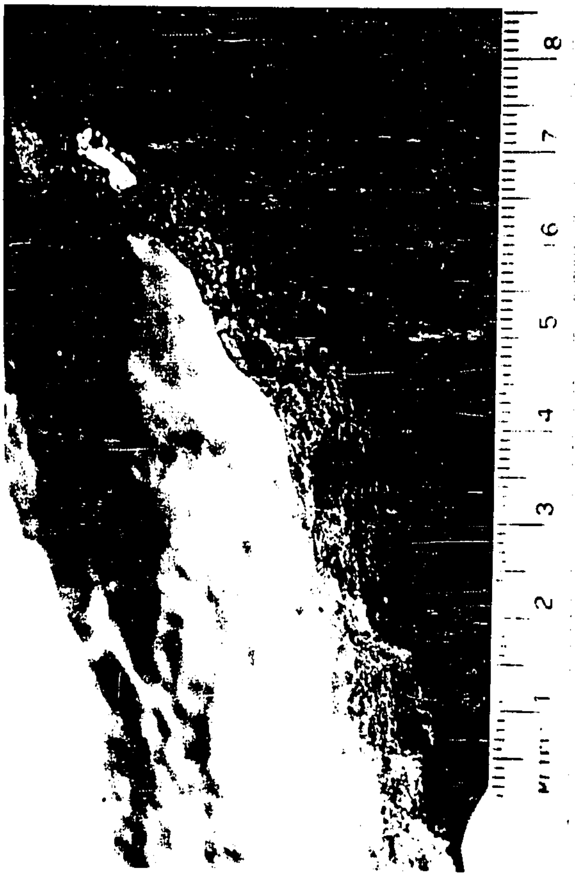
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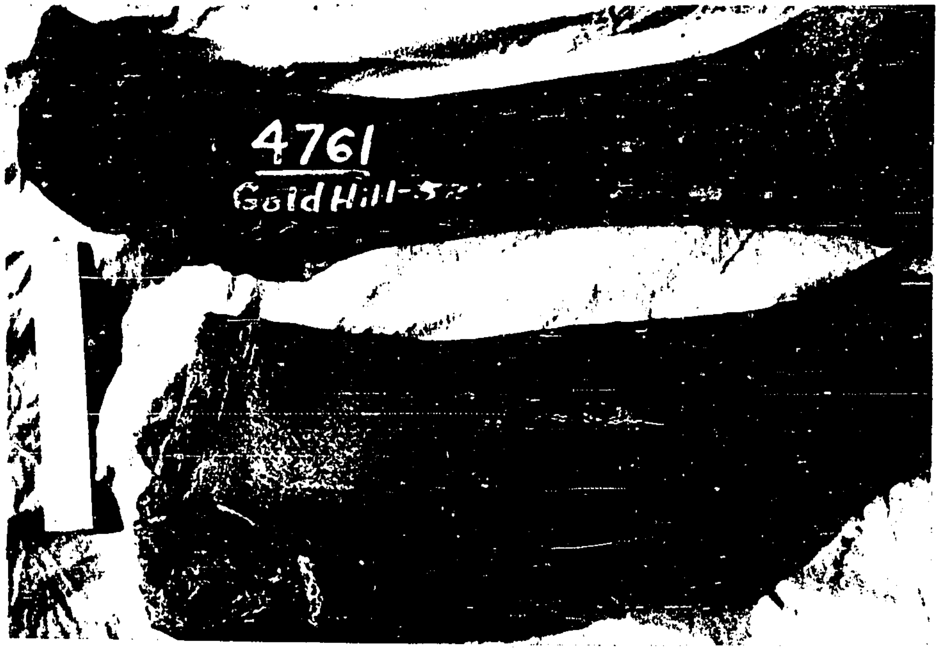
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OBSERVATIONS OF FOSSIL ELEMENT DAMAGE DUE TO GNAWING ANIMALS: THE JONES-MILLER SITE COLLECTION

Introductory Notes

One of the things that human beings do, like most large predators, is create enduring evidence of past behavior: that is, they make sites. It is conceivable that many of the discoverable sites made by hunting and gathering peoples contain some items left over from subsistence or technological activities (see Gould 1980; Yellen 1977; Binford 1977,1978, 1981 in press). It seems to be archeological convention that food refuse or debris from tool manufacturer are interpretable as the most direct representations of past human behavior; however since scavengers and carnivores undoubtedly co-existed with people in prehistory, the possibility exists when food refuse is involved that post-depositional disturbance has taken place. In some cases these foraging animals might have encountered abandoned human campsites, butchering sites, and killsites, and might have gnawed, removed, or redistributed bones.

The subsistence catchment areas of indigenous human groups may overlap or coincide with territories of other predators, especially where the human and other predators' populations are relatively low in number and scattered, as is common for large predators, and there is a great enough herbivore biomass to support several predaceous species having similar econiches (see Estes 1967; Rudnai[1977?]; Schaller 1975; Kruck 1975). Since during the course of foraging journeys many territorial carnivores revisit their own kills months after original feeding (in some cases after years [Haynes unpublished data]), there seems to be good reason to expect even non-fresh, human-produced bone accumulations to have some appeal to four-legged scavengers.

During the Late Pleistocene period in parts of North America, there were more species of predators and carnivores that existed in Recent times, and probably also a much greater standing crop of potential prey animals (see Martin and Guilday 1967; Guthrie 1980; Matthews 1976; Butzer 1971). North America may not have possessed direct counterparts to the highly effective scavenger communities which exist today in south and east Africa, although there is the possibility that some large carnivores such as the dire wolf (Canis dirus) may have functioned much more as scavengers than do timber wolves of today: Kurtén (1968:109) and Martin and Guilday (1967:29-30) describe the dentition of dire wolves as hyena-like, since it is so massive. The dire wolf's carnassials are slightly higher and longer relative to jaw length and toothrow length than are the timber wolf's,* and the dire wolf's jaw bones are much heavier. The dire wolf's head is larger than a timber wolf's in proportion to body size. Regardless of the

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*Dire wolf upper carnassials are generally a little over 30% of the length of the maxillary cheektooth row, which is about 33% of the entire head length, while in timber wolves the upper carnassial is a little under 30% of the cheektooth row length, which is a bit over 33% of the skull length. In spotted hyenas the upper carnassial is closer to 45% of the toothrow length, which is 30% of the head length. Spotted hyenas also possess huge, massive, conelike premolars that become very blunt from wear, and that are specialized crushing structures. Dire wolf teeth and skulls are very similar to timber wolf teeth and skulls; spotted hyenas, however, have a much more forward nuchal crest, putting the temporalis muscles nearer the jaw's fulcrum, and they have higher sagittal crests, allowing more area for temporalis insertion. Hyenas also have lower and more robust zygomatic arches, and much larger and thicker masseter muscles (Buckland-Wright 1969).

similarities or differences between wolves and spotted hyenas, the fact remains that both species (Canis and Crocuta) as well as large bears and large cats are capable of inflicting great damage to bones of large prey animals (Miller 1969; Haynes 1978a,b,c, 1980a,b; Kruuk 1975). The potential for human-produced sites to be disturbed is present and significant in any time period.

Observations

The Jones-Miller site in eastern Colorado was excavated by D. Stanford of the Smithsonian Institution. A final report is in preparation; several preliminary reports have already been published (Stanford 1974,1975,1978). The site contains over 40,000 bones and bone fragments from about 300 bison, and more than 300 stone implements and flakes, including over 100 Hell Gap type projectile points or point fragments. There may be several episodes of mass winter killing of mixed bison herds by prehistoric peoples represented at this site. Stanford (1974,1975,1978) postulates that bison were driven en masse through or into deep snowdrifts between two gently sloping wooded hillsides, then killed with spears while they were trapped and unable to escape. The animals were butchered at the killsite.

There were practically no articulated bones, except a few vertebrae and some lower leg elements; otherwise the bones occurred nonrandomly scattered in a lense or bone bed, sometimes clustered by element or body part, indicating stacking or the use of standarized spots in the site area for processing the same parts of several different animals. Many bones were fractured when fresh, many were carnivore gnawed, and about 200 pieces may have been used as chopping or scraping tools. The greater part of the bones were weathered to the same degree before burial. There were rodent gnaw marks on many elements, and the damage is most similar to that produced by grey or red squirrels (Sciurus spp.) or other species of the same or smaller body size (Haynes unpublished data). There is also on many elements a kind of root etching seen most often on bones in modern assemblages that lie shallowly buried for years or that lie in the upper part of zonal, well-drained soils usually shaded by deciduous trees (Haynes unpublished data).

A cursory examination of femora, tibiae, and humeri revealed a great deal of carnivore gnaw damage. Most of the damage was typical of light to medium utilization by carnivores. Almost none of the damage was of an advanced scavenge type and very little was of a kennel pattern (See Chapter 4). There were some cylinders of long bones lacking epiphyses, typical of kennel pattern, but most such specimens were from subadult animals, whose bones usually do not have hard epiphyses fused to the shafts.

Some long bones were not gnawed at all. Judging from teeth marks, gnawing animals ranged in size from 9 kilograms in body weight to over 40 kilograms. I propose that there are canids involved in the modifications. There are three possible alternative interpretations.

(1) The hunting peoples were turning loose their domesticated dogs, wolf-dogs, or other, small- to medium-sized and occasionally large canids after the bison carcasses were butchered. Some long bones showed stage 1 or 2 damage to an epiphysis while also showing midshaft spiral fractures. The gnawing animals did not make the fractures. Some fracture edges show possible gnaw damage; therefore, these

elements were most likely gnawed after breakage by humans, perhaps for marrow extraction or for tool manufacture. However, all gnaw damage resulted not from long-term kennel gnawing, but from feeding on cancellous bone or cartilage-covered parts of bones. In other words, these was grease or soft tissue present on bones when all gnawing was being done, suggesting that *no* large numbers of scavenging animals spent long periods of time at the site cleaning it up. If dogs did most of the gnawing, it is possible that a dozen or fewer spent several weeks at the site; a larger number of dogs (say 50) could have created the gnaw damage and scatter within a week.

(2) Wolves, coyotes, or semi-wild dogs were scavenging the bone piles after humans abandoned the site in winter. I would expect this kind of behavior from coyotes, dogs, and single wolves or unusually small groups of wolves which could not successfully hunt big game animals such as bison. It is also possible that human hunting caused local decline in bison numbers, and territorial wolf packs that seasonally depended on wintering bison herds may have been left without adequate numbers of prey to sustain them over the rest of the winter.

In wooded habitats or where there is grassland broken up by numerous stands of trees, bison bands may not contain more than a few hundred (or fewer) animals. Larger groups would have to split up to feed on the prairies which are interrupted by woods. Usually these discrete bands, made up of adult bulls, adult cows with calves, other adult cows, yearlings, and very young adult animals of either sex, do not remain close to each other because wintertime feeding involves a lot of daily migrations. Therefore a single band of 100 bison might be the only source of prey animals for dozens of kilometers around in certain ranges. If humans killed all the members of a discrete band, full sized hunting packs of wolves may have spent unusually long amounts of time scavenging the butchered bones in wintertime, because there was no other choice. The scavenging animals apparently were satisfied with their available food at the site, since they utilized the bones as they would have in primary feeding, rather than as in unsatisfied scavenging. In Wood Buffalo National Park I have observed skeletal remains of a mass death episode in which thousands of bison drowned in springtime (see Chapter 7); in two particular areas individual skeletons of several dozen bison lay only meters from each other. When flood waters receded from the carcasses there would have been an enormous amount of fresh bone and carrion found within a limited area and available to wolves. Yet, almost no gnaw damage was seen on the remaining bones. Because living prey had become locally scarce after the deaths, it is possible that wolves simply avoided the area, seeking food elsewhere in the following winter and spring. Even poorly-fed wolves wander very widely in search of living prey (Oosenbrug 1980 pers. comm.;Haynes 1980 unpublished data), so it is possible that many nonterritorial wolves encountered the Jones-Miller bone mass over winter, ate a little softer bone, then moved on to seek prey elsewhere. I think the Jones-Miller bones have been scattered and gnawed by some wolves, but I do not think most of the gnaw damage is attributable to scavenging wolves.

(3) In the summer or fall, wolf families may have relocated their pups to the site of the bone mass, there to take advantage of the abundance of gnawing objects. The medium- to small-sized canid gnawing damage was thus caused by pups, while the rarer heavier damage

was created by adults at rest between times of hunting forays. I think that soft tissue was present when most gnaw damage was done, indicating that the bones did not undergo much decay until buried, and that scavenging did not occur long after the kill and butchering date.

It is possible that all kinds of wild animal activity and domesticated animal activities took place at the site. However, my preferred interpretation is alternative (1), in which dogs for the most part are responsible for the damage. The dogs probably did not live at the site very long, although if they were few in number they may have lingered around the frozen bone mass for a few weeks in wintertime. Most of the dogs would have been about 22-35 kg. in body weight, or somewhat smaller. The site apparently was located on the edge of woods, was wooded, or became so within a few years of the date of deposition of the bones, and was well-drained most of the time. Burial was relatively quick, so that most elements did not weather severely before being protected by overburden; I estimate that all elements were buried within five years.

IX. The Transition from Biosphere to Lithosphere: Bone Deterioration

STABILITY, JEOPARDY, AND PRESERVATION POTENTIAL

Literature Review

Once bones are deposited out of the body of living animals, they are subject to deterioration, which could ultimately end in total disappearance of the elements. Fossilization is simply one stage in the sequence of disintegration, although fossilization gives much more stability to bones in the process of *ex vivo* deterioration. In fact, fossilization may almost entirely stop the process, if the successfully fossilized bones do not end up in depositional environments that are too eccentric or too severe. Because entropic processes are inevitable in this world, one can probably never say that anything (even fossilized and petrified bones) will forever remain in a steady state (or be stable). Therefore, one can only grade the degree of stability achieved by bones under certain conditions.

Stability factors vary widely in different depositional environments. Once bones are at rest in their final depositional environment, their survival depends of their durability. Guthrie (1967) considered bone size and "composition" to be the "forces" chiefly responsible for determining survival of different bones. However, there is a more measurable factor involved. The most direct way to measure the property of durability is by determining overall bone density (weight divided by specific gravity), or the density of particular bone parts.

Brain (1969, 1976) reasoned first that density was the most significant factor affecting destruction of bones; Binford and Bertram (1977:126) also considered the determinant variable in bone survivorship to be density. Carnivore gnawing, weathering and decay, fluvial transport, sedimentary burial, or trampling are processes that affect bones to a degree ultimately due to bone densities. For the purposes of the most simplistic model, carnivores could be considered to differentially consume and destroy the bones of mature and immature prey animals due to density differences, not due to possible differences in the carnivores' motivation when feeding on different-sized animals.

I would point out a basic weakness in this model. A well-fed carnivore may normally eat a porous bone of a juvenile animal, but not a densely-walled bone of an adult; however, a hungry carnivore, if capable, will eat the denser bone. Obviously a factor of purposive, rational behavior by carnivores and human beings must be considered.

Under various soil and climatic conditions there are several different processes acting to destroy or preserve bones. The extreme dryness of deserts produces very brittle fossils that splinter and disintegrate unless soon buried or otherwise protected (see Miller 1975). Caves, especially if calcareous, usually preserve bones well (Guilday 1971b); however, due to the liberation of CO_2 by plants at night (Rolfe and Brett 1969), even in calcareous regions groundwater acidity may be powerful enough to dissolve carbonates in bone. Continually cold and dry climates preserve bones as in a deep freeze, but the effects of seasonal freezing and thawing have not been well investigated (Sutcliffe 1979, 1980). Bones under water may be battered and abraded by rolling across bottom sediments, or they may be severely leached in a few years and become very fragile (see D. Allen 1979:140). As in deserts or arid environments, bones on prairie surfaces may weather quickly, but may also be protected somewhat by growth of grass (Behrensmeyer 1978). Bones in swamps and woods may be protected by shade and available moisture, preventing the too rapid drying which results in splintering and complete fragmentation (Behrensmeyer 1978), and they may be subject to rapid burial by ample covering deposits.

Cornwall (1956) discusses common damage and patterns of fragmentation found in fossil animal bone assemblages, results of post-mortem decay or destruction by natural agencies:

For very large ungulates, skulls are often porous and cellular (which saves weight for the animal but maintains a large surface area); crania are often easily decayed. Jawbones are denser, and teeth, antler, and horn attachments are much more resistant.

Vertebrae, usually porous, seldom survive completely intact. The atlas and axis, being heavier and more solid than most other vertebrae, may preserve better than others. "Pieces of rib shafts are common", but whole ribs are rare (Cornwall 1956:200) except for very large (bison-sized or proboscidean) animals. The sacrum and caudal vertebrae lack prominent processes or ridges, and may be preserved with less breakage than other vertebrae.

On scapulae the vertebral margins are usually "very eroded," while the strong neck, glenoid portion, and spinous portion may outlast the blade (Cornwall 1956:200).

On pelves, the iliac crest is the first part to be damaged, before the ischium and pubis. The acetabulum and the denser bone (of ilium, ischium, and pubis) around it are "the last parts to disappear"

(Cornwall 1956:201).

For humeri, the head and proximal tuberosities decay first. On ulnae, "the shaft may disappear before the more proximal parts" (Cornwall 1956:201). The ulna (or its distal shaft) is usually broken off the radius.

Carpal bones are usually not preserved (or not found). Metapodials may be broken in the middle. Femoral shafts are usually better preserved than the ends. Trochanters are especially "susceptible to decay," and the femoral head may exist as a loose piece. The distal epiphysis is also "frequently found loose" (Cornwall 1956:202). The tibia shaft may be broken, and the distal one third of the element may be found isolated. The astragalus and calcaneus are "not often found broken" (Cornwall 1956:203).

Observations in the Study Area

In this first section I will rate how stable I think bones are that have been deposited in several distinct areas possessing diverse local conditions of humidity, sunlight, and subaerial or subaqueous protection (burial or submersion). These gradations were devised based on my observations of bones in all circumstances, using my knowledge of the length of time the bones had survived. In my opinion, none of these combinations of conditions can be considered perfect for stabilization (in other words, cessation of bone decomposition). The conditions are presented in tabular form, with the most stable factors given first, and least stable factors given last. These ratings refer only to the present state of changes of bones, not to future or potential states.

Most stable (slowest change)	WET/BURIED	(river crossing mucks, pond and lake beds)
	MOIST/SUNNY/BURIED	(open drying ponds, marshes, wet wallows, drying lake beds)
	MOIST/SHADED/BURIED	(wooded poorly-drained levees, low-lying bush, and flood-plains [braided])
	WET	(river bottoms with moving water, channels)
	DRY/SHADED/BURIED	(well-drained, wooded levees)
	DRY/SUNNY/BURIED	(well-drained levees with widely spaced trees, dried wallows, dried ponds)
Least Stable	MOIST/SHADED	(wooded, poorly-drained levees)
(fastest change)	DRY/SUNNY	(open grassland)

If these same factors are impressionistically graded for future preservation potential, the order would be different. This is because while certain combinations of factors can cause changes in bones only very slowly, they may also continue working longer than other factors which quickly change bones. In tabular form, the future preservation potential would be rated as follows, with best potential listed first, and worst potential given last.

Best potential	MOIST/SUNNY/BURIED	minor oxidation, no drying, no leaching in acid soils
	WET/BURIED	no drying, leaching a minor possibility, no oxidation
	WET	leaching possibility, no oxidation or weathering, some trampling without damage
	DRY/SUNNY/BURIED	leaching low, weathering slowed, oxidation possible
	DRY/SHADED/BURIED	leaching danger (acid soils), otherwise protected

	MOIST/SHADED/BURIED	acid soils, leach, low leaching with poorer drainage, low weathering
	MOIST/SHADED	mosses grow, oxidation, slowed weathering, trampling danger
<u>Worst potential</u>	DRY/SUNNY/EXPOSED	quick weathering, trampling

In general, and regardless of localized microconditions of humidity and sunlight, I would rate bones on the following scale of jeopardy (that is, likelihood of being damaged or destroyed), giving the least jeopardizing states first:

Fresh bones still encased in some or all body tissue.

Bones with soft tissue gone.

Grease gone, uncracked.

Weathering cracks appearing, exfoliation, splintering, and deep cracking.

Lichens and moss growing-fragmenting of compacta.

Fresh bones attract living animals which might want to eat them, yet are overall more able to survive almost any temporary weather conditions or any violence due to trampling. Even gnawing by large carnivores seldom seriously damages compact bone tissue of long bones or skulls.

In the absence (or near absence) of mammalian carnivores and scavengers, bones will be naturally cleaned of hide and soft tissue soonest in shady woods, especially where the ground surfaces are covered with decaying organic matter, moss, leaf mold, and litter. In such microenvironments there is an extremely active fauna of arthropods, worms, bacteria, and other microbes which consume soft tissue. If bones are covered with even very thin layers of leaf litter or organic debris, they remain moist for weeks and inviting to microorganisms which eat soft tissue.

Bones lying in shaded woods will be cleaned of most to all tissue except residues of thickest tendons, ligaments, and cartilage around joints, by about two or three months (during seasons when air temperatures stay above freezing day and night, and when there is at least 5 cm. of rain). Bones lying on open ground, such as in meadows or scarcely vegetated ridges, will retain most of the soft tissue for months, possibly the full duration of spring-summer-fall weather, except when rainfall exceeds 12 centimeters. When precipitation is low, the remaining hide becomes very hard and dry, discouraging microfaunal comsumption and decay.

Bones that lie on wet or consistently humid, south-facing slopes (either in open areas or in partly-closed-canopy woods) will be cleaned of virtually all soft tissue, even around joints, by the end of one or two warm months (Figure 44).

If bones or body parts are artificially stripped of hide in wintertime, more remaining muscle and other soft tissue usually survive to the end of summer than on carcasses which have not been skinned or stripped. This is probably because the exposed muscle tissue eventually dries out after extended freezing, and following the thaw is less appealing to microbial or microfaunal scavengers which contribute to decay and tissue consumption.

When large animals die in winter, their leg bones may remain articulated even through the following winter, if subject to little disturbance by scavenging mammals, gravity, or the weight and pressure exerted by settling and melting snow. However, by the middle of the first post-mortem summer (if air temperatures are above freezing in the daytime and most nights, and if the bones do not lie in direct sunlight continually), most long bones become well-greased from liquefying marrow soaking through diaphysis bone from within, and most hide and soft tissue is decayed or devoured. When disturbed, even if slightly (by growing grass, bird scavenging, mild currents of meltwater), bones separate easily. Some bones of lower legs may remain articulated, especially carpals and tarsals attached to phalanges or long bones. Small numbers of vertebrae may remain articulated for a year or more, although by the end of two winters of post-mortem aging they are usually no longer attached, until disturbed by even very minor actions of animals, plants, or other natural agencies.

Horns on bison heads will separate from horn cores very readily if lying in shaded woods, following the thaw (within three months or less), while in open and dry areas with plenty of sunlight horns may never become detached (even if loose on horn-cores). However, it is rare for horns not to become separated from horn cores. Horns easily fall off cores when soft tissue and bone material shrink upon drying. Most bison skulls come to rest upside down following scavenging, water disturbance, movement downhill, or herd trampling disturbances.

Bones lacking a soft tissue or hide cover will dry out and begin cracking within a few hours (unless buried or submersed). Once the grease and marrow has autolyzed or been consumed by microfauna, the bones crack even more and become susceptible to trampling damage. Rodents are attracted to dry and bleached bones for gnawing. Carnivores generally leave such bones alone by this stage. Such bones are still quite hard, and, if not too weathered, enough collagen may survive to keep them from becoming overly brittle. Eventually such bones, if exposed to periods of dry warmth, begin exfoliating and splintering. In shaded areas mosses grow in cracks and openings on bone surfaces, while lichens grow on bones lying in sunnier areas. Cracks in bone tissue may be widened by pressures exerted by growing plant roots and tips. Finally, aged bones splinter and fall apart after a decade or more of weathering.

BONE DETERIORATION (WEATHERING) STAGES

The sequential deterioration of bones over time is remarkably similar in many respects within many different kinds of environments, whether they be arid, subarid, humid, temperate, subartic, or so forth. The time involved for bones to pass through each stage may differ profoundly, however, depending on mean annual temperatures, moisture or humidity levels, and amount of sunlight available. In addition, Warren (1976) found that plants and their root systems functioned quickly and thoroughly in tropical areas to break down human bones which are buried or lie on ground surfaces.

Behrensmeyer (1978) observed the following sequence of ungulate bone weathering in arid African grasslands, woods, swamps, and other habitats:

(1) Stage 0 - No cracks, bones still greasy, marrow remains in medullary cavities, skin or muscle covers skeleton.

(2) Stage 1 - Longitudinal drying cracks appear, even when tissue still covers bones.

(3) Stage 2 - Ligaments and cartilage may persist, but thin flakes of bone tissue peel off surfaces. Edges of drying cracks are angular.

(4) Stage 3 - Surfaces are rough and fibrous. All the very thin periosteal bone tissue has peeled away. No soft tissue remains. Crack edges are rounded.

(5) Stage 4 - Coarse, fibrous surfaces, large and small splintering cracks open up into medullary cavity, with splintering and rounded crack edges.

(6) Stage 5 - Bones splinter, fall apart. Cancellous tissue exposed.

Stages 0-2 may occur within four years, although stage 0 may persist up to one year. Stage 3 usually occurs in four to eight years, stage 4 occurs in 7-10 years, and stage 5 occurs after seven years and up to 15 years after death. Movement through all stages can be slowed by keeping bones wet or protecting them with deep shade and masses of vegetative cover.

The sequence observed by Miller (1975) for bones of horses and cows in a very dry (desert) area of southern California is as follows:

(1) Soft parts removed by scavengers.

(2) Exposed bones crack longitudinally, even when some periosteum remains.

(3) Less than 5% of the periosteum is removed by one year. Most bones are still articulated. Each long bone has one longitudinal drying crack. On single, scattered elements, there may be more cracks and less periosteum.

(4) By one year, 25% of the periosteum is gone, surfaces are bleached bright white, and two or three cracks penetrate into long bone marrow cavities.

(5) By two years, transverse cracks appear on long bones.

(6) By 4+ years, all periosteum is gone, unless the bones are buried, in which case they may still be greasy and articulated by dry ligament.

(7) By 4+ years, all bones are well bleached, exfoliation is beginning, surfaces begin to get powdery, and many longitudinal and transverse cracks develop on shafts of long bones.

(8) By 18+ years, most organic content is gone from bones, the color has become dull grey, exfoliation increases rapidly, and many cracks and splinters occur.

(9) By 30-35 years, color is still dull grey, cracking and splintering are severe, and surfaces are badly weathered. By 20 years, bones have already become too deteriorated to fossilize well.

R.O. Peterson's weathering sequence for bones on Isle Royale can be summarized as follows (R.O. Peterson 1977, 1980 pers. comm.):

0 - 1 year: Presence of hair, rumen contents, hide, and soft tissue on bones. Abundance of these materials usually indicates death the previous winter.

2 years: Most or all dried soft tissue gone from bones. Some epiphyseal soft tissue may survive until about the 18th month after death.

2 - 5 years: Bones bleached white, much lighter in weight. There may be very slight peeling and cracking longitudinally.

5 - 10 years: Bones begin to turn grey. Exfoliation increases. Lichens may begin to grow on surfaces.

Over 10 years: A great deal of surface exfoliation occurs. Bones are dingy grey for the most part (Figure 45).

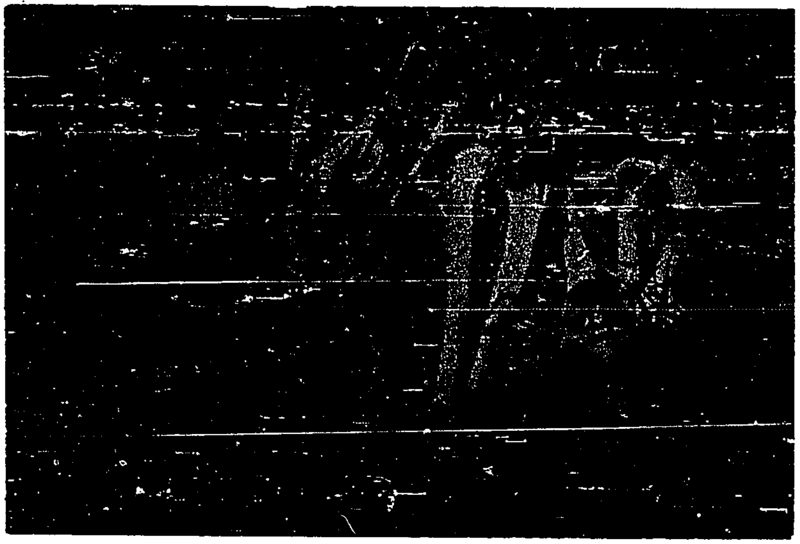


Figure 44. Well cleaned Moose bones (entire assemblage) at site number 9 (79-27), four months after death.

Figure 45. Advanced weathering deterioration of fragment of Moose mandible, collected in Ft. Smith, Northwest Territories. Weathered over 10 years.

Many of the moose bones found today on Isle Royale's ground surfaces (and almost all the bones that are findable) were originally mapped at the time of the animal's death or devouring by wolves. Thus, bones from carcasses dated over 20 years old and younger down to very recent times are available as documented reference materials with which one can compare weathered specimens, in order to estimate original date of death and length of weathering period for the specimens.

The sequence worked out by Peterson appears to fit the bone deterioration patterns observed in Wood Buffalo National Park, Canada, which is also a subhumid-subarctic area. Nearly all of the Wood Buffalo study region is comprised of poorly-drained flatlands, while most of the Isle Royale study region is excessively well-drained sloping uplands. However, most moose bones are deposited in lowly, poorly-drained areas of Isle Royale. Thus, it is probable that potential bone deterioration (for the most part) in Wood Buffalo is very similar to deterioration on Isle Royale. In both study areas the addition of moisture to bones aging _ex vivo_ retards their degeneration. In both study regions over the year there is an extended cold period when air temperatures do not exceed freezing. Also, during this six month period, bones lying on or within ground surfaces are usually covered with snow, and so are not exposed to drying and warming caused by direct sunlight (which is quite reduced, compared to summer months).

In dry and thinly vegetated uplands of Isle Royale or Wood Buffalo Park it is occasionally possible for a cross-country explorer to find cast antler, much of which is decaying. Aging antlers, unlike weathering bone, do not exfoliate much, although they do develop cracks and a grey color from weathering. Oftentimes, the downside of cast antler (or the part in contact with ground or groundcover) is stained a rich rusty brown color. When cast antler decays on vegetated ground surfaces, the palmate portion decomposes first, becoming very friable and crumbly. Main beams survive longest, perhaps several decades. I have found a few fragments of very old cast moose antlers on the dry grasslands of Lake One in Wood Buffalo National Park; these grasslands are in places covered with dried out, long dead willow stems and branches, perhaps the remains of a bush vegetation ringing ponds and marshes that have since shrunken or dried up altogether. Such wet ground may have been much better moose habitat than the present-day large open prairie ringed by densely-wooded sand-dunes and thick forests. Judging from their advanced state of deterioration, the antlers could conceivably have been cast several decades ago. They are light grey in color, with fibrous and rough surfaces. Above-ground weathering usually roughens the surface of bone materials, while below-ground or underwater weathering rounds or smooths surfaces and edges. All antler pieces are of dense tissue from interiors of main beams, and all are still quite hard and solid.

MISCELLANEOUS OBSERVATIONS: ACID ETCHING, LEACHING AND DISSOLUTION, SLOW BURIAL IN MUD, TRAMPLING BURIAL, AND EXTREME DRYING STRESSES

Processes of stabilization and preservation may interact in complex ways to produce unexpected outcomes. For example, bones that would not normally be expected to survive long, such as those lying atop well-drained, sunny, open-ground sediments, may be swept away by unusual floods or may be carried off by foraging animals, later to be dropped in streams or atop ice that eventually melts to become a stream, so that the bones have been redeposited within a protective environment (such as underwater mucks), while all other bones from the same individual's skeleton may remain in place and rot. Bones that are on their way towards weathering disintegration may be fortuitously trampled deep into temporarily water-saturated soils, there to be stabilized and preserved while other bones from the same skeleton eventually disappear.

An extremely large number of bones is deposited during the lifetime of the members of a single hunting wolf pack in the north today. In the study area which I have chosen, the Hornaday Pack (which has apparently existed in the same territory for several decades - see Soper 1945) creates about 20 sites of adult prey carcasses each winter, each site containing approximately 20-50 bones. Most of the elements left lying atop well-drained ground surfaces will probably not be preserved, and will disappear after a couple of decades. Some elements will be destroyed by carnivores, others will be partly destroyed by a number of factors, and others will remain untouched; yet all bones have poor potential as future fossils unless some unforeseen process creates a protective environment for them.

Many bones in open meadows will be partly protected by locally wet conditions and a thick overgrowth each year of sedges, grasses, and forbs, which create tangled and protective covers. Most meadows drain steadily throughout the warm season, until the greater part of ground surfaces are free of standing water; in the drier times of the year, the water may stand only in isolated depressions or between hummocks of growing plants. Bones lying in such shallow water, even in rather alkaline areas or where bedrock is limestone, gypsum, or dolomite, will eventually suffer some etching of tissue surfaces due to the action of root acids dissolved in standing water or released upon contact of the roots with the bone surface (Figure 46). Therefore, bones in sedge fens or wet meadows, especially those that are shallowly buried under humic sediments within the grassroots zone, will show a great deal of surface etching although they will survive much longer than will unburied bones lying on drier ground. In time the humic buildup in such wet areas may create a relatively thick sediment cover for the bones, and they would eventually lie below the root zone; hence, the process of root-acid etching might cease and the bones would be preserved for many centuries in their altered state.

Destructive underwater leaching and dissolution of bones can occur, especially in nearshore areas where shore plants shed leaves and may release root acids into the water. The acids dissolve the calcified matrix of bones. In some aqueous environments this kind of surface destruction is quite advanced within less than 5 years of submersion (see D. Allen 1979). The damage appears as a surface roughening due to the creation of numerous tiny circular pits occurring everywhere on the bone; these pits measure perhaps 1 mm.deep by 1 mm.diameter. Over time the pits enlarge and run together, and cause exfoliation and peeling (Figure 47). The very brittle surface bone tissue begins to splinter into small, irregularly-shaped fragments, until the entire element eventually disappears. I collected an Alces scapula lying on a small sand beach on Isle Royale; the bone had originally been lying within the nearshore waters of Lake Superior for an undetermined amount of time prior to its recovery. The element was very fragile and falling apart (Figure 47), a result of advanced dissolution in the cold lake waters which were probably slightly acidic near shore, due to the presence of much organic debris (and possibly also due to industrial acid rain).

Bones left lying in deeply shaded, thick tree-stands (Figure 48) would be continually buried by leaf-litter or needle-falls, until over time they become enclosed in humic sediments. Tree-stands exist in Wood Buffalo National Park where the soil drainage is fair to good, or in other words on slightly elevated land surfaces. These surfaces may be only a few centimeters higher in elevation than surrounding prairies or meadows. Levels of precipitation are low for the study area, yet the constant addition of organic materials to the shaded forest floor contributes to a lowering of solum pH. The forest soils are zonal, attesting to some leaching and transformations within the sediments. Hence, bones (being made up mostly of a calcified substance) are in danger of being dissolved by the mild organic acids produced in forest soils (Hunt 1972:289). There is a lot of protection for bones (against drying stresses during weathering), but also a lot of jeopardy. Shallowly-buried bones within wooded sediments would probably last several centuries; deep burial is unlikely, except on levees or in gallery forests along streams, especially in the Delta region, where flood occurs each year (ensuring a consistent incremental burial). Therefore, bones in woodlands may remain a long time near the leaching zone (the A_2 or E soil horizon), leading to a low potential for long-term preservation.

There are plenty of shallow ponds and mud wallows in some open grassland areas of Wood Buffalo National Park (Figure 23). The Lake One area and the North Hay Camp prairies were probably much wetter in the near past than they have recently become. Both study areas contain numerous depressions that are either exposed and deep mud or shallow water standing over deep mud and peat. The bones lying within the basin sediments are well-protected unless suddenly dried; a few bones of skeletal site #10 have been exposed recently in summertime, whereas in 1978 and before they probably lay in the shallow saline waters (Figures 25, 26). These bones have generally been stained a light rusty color, and have much of their surface covered with a dried algal staining as well. A 0.5 mm.thick crust of salt precipitate on bone surfaces that were in contact with mud is peeling off in sheetlike fragments. There is minor exfoliation of periosteal bone occurring, but there are no visible longitudinal drying cracks in long bones, even after complete drying. Bones from the same animal's skeleton that are lying in grass out of the bed of the dried-up saline lake are also not exfoliating, are not stained rust-colored, and for the most part are bleached a bright white on upper surfaces. Other bones from the same skeleton were lying 3 meters away within a willow thicket; these elements are not bleached, but are grey and green-stained, due to a fungal growth and lichen growth over much of their surfaces. A thin exfoliating layer is present on the uppermost surface on some of these elements. There are no longitudinal drying cracks in the long bones. Some of the elements in the willow thicket have suffered minor amounts of recent rodent-gnawing and carnivore-gnawing which has exposed lighter grey (nearly white) bone tissue below the grey periosteal tissue. A few vertebrae, ribs, phalanges, one scapula, and one metapodial of this skeleton had become buried (partially or wholly) under about 5 cm.of the lakebed mud (Figures 25, 26). These bones were stained a more uniform and darker rust color, but surfaces appeared free of algal growth or staining and of salt crusting on undersides.

The buried elements are least altered and least in jeopardy of damage due to animal gnawing, trampling, or weathering. The bones lying on the dry ground of the willow thicket were deteriorating quickly due most likely to active lichen growth and drying stresses. Bones lying in the grasses were probably recently deposited there, since upon first examination (in 1979) I noted that grass beneath each bone had been growing at one time, but had become yellowed and flattened after the bones were laid down. I suspect that wolves had found bones in the wet grass at the willow-bush/lake edge, tried to gnaw a few, also redistributed others, then abandoned them. Wolf tracks (from at least four individuals) were seen in the mud near the bone site, but they may have been several months old. A wolf den is located about 0.8 km. from the site, but was not used the year I first investigated the bone site, although it may have been used the previous year (1978). The bones lying on the grass will probably begin to exfoliate in a few more years; lichens will grow on their surfaces within 5-10 years, contributing to their disintegration.

Only the buried vertebrae and ribs, one scapula, phalanges, and one metapodial (which all lay in the lakebed in a linear scatter about 5 meters long) probably have any solid chance at all to be preserved and to become parts of the fossil record of Wood Buffalo National Park as it existed in the 20th century. Elsewhere, at Lake One, I think that only a few isolated elements found in ponds or wallows (the deeper ones whose muds have not completely dried in recent years, as many have) stand a chance of being preserved, while the numerous skeletons and bones lying atop grassland surfaces are destined to disappear after weathering over time into a mass of tiny fragments and splinters. Not all bones of single skeletons have the same likelihood of becoming enclosed in muds, even those bones lying within a tight cluster on wallow edges or atop wallow bottoms, because the insertion of bones into sediments depends on the fortuitous placement of a trampling animal's foot squarely onto the bone, to force the element downwards rather than to slip off and leave the bone still atop the sediments. At skeletal site #11, an adult female bison whose bones lay in a scatter about 20 x 6 meters in area atop grass, 5 meters from the edge of a shallow lake in an open prairie, one scapula was buried with only its vertebral border standing up out of the mud (about 7.5-12 cm. of it visible); the left femur was also buried proximal end downward, and only the distal epiphysis stuck up out of the ground. All other visible bones, including vertebrae, ribs, and long bones, lay horizontally on grass or drying mud surfaces. One horn core of the complete skull was embedded in 1 cm. of mud.

Intensive or routine trampling is common at certain locales, especially in heavy use spots such as the many wallows of the Lake One area, or in traditional river crossings. In these areas, many bones get trampled into saturated muds and many articulated carcass parts may even be buried as units. In 1979 at one well-used bison river crossing on Sweetgrass Creek, I found bones of an adult female bison, possibly poached there by humans a year before. Some of the bones were lying on and in very hard, dried soils that had earlier in the summer been soft muds. The pelvis remained articulated to all lumbar and six thoracic vertebrae. One tibia distal end was buried by 20 cm. of soil, undoubtedly due to trampling by bison moving over them. Bison use of the crossing area had left the ground surface completely bare of vegetation and very rough along the stream bank in an area about 25 meters wide, extending 50 meters from the stream edge back to a grassy fringe at the edge of a willow thicket. Also found were the right scapula (undamaged by gnawing or trampling), the right humerus lacking its greater tuberosities (due to gnawing), the left humerus (also lacking greater tuberosity) articulated to the radius/ulna, the left scapula (undamaged), the right radius/ulna (undamaged), the entire articulated left rear leg(with minor gnaw damage on the femur), and scattered ribs (medial segments). The skull and mandibles were not found. Quite possibly some ribs, bone fragments, phalanges, or other bone elements had also been forced downwards into the ground and were thus not found.

Bones lying on dry, well-drained, and sunny land surfaces suffer the most severe eventual disintegration. On Isle Royale, some bare ridge tops are excessively well-drained, and when subject to bright midsummer, midday sunshine may reach temperatures near 60°C (see Chapter 7). Any bones lying on such surfaces would be quickly heated and dried out, a process which usually creates deep longitudinal drying cracks in long bones. Since most nights on the island are much cooler than are days, some dew may form on bone surfaces and ground surfaces around the bone. If the bone absorbs any moisture during the night (or during periods of rain or melting of snow) then the sudden and severe drying stresses of hot, sunny days would cause much more cracking and splitting than if the bone remained perfectly dry.

Most moose are killed in lowlying areas on the island, however, and so their bones are primarily deposited in shaded and/or poorly drained spots. A few elements each year may be carried into drier uplands, and a few carcasses each year may be situated on well-drained slopes. During my field work on Isle Royale I ventured off trails and cross country a few times; the only examples I encountered of bone specimens in very warm and dry areas were two long bones of a moose calf. The bones had passed slightly beyond the bright white bleached stage, and were becoming grey. In addition, the shaft of one had fragmented longitudinally, possibly from being stepped on or moved about by an animal. The bones had not weathered very long (estimated longer than two years and less than four years), and so exfoliation was not evident. No lichens, mosses, or fungi were growing on bone surfaces. The bones (a radius and an ulna) were found in an open and nearly bare patch of ground on a south-facing ridge top exposed to unimpeded sunlight.

In Wood Buffalo National Park, bones that lie in dry grasslands such as characterize the Lake One area or the zone of ground between the swampy north shore of Lake Claire and the tree-line (Figure 29), are also subject to high summer midday temperatures, discontinuous drying (although rewetting and re-drying are probably much less frequent than in lowlying areas on Isle Royale), and long periods of bright sunshine.

Bison bones are plentiful in this area, most of them having been deposited in 1974 during a spring flood which killed thousands of animals. These bones are weathering steadily, and are too far from the present shoreline of Lake Claire to be buried by yearly overbank deposition. Thus, these bones will most likely not survive much beyond another decade.

CASE STUDY: SLOW BURIAL OF A HORSE SKELETON

In the summer of 1976 the skeleton of a horse (Equus caballus) was observed in a shallow gully in a floodplain adjacent to the South Fork of the Shenandoah River, Warren County, Virginia. The property at that time belonged to the Thunderbird Museum and Archeological Park, in Limeton, Virginia, and was since used as a horse pasture. The skeleton was of a full grown and very old draught horse, and lay in shallow, slow-moving water draining from nearby precipitous limestone uplands 25 meters east towards the river 35 meters downslope, along a very mild gradient on the floodplain. The skeleton was in anatomical order, head downslope, lying on its left side, and all hide was gone. Some soft tissue adhered to a few bones, although it had been chemically altered to a white, spongey substance (adipocere). No bones were observed to be broken or damaged, except ribs and vertebrae which had suffered erosion of edges. At the time of the first observation the skull, mandibles, and one femur were taken for study to the archeology laboratory at Catholic University.

In March, 1978, I returned to the site after snow had begun to melt, and found the remaining skeleton under shallow, slow-moving water, still in anatomical position. Some slumpage of the gully walls had occurred. The gully was over 1 meter deep, 1 to 2 meters across, 4 to 5 meters long. Some ribs and vertebrae had become covered with mud; some smaller bones had probably been completely covered. Most bones were under 15-20 cm. of water and were covered with a film of mud, but it was possible to find elements by fishing around blindly in the water with a hand, since so little movement of elements had occured. Many elements were collected; not collected were caudal vertebrae, lumbar vertebrae, many thoracic and cervical vertebrae, left rear limb bones, left fore-limb bones, some right rear and fore-limb bones, and phalanges. These bones will be periodically observed during the next few years.

All collected bones exhibit irregular staining both from algae and minerals in soils and water. It was also found that bones of a juvenile horse were mixed with the older animal's bones in the gully collection. This younger horse's bones were stained a much darker color, almost black, and probably had lain in the mud of the gully much longer than the older animal's bones. Upon drying, long bones of the older animal, notably tibia and metapodials, exhibited longitudinal cracks.

Rodent gnaw damage was seen on the shafts of some bones, indicating that they were dry at certain times while lying in the gully, although in two years they had been observed only underwater. The older horse's carcass had been dumped in the gully about two years before their 1976 discovery, when the animal had died from old age or related illness. It is not known how long the younger horse's bones lay in the gully.

One splint bone from the older animal had numerous tiny circular pits (about 1mm.diameter, 1mm.deep) in its surface, probably the result of post-mortem acid etching. One tibia had shallower pitting on its surface. The gully contains numerous limestone blocks which had been rounded by solution; due to the shape of the gully, which is a washout, the blocks could not have been transported out of the depression unless further erosion enlarged the gully downslope by incising the floodplain soils. The soils consist of a 25-30 cm. deep plow zone over a silty B horizon, which is up to 3 meters deep or deeper.

The points which are to be made from this imperfectly observed phenomenon are these:

(1) The water cover protected these bones from severe damage, such as gnawing or trampling by animals, or drying and heat stresses during dry seasons, but may have leached organic content from them, thereby increasing their brittleness. Many long bones were still greasy at epiphyseal ends. One cannon bone was soaked in water in the lab, then broken by a blow from a 2¼ kg. quartzite hammerstone; the breakage was spiral and oblique, and the fracture edges are smooth, which is characteristic of fresh bone breakage under dynamic loading. Therefore, even though the bones had aged two years post-mortem, their condition was very similar to that of bones which are aged only a few weeks out of water.

(2) Acid etching, staining (from chemicals in the soil), and erosion do not appear on each bone or in uniform ways. There is great variability within a small environmental area in the conditions of morphological change to bone, but this should not be over-emphasized since only single bones show unusual marks or changes, whereas the greater part of the assemblage is similar in all respects.

(3) Burial of the bones in mud moved a few of them out of anatomical position. Especially affected were ribs and vertebrae, which lack the bulk and weight of most other elements. Upon complete burial, which probably would have taken over five years if sedimentation rates remained constant, the skeleton would still have been close to full articulation. However, if the gully had begun to cut headwards or had extended downslope towards the river, it is probable that many elements would have moved several centimeters out of order. Some bones may even have been washed out of the depression during heavy floods

resulting from rain washing down from the nearby uplands. About 5 cm. of silt a year are deposited on the floodplain near the river, although deposition at the gully is negligible. Thus, all burial sediments have to derive from slope wash. The skeleton would be buried in silts and clays, with some eroded limestone blocks contained within the sediments.

Because I have removed some elements from the skeleton, it may be interesting to note the final disposition of bones after final burial; it might appear that the horse was butchered <u>before</u> burial, rather than that its cleaned bones were disturbed.

Table 9-1

Flow chart indicating observed changes undergone in amount of remaining soft tissue and degree of disarticulation for ungulate body parts deposited in different seasons:

WINTER SPRING SUMMER FALL WINTER SPRING SUMMER

Fresh, fully
fleshed carcass.

Mostly cleaned.
Some pink-stained
soft tissue or
Periosteum dried
very hard. No
articulated units,
except vertebrae
in groups of 2-3.

Some hide and
ligament survive.
Cartilage and
some periosteum
remain. Legs
articulated,
vertebrae
articulated in
units.

Anatomical order.
legs articulated,
vertebrae in
articulated units.
Some hide left.
Bones greasy.

--

May clean faster than
winter deaths due to
more insect activity.

If lying on well-drained
ground, grass and earth
stained dark and oily. Most
hair fallen out, viscera gone.
Flesh dried hard, most muscle
gone. Leg bones coming apart,
ribs disarticulated. Vertebrae
in groups of less than 10.

Greasy bones. Hair
and hide gone.
Bones bleaching.
No articulation.

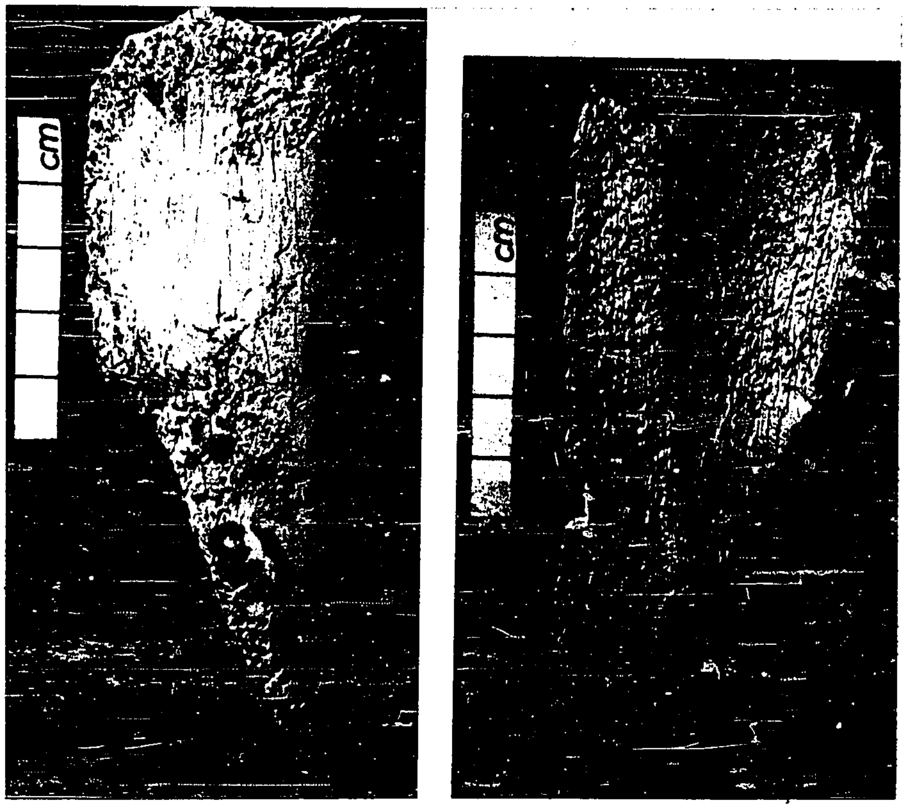


Figure 46. Acid etching.

TOP: Fractured Bison humerus (?) fragment showing root acid etching and rodent gnaw marks on edges. Collected in wet grassland on Bison trail near Lake One, 1979.
BOTTOM: Apparent advanced acid etching possibly caused by shallow standing water on grassland. Specimen is <u>Bison</u> femur collected from Lindenmeier site, Colorado, by F. Roberts (Smithsonian Institution).

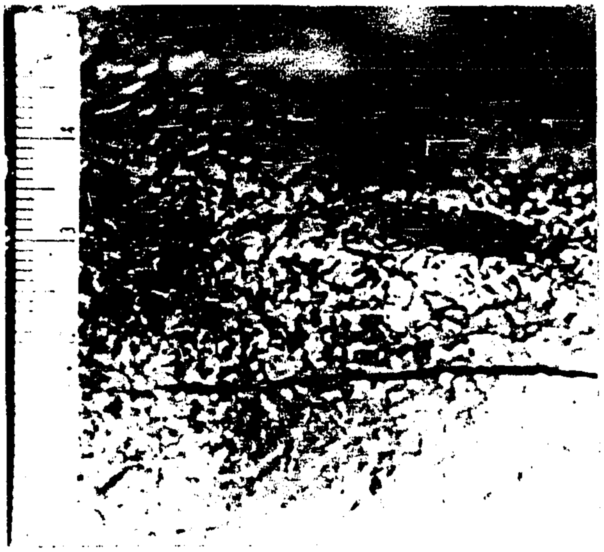


Figure 47. Extremely etched and eroded portion of Moose scapula collected from shallow water at shore of Lake Superior, Isle Royale, summer, 1979.

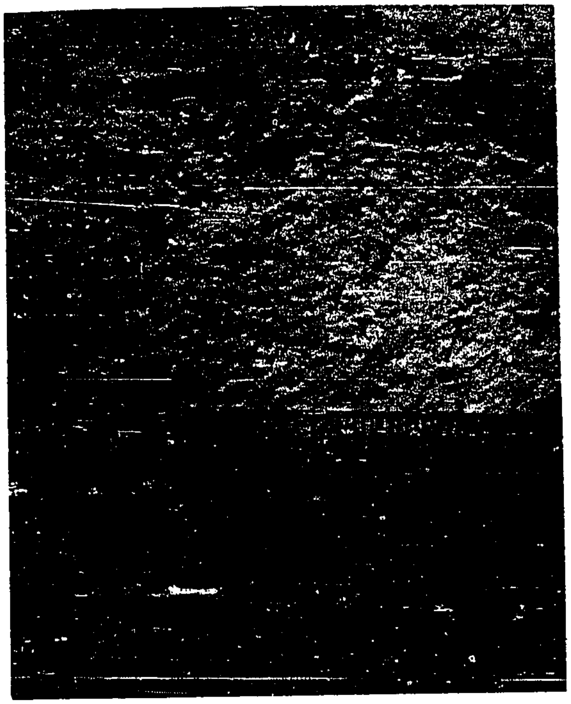
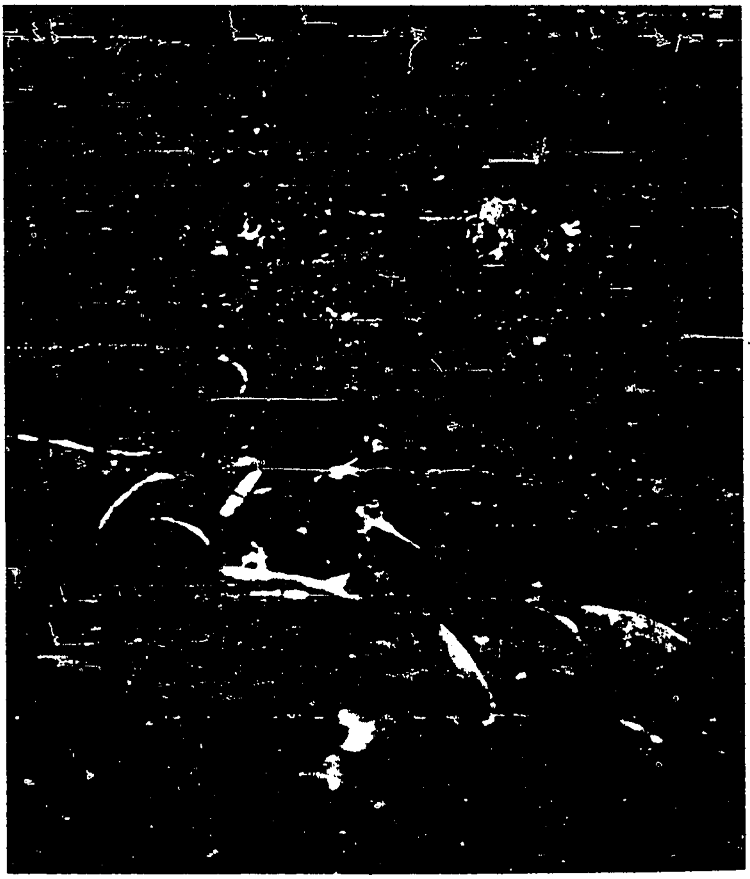


Figure 48. Bones of adult female Bison, skeletal site number 22, lying in shaded aspen poplar woods.



X. Experiments in Bone Breakage, Meat Removal, and Carcass Dismemberment; and Comparisons of Experimental Results with Observed and Expected Natural Modifications of Bones

EXPERIMENTS IN BONE AND JOINT MODIFICATION: BACKGROUND

I experimentally butchered some wild and domesticated animals, and broke a large number of long bones for marrow extraction, in order to observe very basic attributes of deliberately smashed long bones and deliberately cut or defleshed bones. No attempt was made to be exhaustive in analyzing any one task, such as breaking marrow bones under carefully monitored stress levels applied to carefully arranged spots on the bones. Such experiments are currently being performed or planned by other researchers (D. Crader 1979 pers. comm.; A. Behrensmeyer 1980 pers. comm.; K. Davis 1980 pers. comm.). Most of my results are therefore impressionistic or narrative in form, and will be presented as generalizations.

Most bone specimens experimentally broken by deliberate impact were Bos femora, although a few tibiae, humeri, and metapodials were also broken. In no cases were long bones roasted or heated before being broken. The bones were identical to those described in Chapter 4, captive animal feeding experiments. I also smashed a few Bison, Alces, and Equus femora and tibiae; in addition, I butchered six whole legs from adult horses (quarter horses and thoroughbreds), four whole legs of adult cows, and several whole legs of calves and colts, using unmodified stone flakes and prepared bifaces, one of which was hafted in a modified Bos rib segment. I have also skinned or removed meat from several dozen skulls, single bones, or partial legs of adult cows, bison, moose, horses, deer, and elk, using stone tools (mostly unretouched flakes) and (rarely) steel knives.

Fracturing of Long Bones for Marrow Extraction

The marrow in bovid and cervid bones occurs as a single body of thick, greasy material filling up the medullary cavity of the shaft. The substance at room temperature is usually about as hard as a stick of butter. One medium size *Bos* femur (which weighs about 3 kg.) contains approximately 200-300 grams of solid (unmelted) marrow. The marrow in long bones of rhinoceros, elephant, and equids usually contains tabecular bone material in membranes, plates, or "woven" masses attached to the inner walls of cortical bone. Short of melting it and pouring it out as a liquid, marrow cannot be extracted from horse bones completely free of boney material, as it can be extracted from cow bones. Some bones of the ungulate body contain relatively more marrow for their size and more easily extracted marrow (in terms of difficulty involved in fragmenting the element) than other bones. For example, the tibia requires a more exact placement of direct impact blows than does the femur, if the bone is to be cleanly split apart with a minimum of small fragments driven into the marrow. Some bones contain less fatty marrow than others, especially in animals that are undergoing some nutritional stress, as wintering ungulates often do. Usually the bones nearest the trunk of the body are first depleted of fat reserves from the marrow during times of food shortages. When marrow has suffered fat depletion, it appears red and runny, as opposed to its thick creamy appearance when in normal condition (see R. O. Peterson 1977). Also the marrow in subadult animals contains a greater proportion of red blood cells than does the marrow of adults, making the subadult marrow perhaps less appealing or tasty for humans. Thus, it would seem logical to expect humans to be picky about which long bones they choose for smashing, especially in certain seasons of the year, in order to get marrow out.

Spiral fracturing has been defined (usually implicitly) in several slightly different ways. The commonest usage of the word implies "green bone break." This of course explains nothing, and in fact is in error, since dry bones also break spirally. Some investigators distinguish oblique from spiral fractures: in this usage spiral fractures are those breaks which curve around the shafts of long bones and which also have break edges on the outer bone cortex on a different plane from break edges on the inner cortex (see Figure 49,b). If the inner and outer break edges are in the same plane and the break crosses the shaft diagonally, the fracture would be called oblique. However, I will not make this fine a distinction, and I will term any long bone break that curves around the shaft or is diagonal across the shaft as a spiral fracture. INTERSECTING RADIAL FRACTURES are often produced by a blow to a single point on the shaft of a long bone, and are in fact the primary component of some spiral kinds of fracture. These fractures are the result of the intersection of two or more different fracture fronts spiralling around the bone shaft (see Figure 49). Linear breaks across a shaft (at right angles to the long axis of the bone) will be called TRANSVERSE FRACTURES (Figure 50), while breaks running the length or part of the length of a long bone shaft will be termed LONGITUDINAL FRACTURES (Figure 50). There are variations and combinations of these patterns, such as step-fracturing interrupting spiral breaks (see

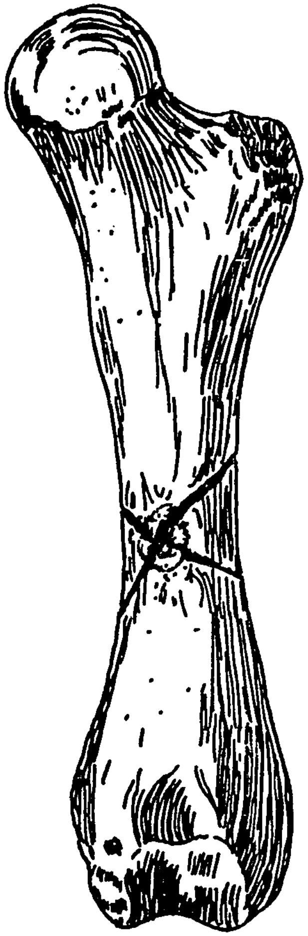
Figure 49,c,d).

When long bones are freshly exposed to air, longitudinal cracks often appear within 12 hours (Miller 1975). These cracks are dessication splits, and are parallel to the prevailing alignment of collagen and apatite crystals in the bone. Collagen and apatite, the major structural components of all bones, are usually arranged in fibers or strings running the long way on bone shafts (see Tappen 1969, 1971). Most artificially induced bone breaks that occur after drying cracks appear will be mixtures of spiral, transverse, and longitudinal fractures (Figure 49,c).

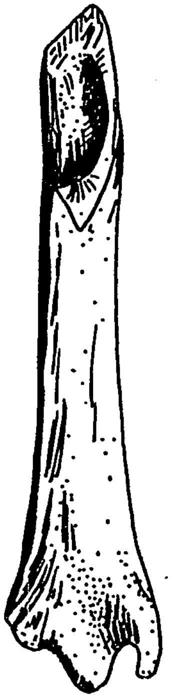
However, aged bone may still break spirally under certain conditions. Hill (1976) states that bones which are subject to torsional stress in life tend to crack and break obliquely after death. Hence, these elements will break spirally when dried or treated roughly after exposure (that is, when gnawed, trampled, dropped). This is probably due to the fact that the collagen fibers in these bones are in places arranged spirally around the shafts. In addition, aged bone that retains some of its microstructural elements, specifically collagen, when soaked in water, can sometimes be broken by impact into spiral configurations.

Figure 49. Fracture morphology.

a: Intersecting radial fractures and ring cracks. Fresh break, due to local and directed blow.
b: Spirally fractured specimen. Fresh break.
c: Mixture of spiral fractures and longitudinal fractures. Weathering or trampling damage (?).
d: Spiral fracture with jogs or right-angle offsets interrupting smooth fracture surface on upper right and left. Result of fracture cutting across small longitudinal drying cracks.



a



b

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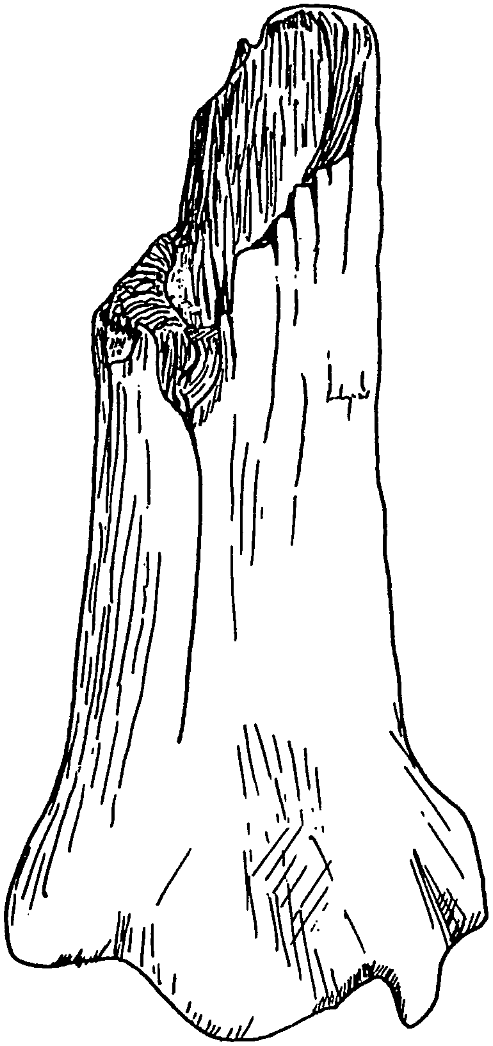


d

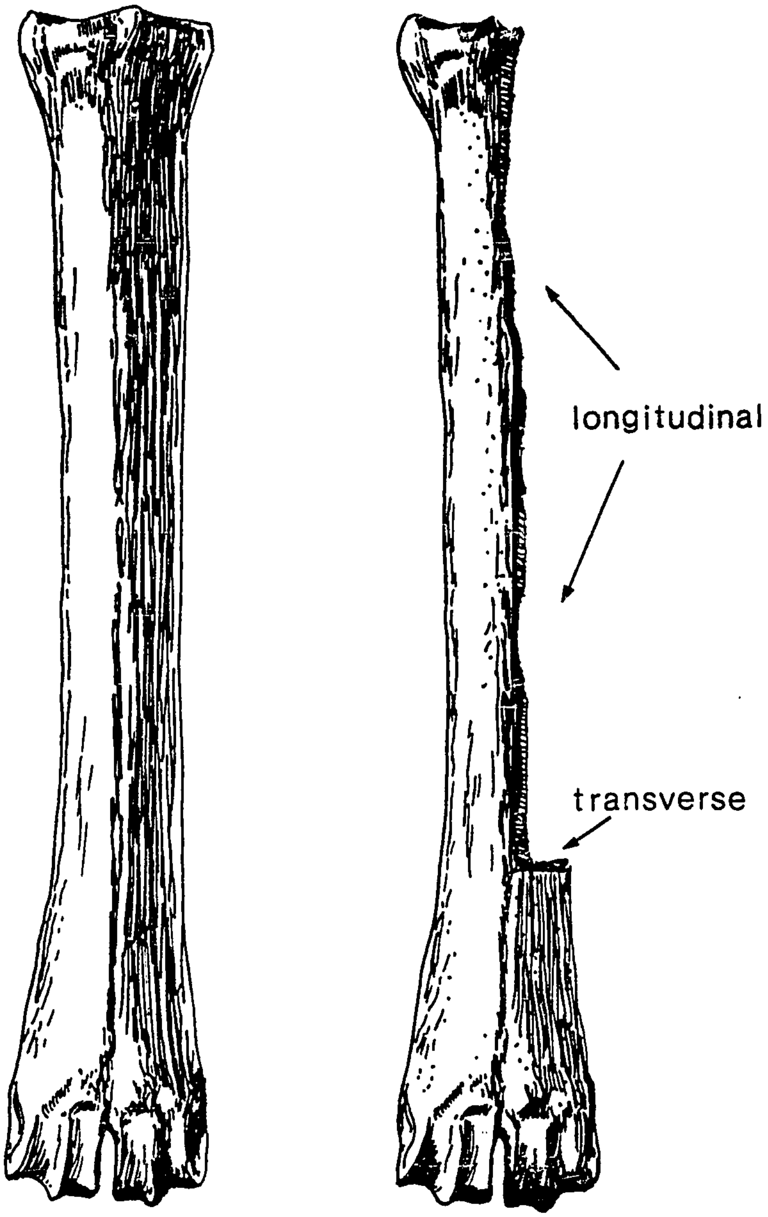


Figure 50. Longitudinal and transverse fractures.
LEFT: Unfractured ungulate metapodial.
RIGHT: Longitudinal and transverse fractures.

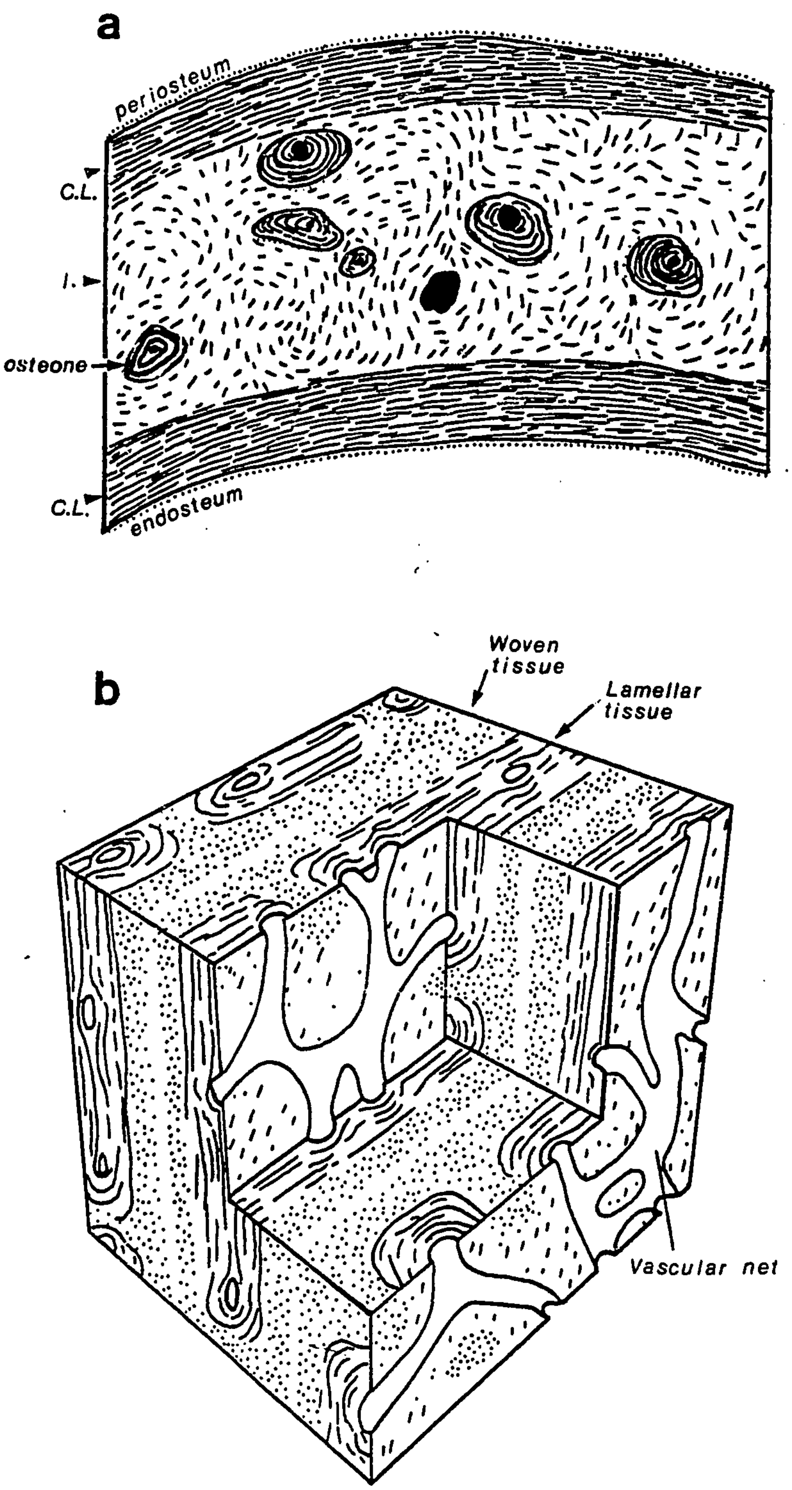


Figure 51. Bone tissue.
a: "Textbook" bone. Section through outer compacta of a long bone shaft. C.L.=Circumferential lamellar tissue. I.=Interstitial bone tissue. After Enlow (1966:94).
b: Block section of laminar bone. From Currey (in Budy 1968:110).

Bone: Natural History

Any discussion of bones must consider the subject from two perspectives: bone as a material or tissue, and bones as whole structural elements of the vertebrate body.

Bone, when examined as an engineering material, is anisotrophic: that is, its responsive properties are not identical when forces are applied to units of bone tissue in different directions (Zarek 1966; Laird and Kingsbury 1973). Also, if part of the material in bone fails under an applied force, the bone as a whole need not fail (Currey 1964). The reason for this anisotrophism is that there are several different substances making up bone tissue, and these are arranged in such a way that certain properties of each substance complement or are superseded by the properties of the other substances. Bone contains living cells imbedded within a solid matrix made up of (1) inorganic minerals in both crystalline and amorphous states, giving hardness or rigidity to the tissue; and (2) organic components, specifically fibrillous collagen and amorphous protein molecules, providing elasticity and toughness (Maj and Toajari 1937). About a third of compact bone tissue is organic material (Bloom and Fawcett 1962:158). Bone also contains liquid-filled pores (Piekarski 1977:610).

If a living bone were cut in two across the shaft, the following elements would be visible: (1) periosteum, containing living cells attached to the hard, mineralized periosteal bone by means of collagen bundles and a network of arterioles and capillaries entering the bone wall; (2) cortical bone, the denser and harder walls of the long bone, made up of parallel fibers of collagen and crystals of apatite, arranged mostly lengthwise along the inner part of the compact bone tissue. Within the cortical bone tissue is sometimes found Haversian tissue, containing a system of vascular channels that supply nutrition to the thick compact bone. The cortical bone matrix containing the Haversian systems is sometimes called interstitial bone, especially if Haversian canals are very common. Microscopically, there appears to be much more intersititial bone than other kind of tissue, and this kind of tissue may also appear to be arranged in layers (lamellae) (Bloom and Fawcett 1962:154; Hayes and Carter 1979:264) (Figure 51,a).

Long bones are hard, nearly hollow asymmetric cylinders of sorts. The interior is usually filled with marrow, a gel-like, grease-like material which stores body fat and also manufactures white blood cells. However, the long bones of some heavy-bodied quadrupeds such as horses, rhinoceroses, or elephants may contain more cancellous bone by volume than marrow (Hill 1953:19).

The main function of bones is to provide support for organs and muscles; therefore, it is not surprising that the structuring of bone materials is so well engineered. The internal (cancellous) bone, much less compact than cortical bone, is made up of hard, spongy-looking trabecular structures, or crisscross networks of tiny struts and beams arranged most thickly near the ends of the long bone cavities. This material can absorb and deflect forces applied to each bone or transmitted from bone to bone (Koch 1917). Like cortical bone, trabecular tissue is comprised of elastic collagen and more rigid apatite crystals. Both the periosteum which encloses the outer bone surfaces and the endosteum enclosing the marrow cavity surfaces are living tissues that serve biological rather than structural functions

(Piekarski 1977:608).

The collagen in compact bone is strong in tension, and the apatite is strong in compression, so that bone has an unusual combination of plastic, elastic, and brittle properties (see Evans 1957; Rooney 1969). Small, brittle apatite crystals are kept from breaking up under forces that pull apart (tension) by being closely packed with their long axes along the length of fibers of collagen (Koch 1971; Currey 1964:8). These collagen fibers, being elastic and deformable, do not transmit cracks as well as does brittle apatite. The structure also helps discourage brittle cracking, because if cracks are propagated <u>across</u> an apatite crystal or set of crystals they would tend to move in new directions (at 90° to the original direction) upon reaching the interface with another crystal. Cracks would also encounter collagen at a right angle, and much kinetic energy would be absorbed as the collagen flexed or deformed (Currey 1964).

Bones differ in chemistry and microstructure according to age, sex, health, species, and particular region of the element (Simkin and Robin 1973; Chaplin 1971; Enlow 1966; Enlow and Brown 1956, 1957, 1958). In general, it can be said of all bones that they must change their size and shape as the body grows. Healthy bones are also capable of healing and regenerating tissue. But bone does not grow simply by increasing its size; the "calcified intercellular matrix of bone is hard and incapable of interstitial growth...There must be a process of sequential adjustments in virtually all areas of the growing bone order to continuously maintain the constant shape and relationships of the bone as a whole" (Enlow 1966:101; also see Currey 1963). During growth there are tuberosities and points on each bone element that must be relocated to accomodate changing proportions and changing positions of muscles, joints, and blood vessels. Thus, bone has to remodel itself by destroying old parts and building them anew elsewhere (Currey 1963; Enlow 1966).

The remodeling of cortical bone oftentimes involves the development of secondary Haversian systems, which are canals that contain blood vessels, nerves, and lymphatic tissue, surrounded by concentric layers of bone tissue (Enlow 1963). These systems are formed by a two-stage process: in the first stage, osteoclasts cut channels through the primary cortical tissue, which is usually concentrically arranged as layers of bone; in the second stage, osteoblasts fill in the channels with newly formed bone tissue. The outer limit of each Haversian structure (called an osteone) is defined by a denser layer of bone, known as a reversal line, which "marks the boundary where osteroclastic tunneling ended and osteoblastic filling began" (Ubelaker 1978:64) (Figure 51,a).

However, compact bone tissue from the large, hollow leg bones of most modern artiodactyls is characteristically _not_ everywhere remodeled into Haversian structures (osteones), as is human bone. The compact outer tissue of _Bos_ long bones, for example, is usually composed of a well-organized, uniformly-arranged laminar or plexiform bone (Currey in Budy 1968:109; Enlow and Brown 1958:204-205; Bouchod 1974:24; Hayes and Carter 1979:264-265) (Figure 51,b). In tissues from older artiodactyls' long bones, scattered secondary osteones may form, but are relatively few in number. Currey (in Budy 1968) found that the innermost part of the compact bone may be entirely reconstructed into dense Haversian bone, although Singh _et al_ (1974) could find no osteones at all in their sample of artiodactyl bone tissues. Bouchod (1974:24) states that Haversian systems are much more abundant in the bones of older animals, and are not as large or common towards the outer part of compact bone tissue.

Plexiform bone is arranged in a uniform and orderly network of vessels and compact tissue, whereas in Haversian bone there are many canals and channels cutting through the bone matrix; hence, one possible advantage to a decreased proportion of Haversian remodeling in bone may be an increase in bone strength, specifically strength in tension (Currey 1959).

In general the long bones of carnivores may contain a greater proportion of the Haversian pattern tissue than do herbivore long bones, although osteones may indeed be entirely lacking in some specimens (Enlow and Brown 1958; Singh *et al*. 1974). The ribs of artiodactyls may be dense Haversian bone, while long bones may contain both Haversian structural patterns and plexiform or laminar patterns. The size of the animal appears to have no consistent, direct bearing on the prevailing patterns of bone tissue to be found: the compact tissue of modern *Elephas* bones is by far mostly dense Haversian tissue (Enlow and Brown 1958:198), modeled from the primary plexiform pattern, in contrast to the prevailing existence of the plexiform pattern in *Bos* long bones. The long bones of modern *Equus*, *Bos*, and *Canis* basically show layered woven-fibred and plexiform configurations on shafts, although secondary osteones may form either in dense, localized patterns, or may be scattered throughout the bone width (Smith 1960:337-338). Currey (in Budy 1968:117) hypothesizes that the remodeling of bones into Haversian systems is an adaptation to provide calcium for the rest of the body:

that is, osteoclastic channeling through primary tissue releases calcium from the bone, making it available elsewhere. This releasing of calcium seems to occur most actively in the ribs and vertebrae of artiodactyls because these elements can most afford to be weakened by losing some minerals, in contrast to the long bones which are under constant heavy use by active big-boned herbivores. In *Bos*, Haversian remodeling of the femoral shaft seems to occur only on muscle insertion points, supporting the suggestion that Haversian remodeling may also be a localized *response* to mechanical stresses in bones (see Budy 1968). However, this latter hypothesis cannot explain why adult human bones are nearly all dense Haversian tissue, because humans are typically well-fed and underworked. The bones of humans and some other primates generally undergo continuous Haversian remodeling throughout life, until there is nearly complete replacement of primary, non-Haversian structure by the Haversian pattern within fine lamellar bone organization (Hall 1978:3).

At any rate, a discussion of animal bone tissue and its structural characteristics would be in serious error if based solely on anatomical and physiological research performed on only human bone tissue. When analyzing fractures on artiodactyl long bones, the bone tissue itself is most often structurally different from human bone, and therefore responds to stresses in a different way (Currey 1959). The greatest difference in response is in tensile strength of the tissue and of the entire element (Ascenzi *et al*. 1966; Currey 1959:94), although on a microscopic level there are probably also significant differences in such things as nature and direction of crack propagation due to a blow on the bone from a hammerstone.

Antler

Antlers are temporarily living bones which grow in a nearly symmetrical pair from the skull of deer, caribou, and other cervids. Antlers are in effect the fastest growing postnatal bones, achieving an often remarkable complexity of form in a very short time, with a rate of growth that may exceed 1 cm. a day (Goss 1963:339; Modell 1969:117). In temperate regions antlers grow annually and during fixed seasons, according to species. During antler formation, ordinary bone materials (fibrous collagen and crystalline apatite) grow from permanent bases (pedicles) on the front of the skull, sharing the rest of the body's blood through vessels within the new bone tissue and vessels in the skin (the velvet) covering the new bone (Bouchod 1974a:22). At this time antlers are as much alive as any other bone in the animal's body.

The early internal structure is trabecular, so that antlers at first are fragile. The soft hairy skin covering them during growth is tactilely and thermally sensitive. But within a few months, when the limit of growth is reached, the velvet dies, is rubbed off in a few days, and a much hardened compact bone is exposed. At this time antlers can no longer be considered living structures, and eventually they are cleanly amputated by natural body process (see Goss 1963). "Live" antlers may be of no use for the manufacture of artifacts, since cortical bone is lacking, but dead or cast antlers are potentially of great use for durable tools or craftwork (Bouchod 1974).

Before being cast off, mature antlers are rubbed and burnished by the animal, who (if male) uses them in ritualized fighting and displays during the rutting season. Polished antler is extremely dense and hard; it has been estimated that each year probably no less than 95% of all caribou and moose antlers in North America are cast without having suffered major breakage (Henshaw 1971:469); however, in one week on Isle Royale Murie (1934:23-24) saw four moose bulls each with one antler broken off a few inches above the base, and another bull with tips broken off the tines on each antler. The breaks resulted most likely from rutting battles with other bulls. However, the condition of these moose may have been exceptionally poor, due to overcrowding and nutritional stress, a result of a lack of predators at the time.

Ivory

Like bone and antler, ivory is a hard material that tends to break in a conchoidal manner when impacted (if it is fresh). "Ivory" may refer to calcified tissues from many different animal species such as narwhal, walrus, hippopotomas, or wild boar; in this discussion, the word refers only to the two continuously-growing maxillary lateral incisors of Loxodonta or Elephas (African and Asian elephants, respectively).

These tusks grow from persistent pulps at their bases; a thin layer of hard and inelastic enamel covers the newly-erupted tusks, but it is soon abraded and removed by continuous use (Brown and Moule 1977a: 14). The whole tusk is covered by a relatively thin layer of cellular cementum, a soft, calcified cement which keeps the tusk attached to its bony socket in the skull. The cementum is incrementally deposited around the tusk roots during continuous growth (Brown and Moule 1977b:57). When the animal is alive, the cementum contains living cells within lacunae (spider-shaped cavities) which are arranged in parallel rows. Below the layer of cementum is dentin; radiating from the central pulp cavity outward to the external surface of the tusk are dentinal tubules, which are microscopic in size (about 250,000 per mm^2 of surface) (Brown and Moule 1977a:15; 1977b:51). These tubules contain protoplasm derived from the living cells which line the pulp cavity; the matrix supporting the tubules contains extremely fine fibers of collagen oriented in two directions (when a tusk is viewed in cross section) but running unidirectionally when viewed in longitudinal section. That is, the collagen runs from base to tip, but is complexly arranged in the dentin of the tusk.

"Although the external morphology of mammoth and mastodom tusks differ from the elephant, no apparent structural differences are demonstrable between the ivory from recent and from fossil elephant" (Brown and Moule 1977a:17).

Dead Bone

It is important to remember that because bone is a living tissue many of its constituents undergo complex chemical changes during the process of fossilization (Von Endt 1979:96). Upon death, the water content of bone normally decreases as do the colloidal constituents of tissues within boney elements (Gurdjian *et al*. 1970). The organic constituents of bone may undergo bacterial decomposition in aerated or unfrozen or undessicated deposits, and may be dissolved away by acids deriving from soils and vegetation (Chaplin 1971). Fats may rapidly decompose through autolysis. After a time the inorganic mineral apatite may recrystallize in bones, and the new crystal may subsequently contain secondary carbonates, which are derived from ground water or elsewhere in the environment (Hassan *et al*. 1977). This often adds weight to the bone (Oakley 1963:26). The bone's content of collagen decreases over time, although some of this fibrous protein may resist decay for millenia (Chaplin 1971). In acid soils the collagen in bone may be preserved while the minerals are dissolved. In alkaline soils, calcite may replace some collagen and coat inner bone cavities (Hassan and Ortner 1977). Acids produced by plant roots may etch and discolor the bone's surfaces (Figure 46). As organic matter is lost, bones may become much more brittle and susceptible to thermal fragmentation and deformation or destruction due to the weight of overlying deposits.

Possible Factors in Bone Tissue Affecting Fracturing

There are several possible mechanisms of fracture in cortical bone. One mechanism may be termed ductile; in this kind of fracture osteones and fibers separate from one another as the interfibrillar cementing substance fails, after the fibers have reached their elastic deformational limits (Piekarski 1977:616). The elastic limits would be defined as the limits of a material to return to its original dimensions and shape when external forces producing distortion are removed (see Koch 1917). The materials in bone tissue being deformed are collagen and apatite, the collagen in long fibers and the apatite in long chains of crystals adhering closely to the fibers. Because bone material is deformable up to a point, impact forces or tension forces required to break it are greater than they would be were bone material perfectly brittle.

In addition to breaking in a ductile way when an external force is applied, bone may also break in a similar manner upon drying out. The structural units of bone are usually oriented in preferred directions.

In long bone tissues, the Haversian canals or cementing zones between osteones may be arranged along the long axis of the element, and weathering cracks may develop along these oriented features, separating osteones from other osteones, or collagen fiber bundles from other fiber bundles, rather than breaking apart each bundle or osteone (Tappen 1971; Evans and Band 1966; Maj and Toajari 1937).

Another kind of fracture mechanism is brittle fracturing. This kind of material failure usually occurs at higher strain rates, where a crack runs indescriminantly across microconstituents in a "quasi-cleavage manner" (Piekarski 1977:616). In other words, the fracture cuts through and across fibers and crystals, and does not merely separate them or go around them (Figure 52).

The amount of plastic deformation in tension (Figure 53) is probably related to the microstructure of bone tissue -- that is, the lamellar, osteonic, or unorganized ("woven") nature of tissue present in bones (Hayes and Carter 1979:264-265; Simkin and Robin 1973:37). Young bones can absorb more energy from tension or impact (due to a higher proportion of lamellar tissue [Evans and Bang 1966]), and may produce more of the ductile kinds of fracture. Much fast-growing bone tissue may also be of a woven nature: its collagen and apatite lie randomly in an amorphous matrix, and show no greater or lesser strengths in any one direction (Currey 1964:8-9). Young bone also contains many spaces and pores that are liquid-filled or filled with unmineralized tissue (Figure 54) (Evans and Bang 1966). Fracture surfaces in young bone might show large areas of "pulled-out" osteones, the results of energy-absorption during impact (Piekarski 1977:618). Temperature also affects the ability of bone tissue to absorb energy, the peak probably being reached at 0°C

(Bonfield and Li 1966). Dynamic loading of bones generally produces brittle failures, where "cleaved" fracture surfaces are seen (the fracture cutting through osteones and collagen/apatite fibers) (Saha and Hayes 1976). High-speed blows require less energy to break visco-elastic (flowable-deformable) materials such as bone than do low-speed loading, possibly because less kinetic energy from the higher-speed impact goes into deforming the tissue before it fails (Alexander 1968: 122). On the other hand, under a very short duration of force application, less water vapor or fracture debris can enter the propagating crack and penetrate to the immediate crack zone (the "reaction zone"), adding energy to keep the crack moving ahead (Lawn and Marshall 1979:70,78).

The dissemination of force in loaded bone tissues is similar in dry and fresh bone (see Gurdjian et al. 1970), but dry bone cannot deform as much under tension, hence tends to break more easily (that is, with less force required) in a brittle manner.

A great deal of research has been performed on the strength properties of bone tissues, yet it is still "not at present possible to relate these properties of bone as a tissue to the failure of bone as a structure" (Hayes and Wright 1977:1173; see Hayes and Carter 1979: 284-298). However, because generalized mechanical models of rock fracturing can be usefully applied (for example, see Hayden 1979), even though all rocks are not identical, it seems possible that general models of bone fracturing should also be usefully applicable, even though all bones are not identical. Such a general model of fracture mechanics is presented below.

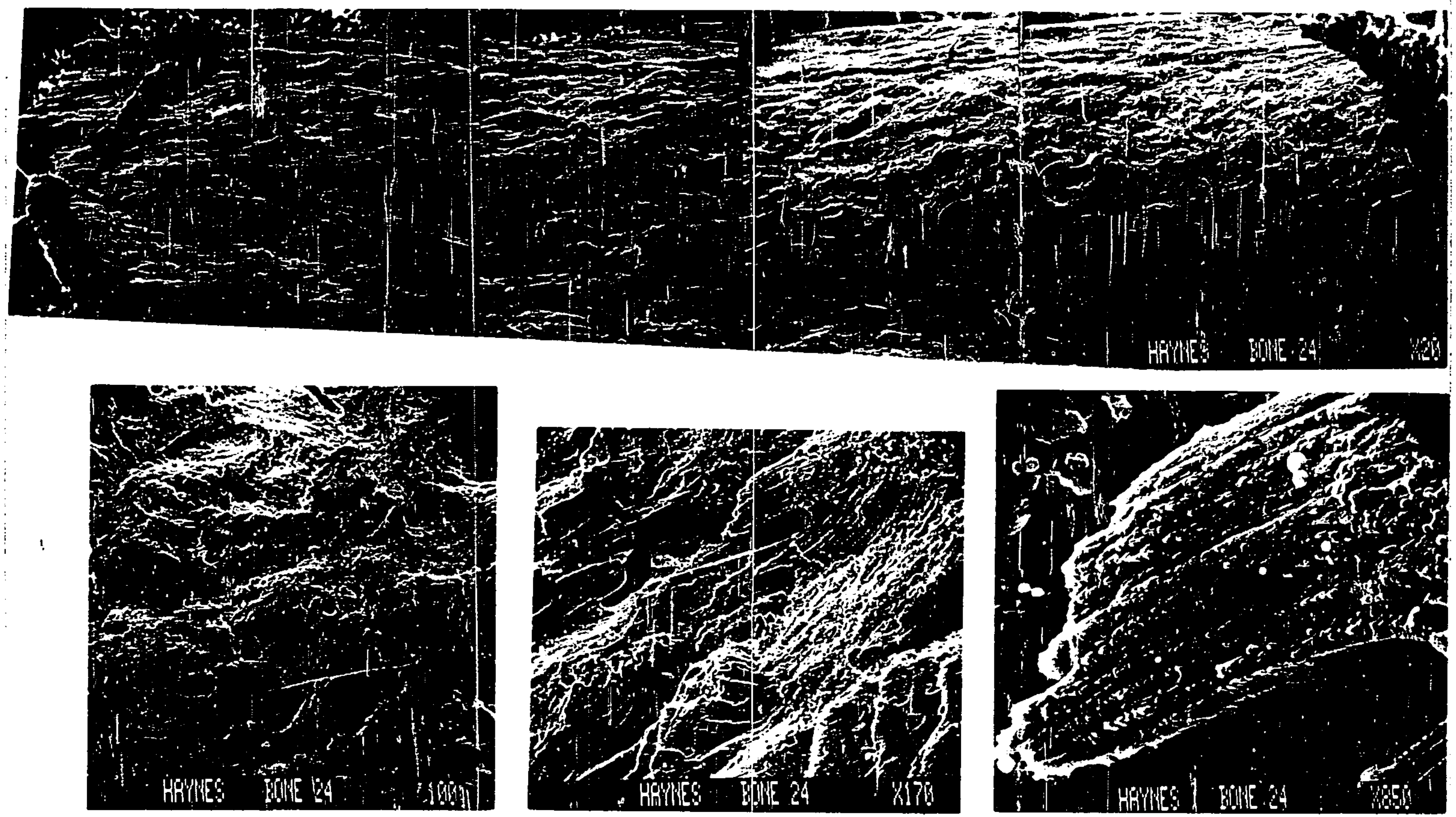


Figure 52. Brittle failure (impact fracturing).
TOP: SEM photograph of fracture surface of a flake removed by percussion from <u>Bos</u> femur shaft.
BOTTOM LEFT: Close-up of rough fracture surface.
BOTTOM CENTER: Enlargement of part of above photograph.
BOTTOM RIGHT: Extreme enlargement of brittle-failure fracture (note cleaved structural elements).

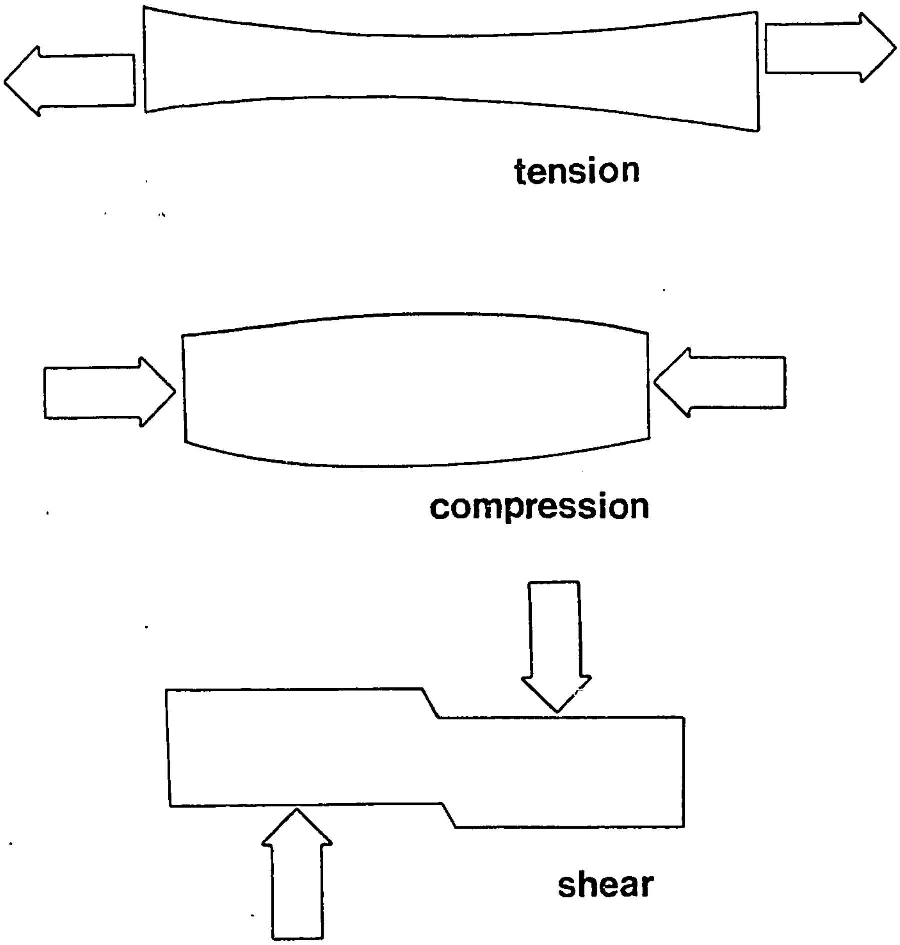
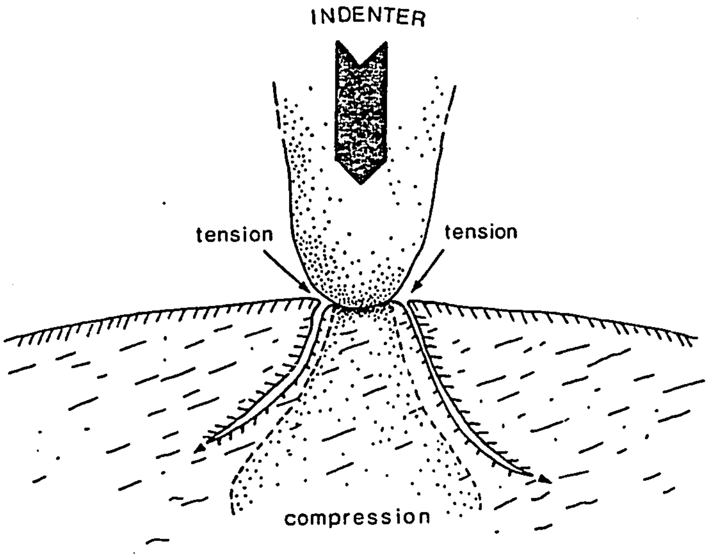


Figure 53. Stresses and bone failure.
TOP: Tension, compression, and shear.
BOTTOM: Impact fracturing.



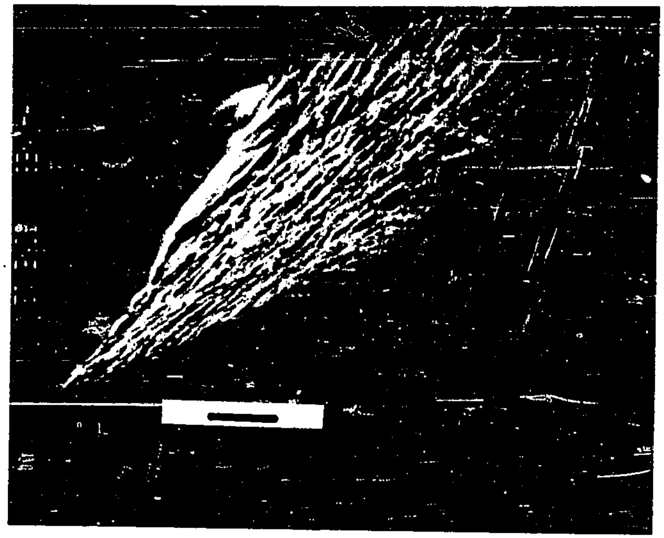


Figure 54. Section of bone from compacta of subadult Moose long bone. Note many spaces between calcified tissue on right (outer cortex) surface. Scale bar = 375 microns.

Fracture Mechanics

As mentioned above, bone is a composite or polyphasic material, a solid containing several substances mixed together but retaining some separate properties of each phase (Alexander 1968:117-118; Currey 1964). Many discussions of bone fracturing consider bones to behave much as a brittle solid (see Bonnichsen 1979 and Rooney 1969:106), but the materials making up bone tissue are also capable of some other kinds of responses to forces. Bone is somewhat elastic and plastic, and it may yield or deform before fracturing when forces are applied to it. A brittle material would simply break abruptly without "yielding", or without deforming up to a point that initial dimensions can be re-assumed after the force is removed.

There are several important variables to consider when examining the properties of bone responding to applied forces (otherwise known as loading): these would include the rate of loading (such as static loading, where there is constant contact between bone and force applicator; or impact loading, where there is a dynamic, moving applicator of force not previously in contact with the bone); direction of load (such as perpendicular to bone surface or tangential to it); and state of loaded surface (smooth or rough). Lawn and Marshall (1979) discuss these variables in regard to stone fracturing. My discussion follows their terminology and modeling.

Changes in each of these variables have unique effects on bone fracturing. For example, it was mentioned earlier that high speed blows may require less energy to break visco-elastic materials than do lower speed blows (Alexander 1968:122).

When bone is loaded by an external "indenter" or hammer, the load appears to be compressive at the point of impact, but shear and tension components are also present near or within the contact area (Figure 53, bottom).

Plastic deformation as a viscous flow may be activated by the shear component, while compression may cause compaction and permanent deformations. However, the tensile component may result in failure (fracture), just as it invariably does in brittle solids (see Rooney 1969; Currey 1963; Lawn and Marshall 1979), especially on the convex side of the bending tissue (Rooney 1969:108).

It has been theorized that fractures or cracks which lead eventually to fracture initiate from micro-flaws within the loaded material. These flaws may be present before loading, and may simply be pores, structural weak zones such as cement lines or interiors of Haversian canals, or tiny damaged areas. These flaws are often called Griffith cracks, after the original theoretician who described their possible importance (Griffith 1920). In Griffith's theory, once an impactor contacts the surface of a brittle solid, a dominant flaw located in a region where tensile forces are great will develop and propagate as a crack. In isotrophic materials (that is, materials with no preferred orientation of structural components) the crack will propagate closely perpendicular to the greatest tensile stresses (Lawn and Marshall 1979:66). Bone is anisotrophic; cracks initiated in bone may show a tendency towards "preferred cleavage," being continually held up from simple straight-line propagation by seeking available paths of least resistance through or around fibers, liquid-filled pores, or lacunae. Therefore, there is a mixture of stress control and cleavage control on the nature and direction of fracture propagation.

Lawn and Marshall (1979:68) describe the dynamics of impact fracturing using a blunt indenter thus:

> Directly below the indenter, in a tear-drop [shaped] region, all stresses are compressive...On the free surface of the specimen outside the contact circle the stresses become strongly tensile.

In normal loading with a blunt instrument (following Lawn and Marshall's model), there are several idealized, isolable stages in the development of a crack. First, the indenter subjects pre-present flaws to increasing tension outside the expanding contact circle (the circle expands because the force is being continually applied and the contact between bone and indenter also increases over time). A favorably located flaw attains its critical "Griffith configuration," and then runs at high velocity <u>around</u> the contact, forming a ring crack. It is also driven downwards by the indenter, leaving the surface area of highest tension. As the ring crack is driven ever downwards by further loading (still taking place within a tiny fraction of a second), the contact circle continues to expand, and the ring cracks may deviate outward in avoidance of the compressive zone. The ring then develops into a full Hertzian cone-shaped crack, which will probably be asymmetric in bone, due to the preferred orientation of micro-structural elements. The cone's longest dimension will usually be in the same direction as the bone's long axis. However, structural orientations in bone may vary considerably due to very local forms and morphological eccentricities (see Dempster 1967), and the longer dimension may not necessarily be the same if the point of impact is shifted even slightly on the bone.

Most indenters are not perfectly blunt or perfectly sharp.

Therefore the reaction of bone to real indenters may not directly correspond to the idealized scheme presented above. Initial contact may result in the formation of a Hertzian cone, but further loading may cause multiple ring-cracks to appear, as well as cause subsurface plastic flow and microcracking due to the presence of residual stresses. Downward-extending median cracks and sideways-extending lateral crack systems may develop, and a crush zone may form around the contact site. An interlacing network of microcracks may develop (Lawn and Marshall 1979: 76). In addition, because animal bone may be layered (that is, organized into circumferential lamellae), its lamellae or groups of lamellae may separate within the cone during the formation of lateral subsurface cracks. Even when lamellae do not separate, fresh bone (upon receiving a blow) releases small splinters or flakes which are driven into the marrow cavity, leaving their negative impression or scar on the compact bone that was impacted (Figure 55, top and left). Bonnichsen (1979:42) calls these features "negative impact" scars at the point of impact. Bonnichsen states that these scars or the fracture surface of bone also may exhibit "hackle lines" radiating outward from the point of impact. The flakes released from these scars will also sometimes show these "hackle lines" (also see Bonnichsen 1977:120-121). These lines probably correspond to what Cotterell and Kaminga (1979:110) term "lances," and Crabtree (1972:64) calls "fissures" or hackles: that is, small ridges and troughs running in the direction of fracture propagation, and "common to both pressure and percussion flaking" (Cotterell and Kamminga 1979: 110). Crabtree states (1972:64) that the presence of fissures "on the bulb of force usually indicates that a percussion technique was used."

Because long bones are in effect hollow cylinders, the fracture front initiated in the compact bone is propogated not continuously downward (as it would be were one fracturing a solid stone core by striking a proximal platform), but outward within the compact bone. The bone, if it were miraculously unrolled from its cylindrical shape and laid out as a flattened surface, would be seen to flex downward from the force of the blow, the greatest bending occuring directly below the point of impact.

The bending of course creates tensile as well as compressive stresses. The bone material fails first in tension, and several cracks may propagate as a radial pattern centering on the impact area.

If the bone is now rolled back to its real shape, that is as a cylinder, it can be seen that the radial fractures form spiral breaks around the bone's shaft (Figure 49). The radial fractures may not be perfectly symmetrical around the impact area, due to a number of factors such as preferred orientation of the bone's microstructural elements (as suggested by Dempster 1967 and Tappen 1971), presence of thicker bone tissue or differently organized tissue in various parts of the bone, or unevenness of the impactor's contact surface. The fracture fronts may actually intersect each other, or may reach internal cancellous bone near epiphyses, and may be deflected away to zones of lesser resistance (Bonnichsen 1979:43-44). The fractures might also terminate at epiphyses, and not be deflected in new directions. In many cases, fractures might cut well into epiphyses and cancellous bone tissue, although with fresh and unmineralized bone it is practically impossible to create a fracture front which entirely cuts through an epiphysis, terminating by removing part of the articulating epiphyseal end. This kind of fracture might easily occur in mineralized bone (see Bonnichsen

1979 and Morlan 1980), where even cancellous tissue has become quite brittle through the addition of inflexible inorganic materials and depletion of organic materials.

When fresh bone is impacted, the resulting shaft fragments are "almost always longer than they are wide" (Bonnichsen 1979:43), due to the preferential orientation of bone structures. Collagen, one main structural element in bone, is arranged in long fibers forming osteones or lamellar bundles, and resists breakage more so than can the cement lines between osteones and bundles, as described above. Propagating cracks might travel between separated fibers a long way before moving transversely through them or through canals separating them. In addition, because osteones branch laterally, and the borders between osteones and matrix bone are weaker zones within the bone, it is probable that propagating cracks would move transversely upon encountering branches (Evans and Bang 1966).

So far the discussion has been most concerned with long bones impacted deliberately or otherwise by a hard impactor. Yet it has also been found (see Dempster 1967; Tappen 1971; Maj and Toajari 1937; Hill 1976) that because cracks propagate more easily in certain directions (aligned parallel to lamellar borders or osteone systems), other kinds of processes may initiate and encourage spiral fracturing of bones.

Many bone surfaces reveal orientation patterns of microstructural elements arranged in spiral (actually, helical) ways. These occasional spiral patterns of osteones and collagen fibers might of course control or influence the direction of cracks occurring in weathering. During drying of bone, "tensile stresses and strains are created in the bone as a result of which the bone shrinks and separations occur along the cement lines" (Evans and Bang 1966:152) between microstructural elements.

It is not illogical to expect that bones fracturing under higher energy conditions, such as high-speed impact, might show more cleaved and broken collagen bundles or osteones than bones splitting apart under lower-energy drying stresses (P. Shipman 1980 pers. comm.), although either kind of fracture might show relatively few (or relatively many) broken osteones or collagen bundles, depending on the degree of bone remodeling (or number of Haversian structures) that has developed locally.

From time to time there are found fossil bones (of Pleistocene age or older) in which are discernible some filaments of collagen and crystals of apatite, even if partially degraded (see, for example, Doberenz and Wyckoff 1967). In these specimens it might be possible to distinguish high-energy, pre-fossilization breaks (Figure 52) from low-energy, pre-fossilization breaks (Figure 56), and also to distinguish either kind of fracture from post-fossilization breaks.

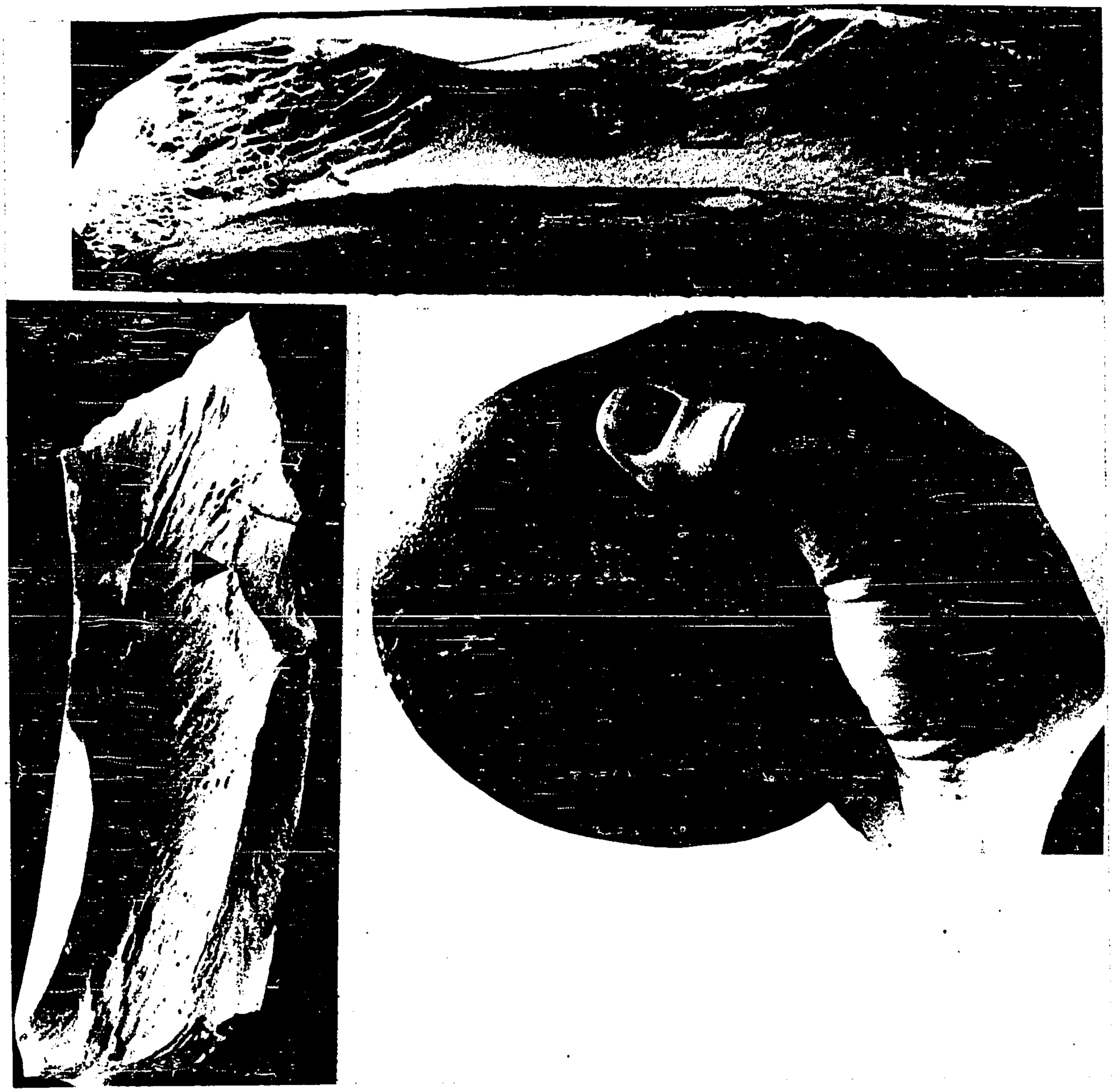


Figure 55. Impact fractures and impactor.

TOP: *Bos* femur shaft fragment. Arrow points to impact splintering notch caused by repeated applications of hammerstone.

BOTTOM RIGHT: Cobble used to fracture long bones.

BOTTOM LEFT: *Bos* femur fragment. Arrow points to impact splintering notch caused by blows from hammerstone.

SUMMARY OBSERVATIONS OF EXPERIMENTS

Most long bones were struck with an unmodified quartzite river cobble which weighs 2¼ kg. (Figure 55). The swing of the blow was begun above my head, then brought down quickly and forcefully to land on the bone specimen. Some specimens were struck with a cobble whose striking surface had been bifacially flaked, in order to examine any resulting differences in bone fracture morphology.

(1) Unless periosteal soft tissue is first removed from bone shafts, it is difficult to detect the successful radial fracturing of long bones after application of hammerstone blows. The periosteum hides the fracture separation and holds shaft fragments tightly together. Periosteal tissue also may absorb some kinetic energy from blow applications. However, even if periosteum is not scraped away, a distinctive crack can be heard when the bone shaft is fragmented. When fresh, periosteum is not difficult to remove since it is tough and can be peeled off in long pieces or long strips.

(2) Marrow is much easier to extract from Bos femora when the bone is first stripped of most periosteum, then struck a hard blow near the center of the shaft on the flattest and smoothest part. Such a blow usually creates long, pointed shaft fragments, a number of smaller splinters and fragments, and two separate epiphyseal ends (distal and proximal) with some shaft compacta attached. The best femoral break spot appears to be near the center part of the shaft. If impacted at the diaphysis' center, a blow of lower energy will suffice to fragment the element than if it is impacted at other spots along its length.

(3) The epiphyseal ends should be resting on a hard surface for

the blow to create enough stress to fracture the bone. It is not necessary to support the center shaft (at a point opposite the point of loading) but such support usually gives the impact blow added effectiveness in fracturing the compact bone.

(4) Fracturing may initiate at support points, as well at points of impact loading. However, while fractures initiated at impact loading points usually are radial, with acute angles between at least two different propogated cracks, the fractures initiated at support points most often propagate in only two directions, and the two cracks create obtuse angles (Figure 55, top: the lower border of top specimen, on the left side, shows an oblique angle where the bone surface rested on a hard support).

(5) Occasionally impact blows will crush and deform bone at the point of loading, but will not create cracks that travel through the bone. Such unsuccessful blows are probably too low in kinetic energy, or are applied at too low speeds to initiate fracture fronts. In addition, the presence of thicker bone walls or of cancellous tissue within the bone's medullary cavity can allow bone to absorb more energy before failing. Increasing the number of blows in one spot leads to splintering and creation of numerous small fragments at the impact point when the bone finally does fracture apart (Figure 55, far left edge of left specimen).

(6) The heavier weight of the hammerstone and relatively small surface at its impact point are factors that create easier fracturing. The angle of the impact edge is not as important a factor: in other words, a flaked chopper edge has no advantage over a rounded cobble edge if the rock is not heavy and if the impacting area is very large. The

blow must be concentrated on the bone to create clean fracturing rather than splintering and shatter which dirties up the marrow.

(7) Many shaft fragments produced by impact loading fractures are sharp edged. That is, the outer periosteal compact bone surface in many places forms an acute angle with the fracture surfaces.

(8) The placement of loading at different points on particular elements produces different fracturing patterns for those elements. Yet, sometimes, even the placement of loading at the <u>same</u> points on same elements leads to different patterns (that is, different numbers of shaft fragments, different fragment shapes). The <u>best</u> placement is generally predictable (the placement which will cleanly fracture the bone into segments from which marrow is most easily and cleanly extractable).

(9) Fresh bones, when impact loaded, break <u>most often</u> in radial/oblique (spiral) configurations with most shaft fragments longer than they are wide. Dry bone (aged one to two days out of water in air temperatures above freezing and below 15°C) will also spirally fracture for the most part, and will show point-of-impact splintering. Drier bone aged over two days will break in spiral and sometimes linear (longitudinal and transverse) configurations, also with impact splintering at the loading point. Bone aged over one year, if dry, not weathered beyond three years, and lacking grease and soft tissue, will seldom fracture with impact splintering at the loading point. Fracture types will probably include spiral/oblique patterns, but the fracture surface will much more often be at right angles to the outer bone surfaces, and will much more often be pebbly or roughened, as compared to those on fresh or green bone. Shaft pieces may not be any shorter

than pieces from fractured green bone. Bones that are weathered over two years, if degreased and not cracking or exfoliating, when soaked in water until they no longer float and then struck with a hammerstone will often show point-of-impact splintering. Fracture types will be spiral and longitudinal. Fracture edges will be less smooth than on green bone.

(10) On several occasions I attempted to break long bones of _Equus_ while flesh and hide still covered them. In all cases, an enormous blow (or series of blows) was required, and in _no_ cases (out of six attempts) were impact splinters seen on the fractured bone at the point of loading.

(11) An unbroken long bone, when subject to some warmth (even in the form of intermittent or occasional sunlight when air temperatures do not exceed 10°) will become somewhat greasy from the marrow within soaking through compact tissue. When such greasy bones are frozen (before excessive aging, say in less than two weeks after removal of the bone from a fresh carcass) and are impact loaded, they will break in a brittle manner and in a delamination manner. That is, the entire bone will fail in bending, so as to fracture almost transversely, while circumferential lamellae separate in layers or groups or layers. This latter behavior is probably due to the fact that the different layers are differentially greasy from melting marrow and red blood working outward through diffusion; the presence of grease in bone causes differences in freezing behavior (such as expansion or contraction) and fracturing behavior (such as brittleness). It appears that frozen, slightly greasy bone may be much more inclined to fracture in circumferential flakes or layer-spalls than unfrozen, ungreased specimens.

(12) Modern horse bones are relatively more difficult to fragment than Bos bones, due to a greater irregularity of surface topography, and to a greater thickness of bone walls; that is, higher energy blows seem to be required, and the placement of impact loading on the shaft is much more crucial. There is also a great deal more trabecular bone tissue within the medullary cavities of horse femora, tibiae, and humeri. This cancellous material of course can absorb energy from impact loading, thereby discouraging failure of the bone element.

NOTES ON MEAT-STRIPPING AND DISJOINTING EXPERIMENTS

Meat-stripping experiments (butchering of fresh animal parts) were carried out not with the intent of creating cut marks, scrape marks, or other tool-use damage on bone surfaces; these experiments were performed to see how one could effectively use stone tools (for the most part unmodified flakes large enough to hold firmly in one hand) in removing hide and muscle masses from bone and in disarticulating joints. The aim was to use the tools very carefully, so as to avoid damaging sharp working edges. However, even the most careful of butchering manipulation, such as using the tools deliberately to cut soft tissue off bone whose topography was well known, often resulted in some marking of bone surfaces, although most of the time the marks were very slight and perhaps easily overlooked if a bone examiner did not expect to find such damage upon close inspection.

I am in no way a fully-experienced, expert butcher, perfectly accustomed to utilizing flaked-stone implements on fresh carcasses. On the other hand I am not a dabbler or a neophyte: I have been dismembering, skinning, and meat-stripping fresh animal parts for several years, and I am much more efficient at these tasks than I was the first times I tried them. I have several times completely stripped the enormous leg of a thoroughbred horse to bare bone in a few minutes using one unmodified flake, whose surviving edge was still adequate to strip other fresh horse legs of hide and meat. To those who have never tried these tasks, this may sound unimpressive, but it has been my own personal experience (and I have observed in others) that stone-tool users who do not have at least a few hours of practice with their tools will make such mistakes as inadvertently twisting them a slight bit while cutting (thus, breaking them or flaking edges), or will cut down hard against bone in order to slice through slippery, bloody muscle, or will neglect continuously to clean tool edges and surfaces of blood and grease, which make even the sharpest cutting implement feel dull because it is so hard to grasp securely. I have destroyed or dulled enough tools to make me aware of many ways to avoid doing it again; I have learned how to be careful with my stone tool edges, while at the same time using them in much more efficient, quicker ways to complete my butchering tasks.

I do not mean to state here that _my_ cutting experiments are _replications_ of prehistoric peoples' butchering activities. The experiments were attempts to _simulate_ actions of butchering by peoples who valued their stone tools, but who also expected to create some (hopefully minimized) wear on them.

SUMMARY OF MOTOR ACTIONS IN MEAT-STRIPPING AND DISJOINTING LEGS

(1) Hide was first removed by slitting an opening in the thinner tissue covering a lower leg bone above the hoof, inserting a hand and pulling the skin back, peeling it off the muscles just as one peels off a sock. Usually the hide is rather firmly attached to muscles with a papery, fibrous tissue which can be easily slashed with a flake edge. However, a duller-edged stone chopper or a bone chopper are more efficient for punching hide off muscle, because their edges will not inadvertently slice through the hide, as very sharp stone flakes occasionally do, ruining a potentially useful piece of skin.

(2) Muscle masses were outlined by slashing with a flake between myelin sheaths (which enclose the individual or grouped muscles). This served to loosen the muscles, which were then sliced away from bone and from each other.

(3) Eventually, after superficial muscles were removed, deeper muscles were cut away at or near points of insertion in bone, using a series of short slicing actions. From time to time it was necessary to use a flake to scrape muscle tissue off bone shafts in order to separate it completely. The insertions of some muscles are composed of very tough, fibrous tendon or ligamentous material, which is much harder to cut with stone (or steel) edges than is ordinary red muscle.

(4) Bones at joints are held together by ligaments that are strongly attached at the articulating epiphyses of each respective element. This material was cut through with a sawing motion, being careful not to press too hard against bone, or was chopped apart with bone choppers (which are very poor tools for this purpose. In my

opinion, bone choppers function much more effectively when used to separate muscles masses or to divide muscle meat).

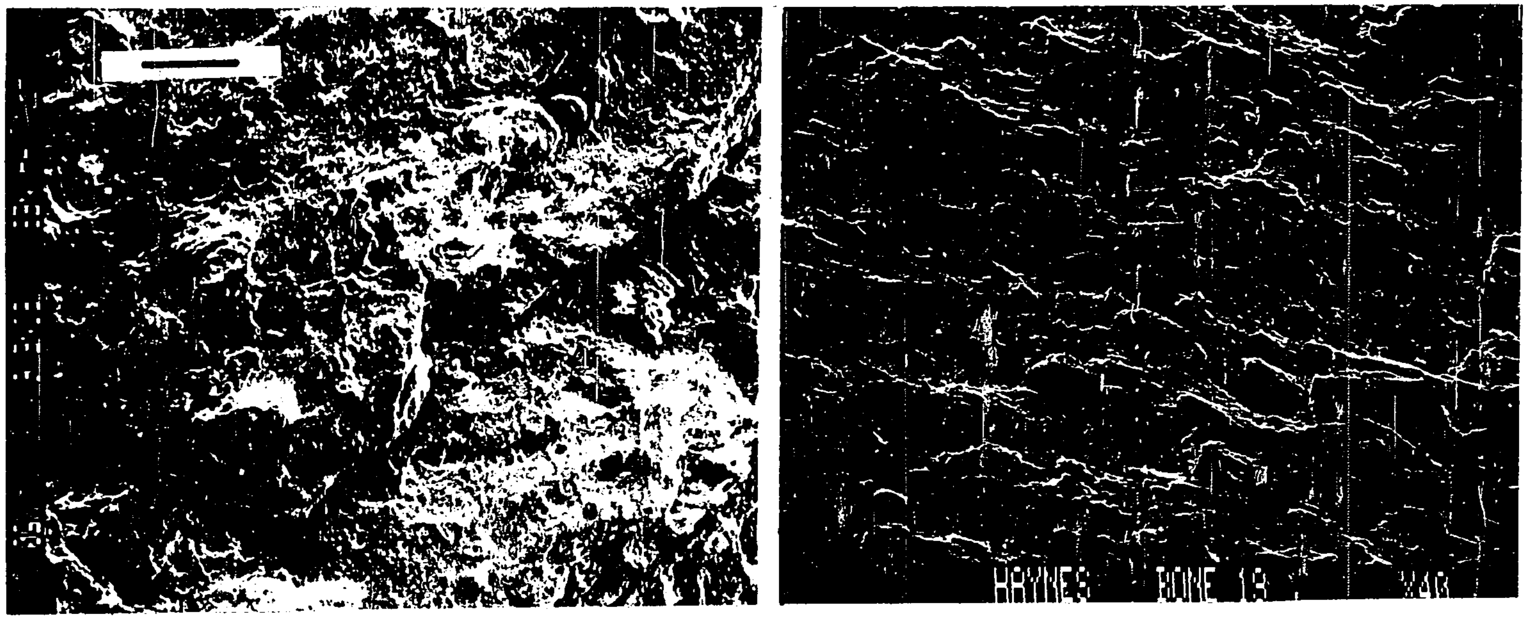


Figure 56. Weathering fractures.

LEFT: SEM close-up of fracture surface of cortical bone flake separated during years of drying of Bison long bone (subaerial weathering). The bone had lain several years in a saline lake. Scale bar = 250 microns.

RIGHT: SEM view of fracture surface of flake from Horse humerus weathered over five years in Algonquin Provincial Park, Canada.

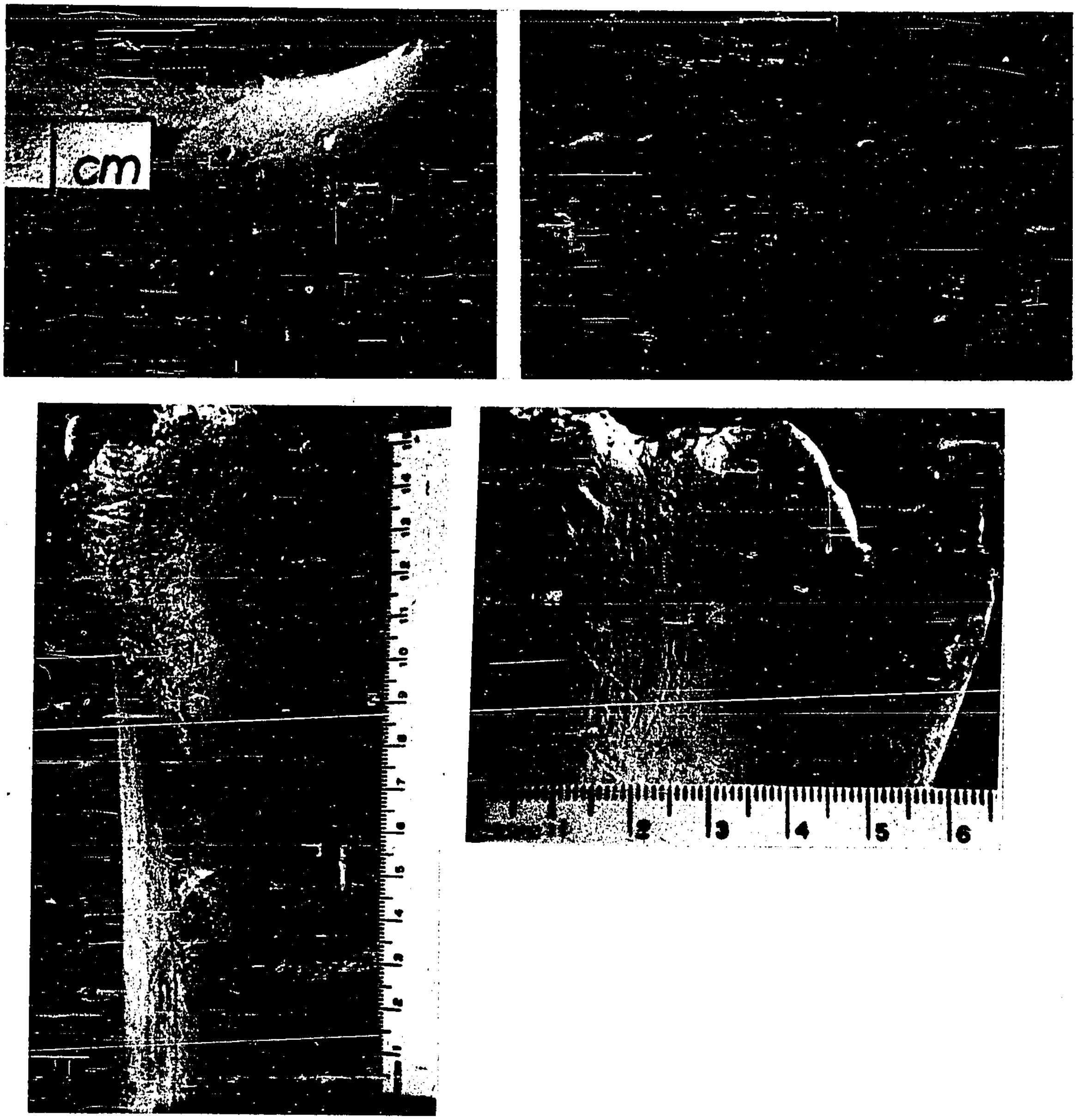


Figure 57. Gnaw damage and breakage.

TOP: Two photographs of Bison yearling long bones chewed by wolves at killsite.

BOTTOM LEFT: Tibia from adult female Bison, heavily gnawed by adult and subadult wolves at rendezvous site in Lake One area, Wood Buffalo National Park.

BOTTOM RIGHT: Close-up of fractured proximal edges of above specimen.

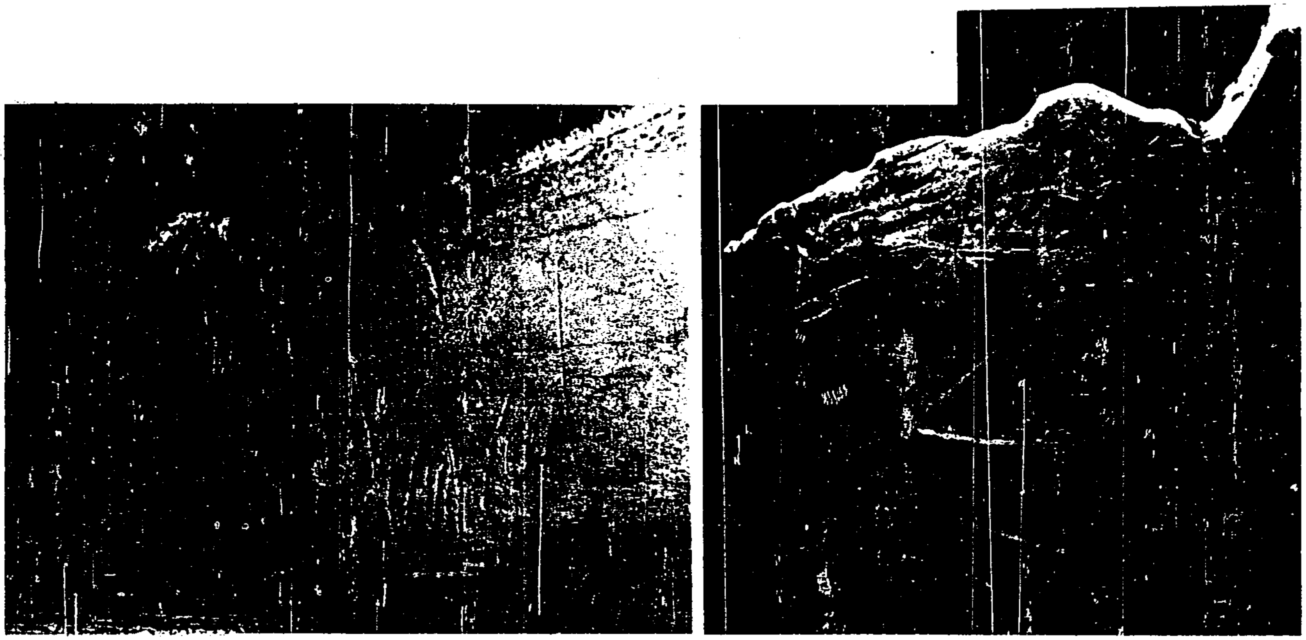


Figure 58. Tooth marking from wolf pups and adults.
LEFT: Gnaw marks from wolf pups on specimen illustrated in Figure 57, bottom.
RIGHT: Bison subadult femur shaft, proximal end gnawed off, showing tooth marking from wolf gnawing.

Figure 59. Various kinds of chop and steel tool cut marks.

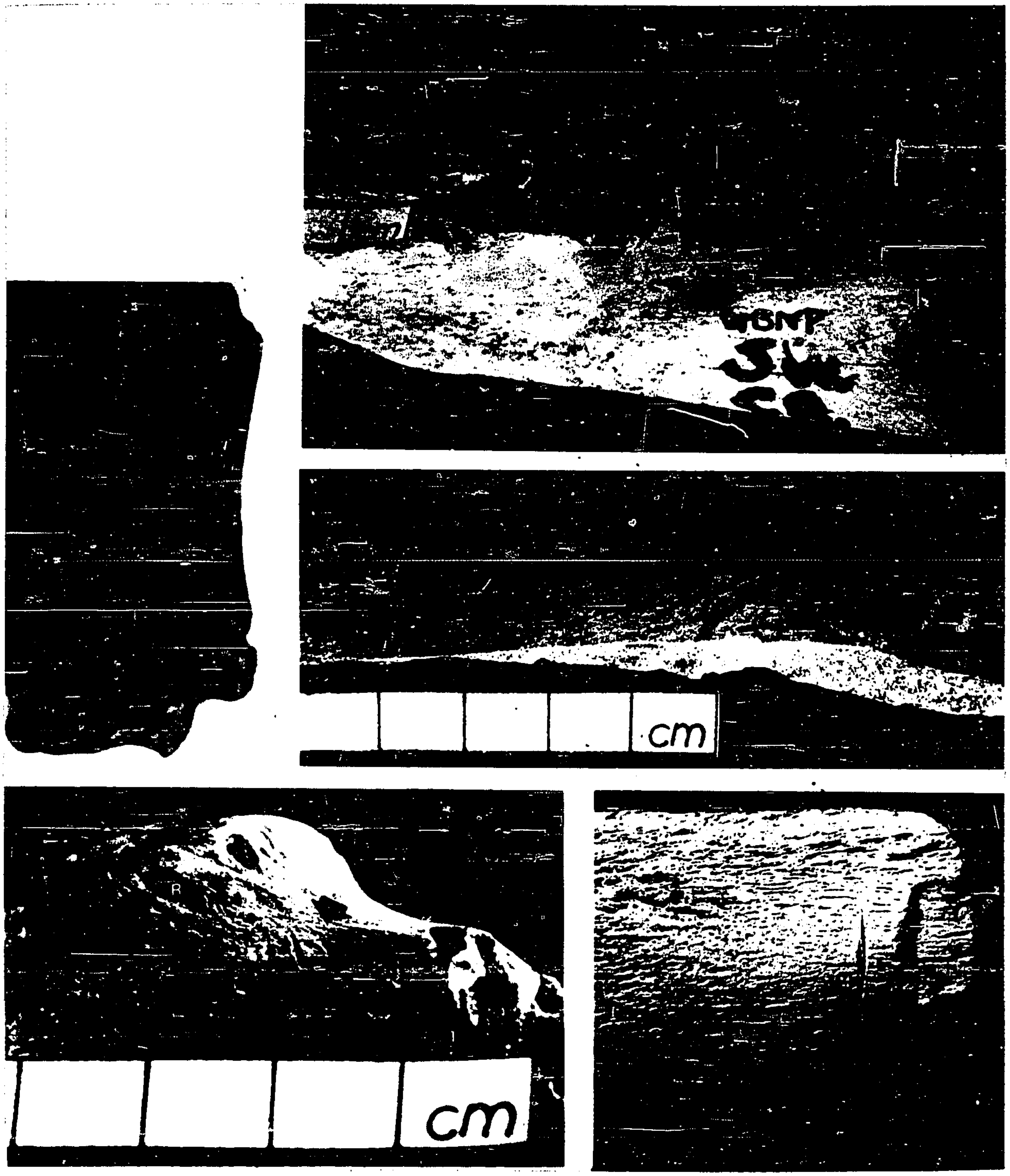
TOP RIGHT: Four impact points on Recent Bison tibia crest, the result of axe blows intended to separate lower leg from knee.

TOP LEFT: Subadult *Bos* tibia distal end, showing slice and chatter marks where tool edge was scraped downward against bone to cut ligament attachment. Specimen from a Pleistocene-Holocene age spring bog in northern Virginia.

CENTER: Tooth marks and scrape-filleting marks made by steel tool. Tool marks are most apparent to left end of specimen, which is Recent Bison bone from Wood Buffalo National Park.

BOTTOM LEFT: Large arrow points to light axe-blow damage, smaller arrow (situated below "R") points to rodent gnaw damage.

BOTTOM RIGHT: Recent Moose rib segment with steel knife cut marks.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RESULTS: OBSERVATIONS AND DISCUSSIONS
(NATURAL AND CULTURAL MODIFICATIONS)

Only many more replicative experiments or simulations of tool use will contribute the evidence necessary to establish solid determination of the agencies responsible for modifications on bone element, when there is a question of cultural versus natural agency.

TOOTH MARKS: When an animal bites down hard on compact bone (which behaves as a plastic up to a point), the teeth usually leave impressions as pits in the bone surface (Figure 57, top); when the animal moves its teeth on the bone, the impressions may be in the form of furrows, scratches, or incisions (Figure 57, bottom). Some carnivore gnaw marking seems haphazardly placed, but is usually most apparent near the ends of the remaining bone or bone fragments, especially on shaft fragments from near epiphyses (Figure 57, bottom right). On epiphyses, cheek teeth may be used to grind or shear off cancellous or thin compact bone, creating grooves where the cusps pressed deep into, and moved through, the tissue (see Haynes 1980a:figures 6 and 7). Such furrows may appear similar to chopping damage as done by stone, metal, or bone implements having relatively low-angled edges. Bones that are otherwise un-gnawed but which have such grooves may actually have been chopped.

In gnawing, bone tissue is first depressed by the teeth, then strongly scraped away. Eventually different concentric layers of tissue (bone lamellae) are broken through by the moving teeth; consequently the groove produced in compact bone is seldom flat-sided and smooth unless the mark is a deformation rather than an incision (Figure 58). A chop mark or deep scrape made by metal tools is usually very smooth-sided, and there may be extremely fine, parallel ridges and troughs in the direction of the chop, covering all of one side of the depression in compact bone. These marks are caused by microscopic flaws in the cutting edge (saw teeth). When cancellous bone is involved, none of the attributes mentioned above may be recognizable.

CUT MARKS: A tool cut usually leaves a sharp-edged impression in compact bone, and when moderately deep may appear dark when viewed with somewhat oblique light, because of the narrowness of the cut's width; whereas the bottom of tooth marks is usually visible, even on those produced by the small and very sharp teeth of wolf pups, other small carnivores, or sharp-toothed rodents (Figure 58, bottom, and Figure 59). Cuts 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. True tool cut marks should be localized on most bones, and should logically not be everywhere common. The edges of actual cut marks are usually well-defined and relatively straight, at least for part of their length, while carnivore tooth marks may waver. Most carnivore tooth marks are made by the teeth of adult animals, which have relatively blunt cusps; hence, these teeth marks are characterized by uneven edges and incomplete slicing through bone lamellae (Figure 56).

Tool cut marks may be very short in length, and may occur as sets of parallel incisions (Figure 59); a true tool mark may skip over depressions on bone surfaces, especially if the tool has a regular (straight) cutting edge, so that single stroke cut marks left on irregular bone surfaces may be discontinuous. Carnivores also leave interrupted grooves, furrows, or scratches, but gnawing damage will generally follow bone surface irregularities. The results of rodent gnawing vary considerably with different individuals and with different species, but most gnawing damage done by rodents will closely conform to bone surface topography. The length of the grooves or scratches produced by gnawing rodents depends on the mechanics of the jaw and the size and shape of the bone part being gnawed. The width and depth of the gnaw marks depend on the hardness of the material being gnawed, and on the number of times the rodent draws its teeth over the same spot (Haynes 1978a) (Figure 8).

Rodents most often gnaw prominences or ridges or edges, producing facets on them. Rodent gnaw-damage may be very localized on any one specimen, or may be all over the element. In some geographic areas where gnawing rodents and lagomorphs are present, cast antlers may be habitually gnawed, yet bones may seldom be touched, as for example in Isle Royale National Park. In eastern North American woods and fields, antlers and bones on the ground surface may be entirely consumed by rodents (and possibly rabbits) with a few years.

While ideally the marks left by stone tools used to cut against bone should be scarce and scattered (although located in rational, practical, and patterned places on bone for the most part), in reality such cut marks are oftentimes problematically common on certain elements (Plate 6). It can be argued that deep and abundant cut marks on bones are unnecessary; that meat and periosteum can be stripped without the need to cut deeply and repeatedly into hard tissue. Indeed, were stone tool-using peoples concerned mainly with the conservation of cutting implement edges, then they would not have unnecessarily dulled their tools by cutting too hard against bone. In some cases, where muscular

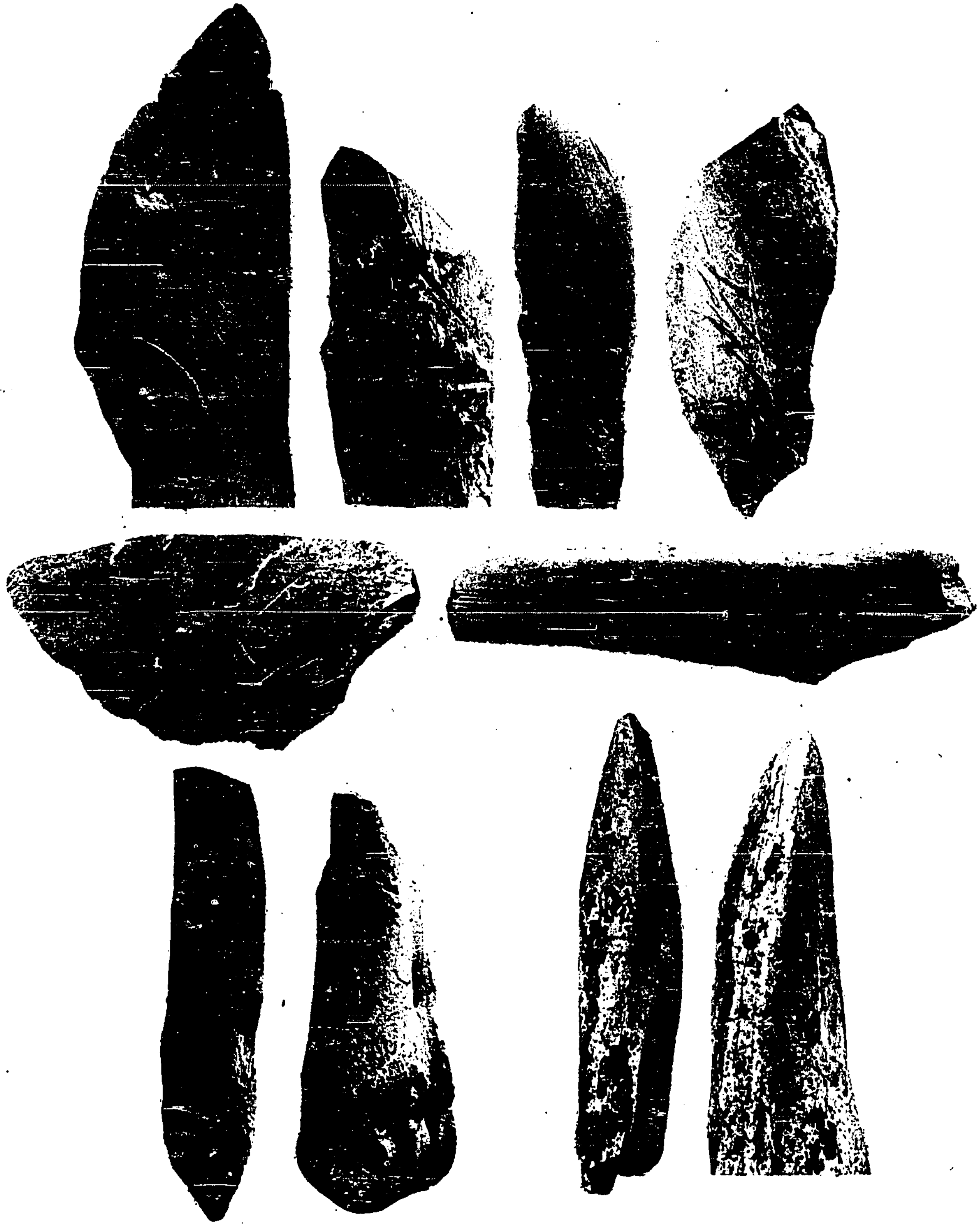

Plate 6. Marks of butchering, evisceration, skinning, meat stripping, or tool use and manufacture on mammalian bones from La Quina, France. All illustrations from Martin (1910).

strength fails or where meat is too bloody to be securely grasped and yanked off bone, there is an inescapable necessity for using edged tools to cut against bone. It would seem more parsimonious to use a sharpened tool to cut through muscle or ligament stretched tightly than to cut through such soft tissue pressed against bone (as a person with a steel knife slices bread against a wooden cutting board, with no regard for wear on the knife edge). On the unmodified flakes I have used as butchering tools, noticeable edge damage (dulling or micro chipping) occurs for the most part only when the flakes were used to slice or scrape muscle against bone. Otherwise, use on muscles and tendon seldom created edge damage or dulling, unless there was leverage. When a flake was used to cut against bone, its edge soon lost almost all efficacy as a meat-cutting tool.

Regardless of this modern day archeologist's musings on the practicality or logic of prehistoric stone tool users, the fact remains that some human activities of animal dismemberment or meat stripping may have occasionally or frequently produced much damage to bones. In these cases the efforts involved in restoring a tool's edge (or making a new tool) were probably less undesirable to the people than the efforts or time involved in using the available tools in much more careful ways.

SPIRAL FRACTURING: As discussed in Chapter 4, Buckland (1822, 1824) recognized that large carnivores may break fresh long bones of herbivores in ways deceptively similar to the ways humans break such bones (see Buckland 1824: plate 23; also see Dawkins 1874:282). Breuil (1938, 1939) also pointed out the possibilities that hyenas and wolves could break fresh long bones of certain size animals (horse and ox for hyenas, deer or smaller for wolves). P'ei (1938, 1939), Koby (1964), and

Zapfe (1939) (among a few others) published their observations on carnivore capacities to break up long bones. Dart (1964) acknowledged that hyena could fracture bones, but he insisted (as did Breuil in 1938 and 1939) that humans fracture bones differently than do carnivores. According to Buckland (1824: plate 23) gnawing carnivores leave semilunar notches in the fracture edges of bone shaft fragments, these notches being the marks produced by separate teeth. These indentations may be very similar to the notches made by impact of a hammerstone (Figure 60). On the other hand, according to Breuil (1939:2), only humans can break up bones longitudinally, by striking blows at the end of the bone. Also, by using a hammerstone and anvil, man breaks up bones and produces "flakes arranged in the form of a butterfly's wing round the spot struck" (Breuil 1939:1) (Breuil is describing the fragments resulting from intersecting radial fracturing.) In other words, man strikes bone shafts and creates spiral fractures on the bone; individual fractures may intersect and create pointed or bi-pointed shaft fragments.

For Breuil, as for many other researchers, the problem of distinguishing causes of fracturing (man versus animal) was solved long ago. The Nunamiut Eskimo Simon Paneak in 1950 or 1951 showed William Irving how to "distinguish man-made from carnivore-made fractures of bone at a glance: man-made fractures curve systematically and smoothly through the main shaft of the bone, whereas those made by carnivores are irregular and tend to occur at the ends of bones" (Irving 1975:7 and 1978:98-99). But Figures 14 (top), 60, 61, 70 illustrate carnivore-created fractures that cannot be distinguished using such criteria. In Irving and Harington (1973:340) it is stated that "no carnivore can break a mammoth leg bone," even though no one has ever watched an extremely large carnivore such as Arctodus eat fresh mammoths.

The patterning of fragmentation expectable from modern carnivore gnawing of ungulate long bones is discussed below.

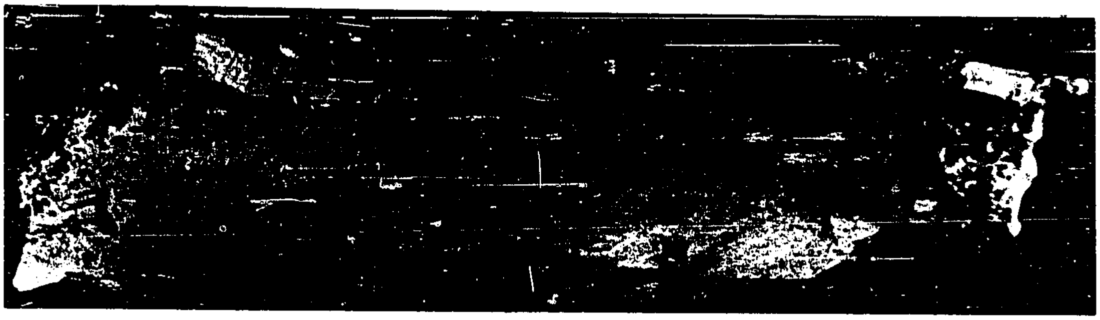

Figure 60. *Bos* femur fragment broken by captive Spotted Hyena. Arrows point to notches and splinter scars caused by Hyena's teeth.

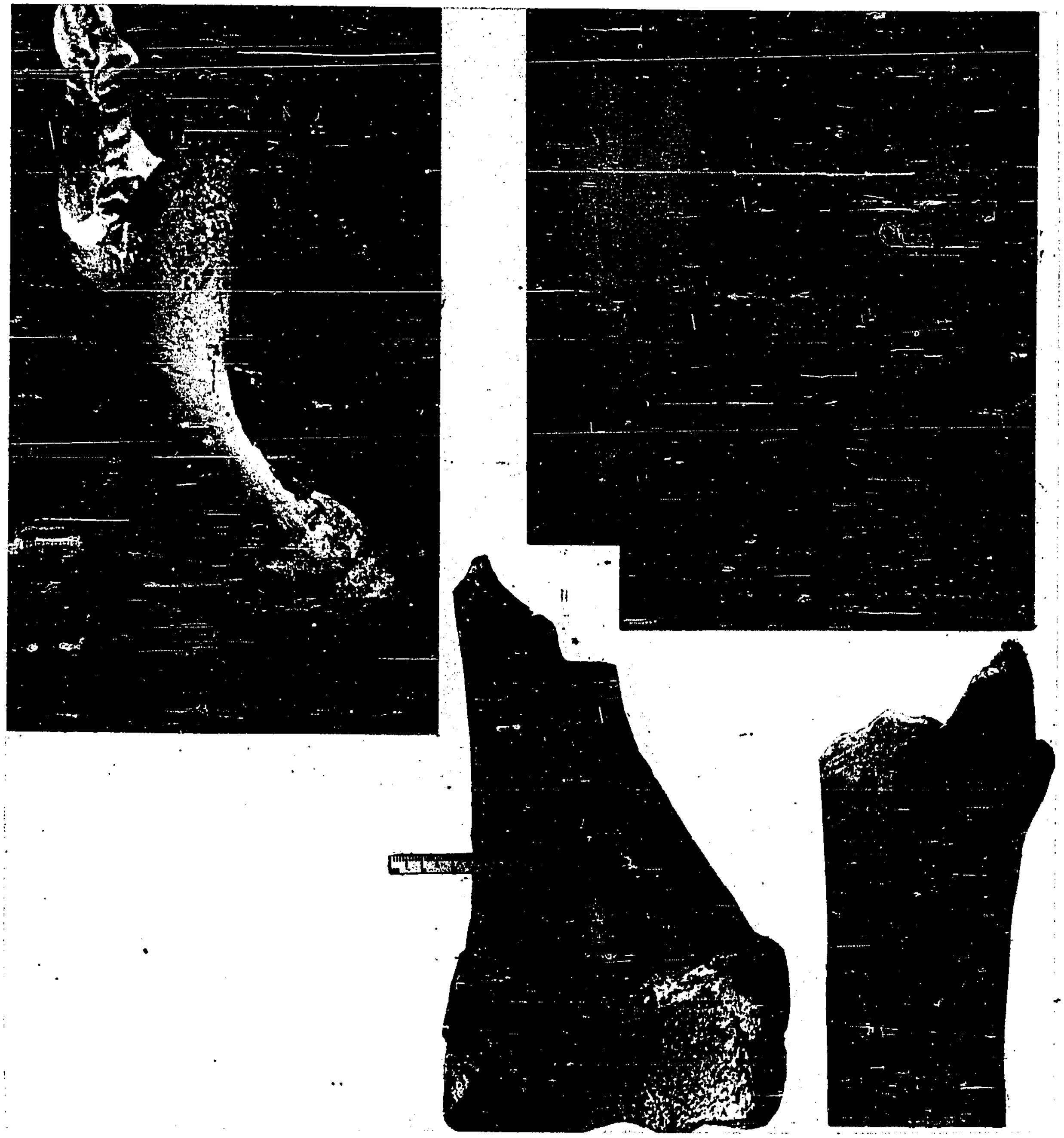

Figure 61. Wolf gnaw-damage, trampling fractures, and gnaw flaking.

TOP LEFT: Bison yearling humerus broken and tooth marked by wolves at killsite.

BOTTOM CENTER: Adult male Bison humerus spirally fractured by trampling Bison after wolf gnawing and weathering.

BOTTOM RIGHT: Specimen illustrated in Figure 58, showing spiral fracture caused by wolf gnawing. Scale same as for above.

TOP RIGHT: Two views of Bos radius flaked by captive Spotted Hyena.

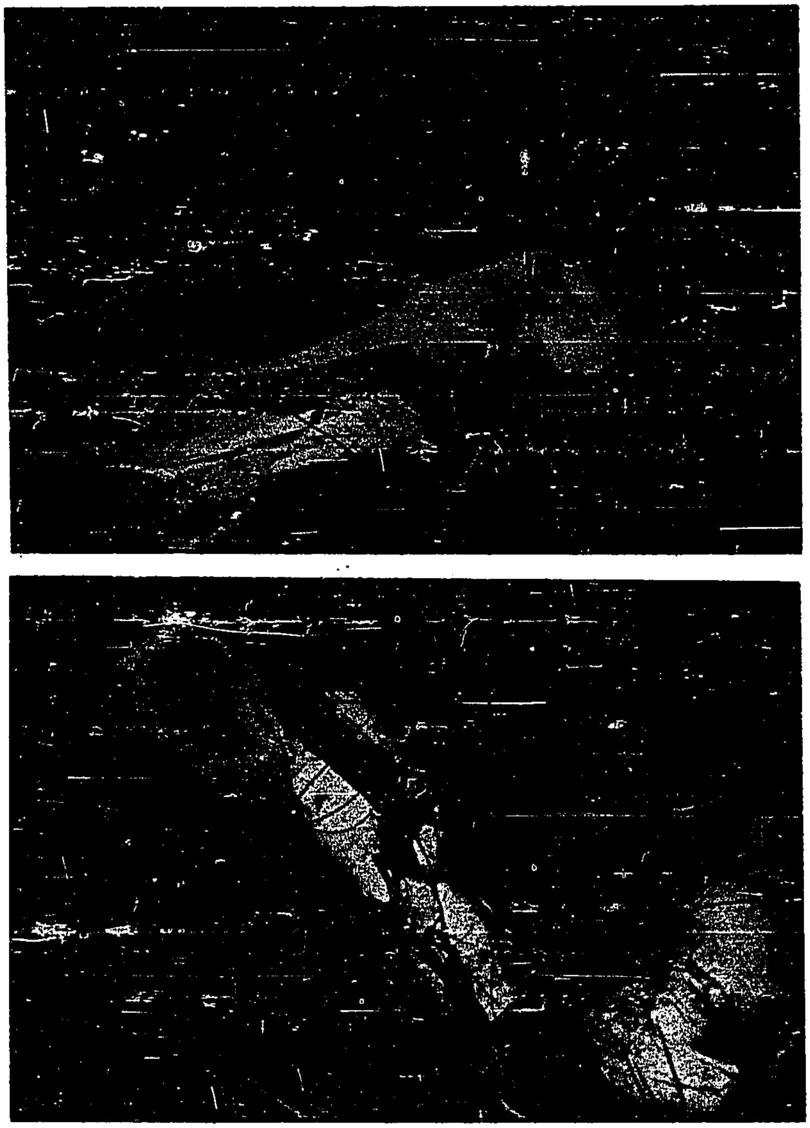

Figure 62. Two Bison long bones trampled and fragmented by Bison, photographed *in situ* near Hay Camp, Wood Buffalo National Park, August, 1980.

GNAWING DAMAGE AND BONE BREAKAGE: A RANGE OF POSSIBILITIES: My sample may be too small for indiscriminant generalizations, but some idea can be least be gained of the various damage types produced (or potentially produceable) by large canids and large bears, which gnaw or feed on skeletons.

When large carnivores gnaw on long bones from adult bison, moose, horse, or similarly-sized animals, they will seldom, if ever, successfully crush the bones to fragments between their jaws. Instead, gnawing of adult moose or bison long bones begins at an epiphysis and may continue as the cancellous bone is consumed, until the bone shaft is entirely opened up at one or both ends (see Bonnichsen 1973). The shaft may then be broken apart by pulling pieces off with the teeth (Figure 61, top left). Bones with an epiphysis partially or completely removed by gnawing may also develop spiral fractures upon weathering, tissue drying, and shrinkage of the tissue's microstructural elements. Such cracks are probably stress-related, some or all of them having been initially produced (although not necessarily visible on freshly gnawed bones) by carnivores levering, pulling, and applying forces to the bone during gnawing actions (Figure 61, bottom far right). Gnawed bones are also likely to fracture easily when kicked or trampled by bison, moose, elk, or deer moving over older kill or skeletal sites (Figure 61, bottom center). If the trampled bones are not badly weathered (length of weathering over one and under four years) and have not developed many longitudinal drying cracks (see Miller 1975; Bonnichsen 1979; Morlan 1980), some of the trampling damage may be spiral, with characteristics of fresh bone breakage (rather smooth fracture surface which is not always at a right angle to the element's outer surfaces, no jogs or offsets in line of fracture through shaft, etc. - see Morlan 1980 for good illustrations and discussion) (Figure 49,c,d).

On bison ranges the most common trampling damage that I have recorded is simple splintering of vertebrae, ribs, and scapulae; older, somewhat weathered long bones (weathered five years or less) are also split into longitudinally and transversely broken fragments, as well as truly spiral configurations (appearing as intersecting radial fractures). Nasal bones and premaxillary bones may be kicked off skulls, and teeth may be broken out. All bones are somewhat scattered when much trampling occurs (that is, the bones may be spread in a circle with a diameter of several dozen meters). Mandibles may be splintered, and all that may eventually remain are toothrows. Pelves may be broken into two or more parts. Occasionally long bones may be trampled and spirally fractured although they are hardly in a very fresh condition (length of weathering period greater than four years). I have found fragments of such fractured bones usually in shaded and seasonally wet areas (river crossings, lake bottoms, bison wallow/ponds) where the deteriorating effects on bones of _ex vivo_ drying and weathering are considerably reduced. However, the bones in such areas tend to disappear into the mud due to animal traffic, and are rarely visible. Since these are the types of localities which may actually produce assemblages of _preserved_ fossil bones, major efforts are being made to inspect these areas.

Most bison skeletons (from wolf kills or other natural deaths) are imcomplete after scavenging, which tapers off significantly (but may not truly cease) after the first summer following prey death. At killsites which are less than five years old the shafts of remaining long bones are rarely found broken, unless the prey animal was a calf or yearling. I have found only four fractured long bones in about three dozen discrete skeletal sites of adult bison, even in areas where there is heavy bison traffic from time to time. One bone, spirally fractured in the center of the diaphysis, was a large humerus from an adult male, date of death (probably due to predation by wolves) estimated at 1970 (Figure 61, bottom). No other long bones at this skeletal site were fractured. Other fractured bones were found in small clusters at a carcass disposal site, and so their placement was probably affected by human behavior. However, the breakage of these latter specimens is undoubtedly due to trampling after at least three years of weathering (Figure 62). These small sites probably represent redistributed body parts of bison dying elsewhere. Other spirally fractured long bones which have been found singly or in artifically created bone piles, accumulated during animal disease-control slaughters over a decade ago, may have been broken during carcass disposal activities. Most specimens have been eliminated from consideration here because of the possibility that humans broke them. Bones at dens or other sites where weaned wolf pups and adults live in summer may be spirally fractured, but are usually well marked by teeth (as in Figure 57). From time to time, wolves deliberately move their pups to convenient sites of carcasses to create temporary homesites, and so prey bones at these locations are extremely well gnawed and broken.

Some long bones of adult moose have been found spirally fractured, in all observed cases a result not of trampling but of secondary scavenging by wolves, occurring approximately 3-6 months after the moose were killed and originally fed upon by the same or other wolves.

Scavenging fractures often have a few jogs and right angle offsets on the curve of the fracture surface (see Haynes 1980a:figure 9, specimen on far left), due to the presence of drying cracks in the bones before gnawing animals broke them up.

Black bears seldom fracture adult bison or moose long bones. When they do, it is probably because wolves have first gnawed off an epiphysis (the distal or proximal end of femora, the proximal end of humeri, the proximal end of tibiae, or the distal end of radii).

Brown bears and grizzlies scavenge carcasses most actively in spring, early summer, and fall. If the carcasses are wolf-kills, then usually only articulated lower legs and cleaned axial bones remain at the site by the time bears find it. I have examined only a small sample of bones from black bear scavenging, although it is apparent that bears, like other scavengers, prefer to eat hide, ligament, muscle, or dried viscera before finally gnawing individual bones. Scavenging animals are hungry, but can be expected to methodically eat those parts of prey remains which are easiest to eat before consuming the skeletons themselves. If scavenging bears are extremely hungry in spring after emerging from their winter torpor, or in winters following poor autumn berry and mast yields, they would most likely make strong efforts to feed on available bony elements or to break apart long bones to get marrow. It is perhaps only armchair speculation to consider it non-adaptive for bears (with their omnivore tooth patterns) to have to rely on bones as food resources part of every year. Many large bears are no doubt capable of breaking bison bones, but I have no idea under what conditions of privation such behavior can be expected. Long bone breakage by bears may be routine even when food is relatively plentiful. There are many unanswered questions that should be of interest to experimental ecologists with concern for the recent or the remote past.

FLAKING OF THICK BONES: On rare occasions wolves and other carnivores observed in this and related studies (see Haynes 1978a,b, 1981 in press) have forced long flakes of cortical bone off long bone shafts (Figure 61, top right). More often flake-like fragments are broken off which retain some of the periosteal and endosteal surfaces of the bone shaft, at least at one end, and terminate with sharp edges at the distal end (Figure 63). These flakes or spalls may have flat proximal ends that appear grossly similar to striking platforms on artifactual materials, but there is usually gnaw damage to the surface of the bone and some edge rounding at the proximal end. Flakes detached by carnivorous animals, through pressure or leverage, may also (but seldom) show ripples and hackle lines on ventral surfaces (see Crabtree 1972 and Bonnichsen 1977 for terminology). When fresh bones of large ungulates are gnawed, the flakes produced may be longer than 10 cm. in length.

It is of course possible that huge-jawed species such as <u>Arctodus</u> (a carnivorous bear [Kurtén 1967]) could have levered off shaft fragments, creating flakes and flake-like spalls, in efforts to get at marrow within long bones, and would not have left unmistakeable tooth marks on the proximal ends of released flakes. Whether this kind of exertion would be adaptive (as stated above) it a moot point. There is certainly no doubt that in the case of mammoth long bones, the effort required to break up fresh cortical bone would have been enormous; yet I believe it is possible that hugh bears could do it, especially on bone specimens with epiphyses damaged by earlier gnawing. However, I wouldn't expect bears routinely to break up such large bones. I do not think that the hypothetical potentiality of gnawing by bears can be realistically used to explain broken mammoth bones in any assemblage.

Wolves or other large predators would be capable of breaking up some mammoth bones by first gnawing through epiphyses, then levering back the cortical bone. I do not think wolves would often have done this. Signs of gnawing on a fractured mammoth long bone have been observed in the case of a Pleistocene specimen collected in Alaska (Figure 43). The proximal end of this particular tibia was gnawed, but the distal end had been completely removed. It is possible that gnawing on elephant size prey remains may begin at the feet (see Douglas-Hamilton 1978:236) and work up the carcass, in contrast to gnawing and disturbance of bison or similar-sized animal carcasses, which begin at pelvis or shoulder, and work only partially down legs. There is no description available in the literature of documented carnivore utilization of elephant carcasses, so it is not possible to postulate sequential bone damage stages and element disarticulation (see Coe 1978 for a study of natural decomposition, and Beard 1977 for dozens of uncaptioned photographs of east African elephant carcasses and skeletons. See discussions in Chapter 8). If carnivores or scavengers were breaking mammoth bones, they must have been exceptionally hard up for food. Such a reaction to privation (habitual fragmenting of large bones) might in fact be expectable during times of megafaunal extinction; if megafaunal extinctions occurred very quickly, as a response to rapid climatic change, then carnivores would probably have at first underutilized herbivore carcasses, due to their sudden abundance. During the terminal stages of extinction, carcasses would have been over-utilized as prey

Figure 63. Two views of Equus tibia and flake, proximal end of shaft, fragmented by captive wolves.

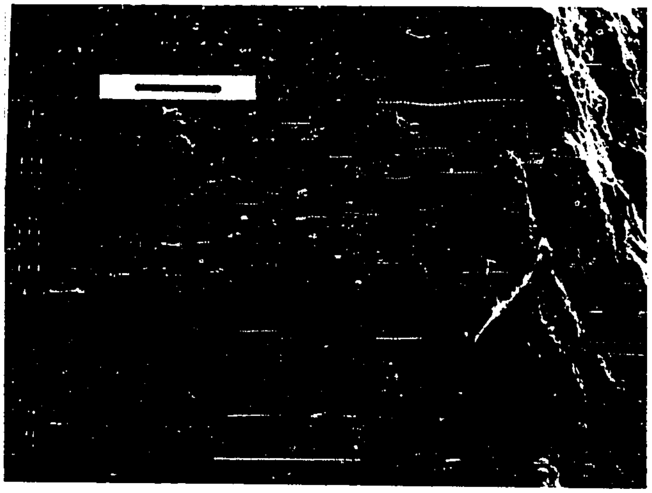

Figure 64. SEM photograph of part of experimental Equus tibia chopper. Utilization rounding runs up and down on the right center part of the photograph. Scale bar = approx. 200 microns.

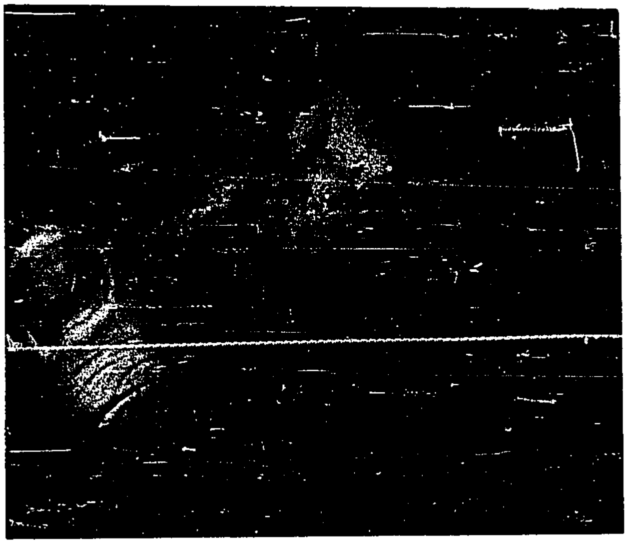

Figure 65. Experimental Equus femur shaft chopper use-edge, showing use-wear flaking and blunting.

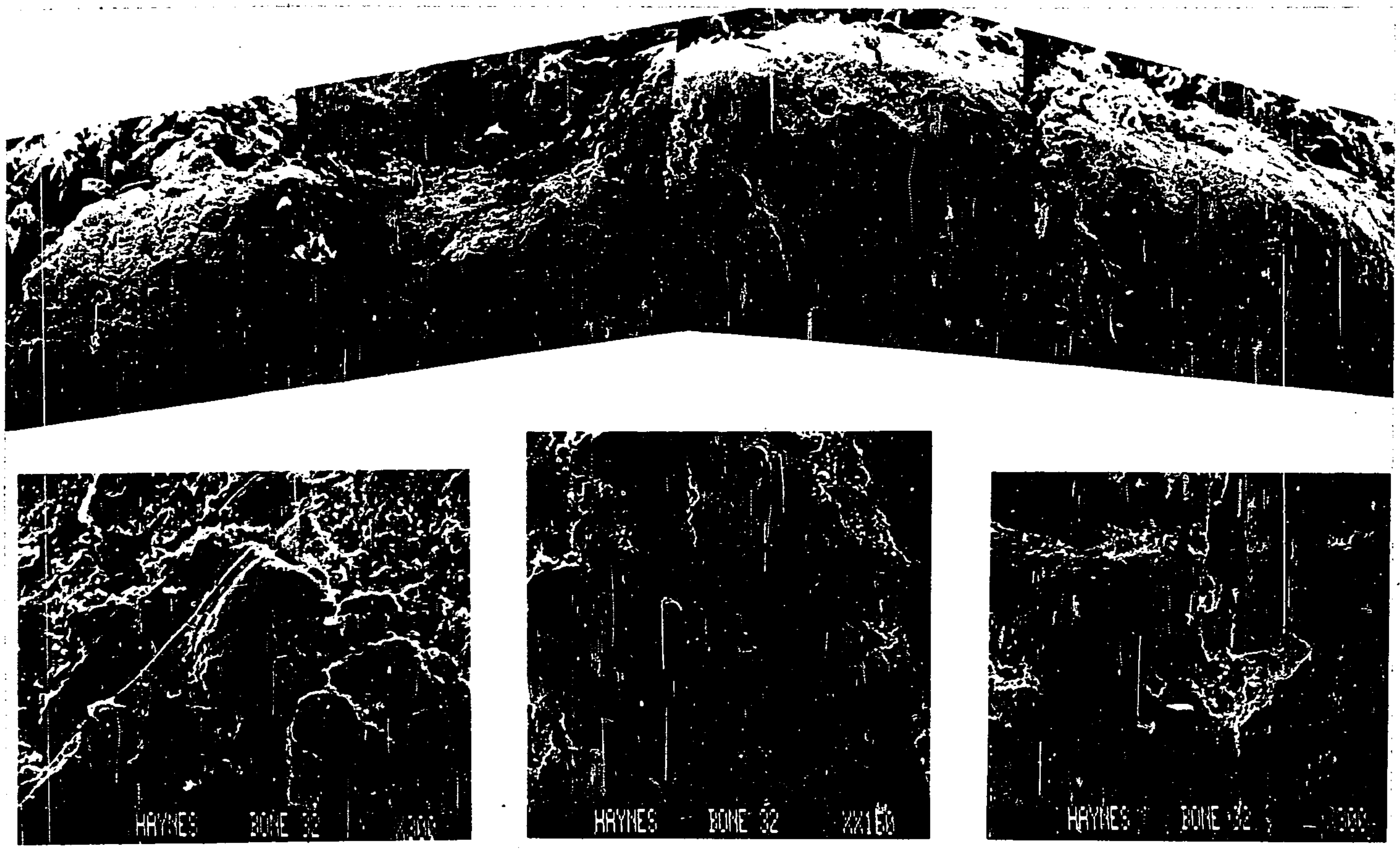

Figure 66. Edge-rounding from tool use.
TOP: Wolf gnawed Bos rib fracture edge showing rounding due to use of specimen to dig in silty sediments.
BOTTOM row: Deformation and scratching of surface of above specimen, seen in close-up.

Figure 67. Edge rounding from gnawing. *Bos* femur fractured experimentally for marrow extraction, then given to domestic dog. Note extreme fracture edge rounding in close-up on right.

availability dropped critically and predator numbers would also have severely dropped (see Haynes 1981 in press).

FRACTURE-EDGE ROUNDING: During this research I observed several agencies that created abrasive rounding of originally-sharp fracture edges. I have also anaytically isolated several probable or possible processes that might have accounted for edge-rounding on some collected specimens.

The observed processes include:

(1) Tool utilization. Fracture edges round when a bone fragment is used as a meat chopper (Figure 64), hide scraper, or digging tool. Edges used to chop through meat are practically useless once they acquire smoothed facets produced from use, simply because these implements were abandoned long before such utilization damage had occured. Edges used to chop apart bone joints oftentimes showed step-fractured or crushed appearances, due to their impaction against other hard tissue (Figure 65). Edges used to dig in the ground were smoothed and became slightly polished if utilized past the point when their effectiveness as dirt-stabbing implements became noticeably poor. These latter edges also showed (at high magnifications) scratching in the form of sleeks and striae (Figure 66). These striae are numerous and are found on much of the rounded edge surfaces, and are similar to striae recorded on stone tool edges used to saw fresh wood that is covered with eolian silt (Fedje 1979).

(2) Gnawing by animals. The gnawing animal either licks and uses its teeth to grind edges smooth, or abrades the fracture edge against its paws or the ground, to create edge rounding (Figure 67). Saliva alone could not dissolve bone surfaces, although regurgitated stomach acids may

enter a gnawing animal's mouth from time to time contributing to bone surface erosion.

(3) Chemical weathering. Because sharp fracture edges are simply the very thin intersection of two separate bone surfaces, each of which weathers or loses some constituents due to decay or dissolution in water, the rate of weathering or decay of the edges may be reckoned to be about twice the rate for each single surface. Therefore, it is expectable that thin, sharp edges will weather to a rounder shape relatively quickly, before flat surfaces of bone show any weathering deterioration (Figure 68, Figure 69). Very mildly acidic groundwater leaches salts from bone material, contributing to a loss of surface area and volume. Even rainwater is usually slightly acidic, due to the presence in solution of atmospheric compounds such as carbon dioxide and nitric acid (Cornwall 1958:77), and also due to the presence of fine, floating wood ash in the atmosphere, not uncommon in densely-forested northern wilderness areas where fires burn uncontrolled. Therefore, bones which are subject to soaking by rain or melting snow may be slowly leached of calcium and other salts, even if they lie atop ground surfaces. Also, in areas where air temperatures rise above freezing (even if briefly) during the year, blue-green and diatom algae, fungi, bacteria, lichens, and mosses colonize the surfaces of bones; growing plant tips enter cracks where they release a great deal of carbon dioxide during normal life activities. The presence of CO_2 creates a local environment on bones surfaces that is acidic. Lichens during growth release some kinds of organic acids, and the decay of lichens, mosses, and microorganisms also produces different organic acids (Gerasimov and Glazovskaya 1965:24-25).

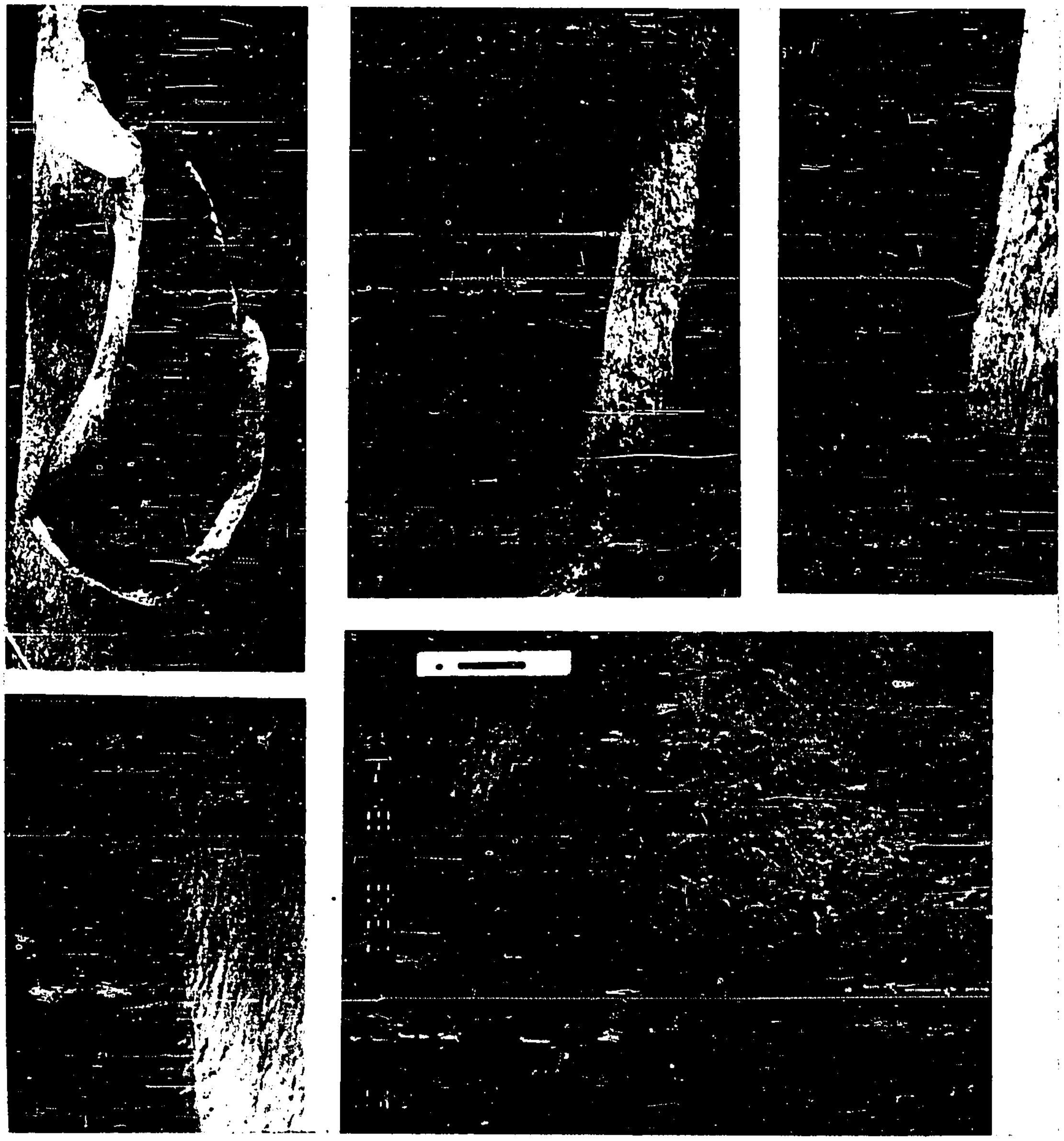

Figure 68. Edge rounding due to weathering. Bison femur fractured when fresh by a poacher, then lightly gnawed by domestic dogs, floated downriver approximately 8 km. in a flood after spring thaw, and abandoned for five years. Edge rounding is slight but noticeable, due to chemical weathering (dissolution). Scale bar in SEM photograph approx. = 190 microns.

Figure 69. Bison tibia fractured by poacher. Edge rounding is due to approximately five years of weathering.

Figure 70. Edge rounding due to light trampling. Subadult *Bos* tibia shaft, fractured by captive wolves, then buried two years in sediments which rodents burrowed through. Step-fracturing and localized edge crushing caused by wolves. Edge rounding is due to low energy trampling by wolves and rodents.

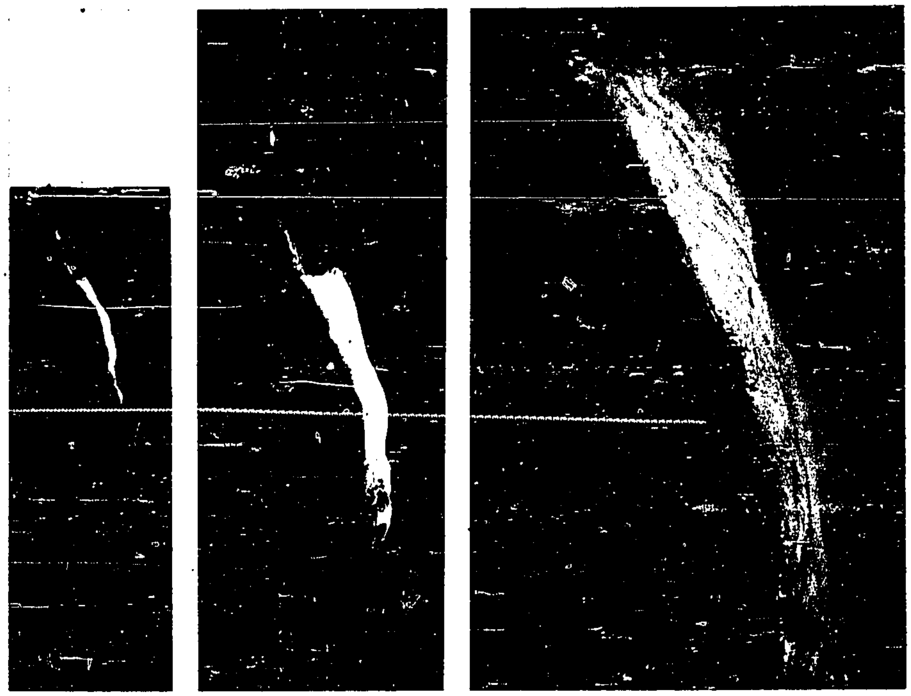

Figure 71. Fragment of long bone of subadult Bos. Specimen fractured by captive wolves. Edge rounding is localized, and is due to wolf gnawing and rodent trampling.

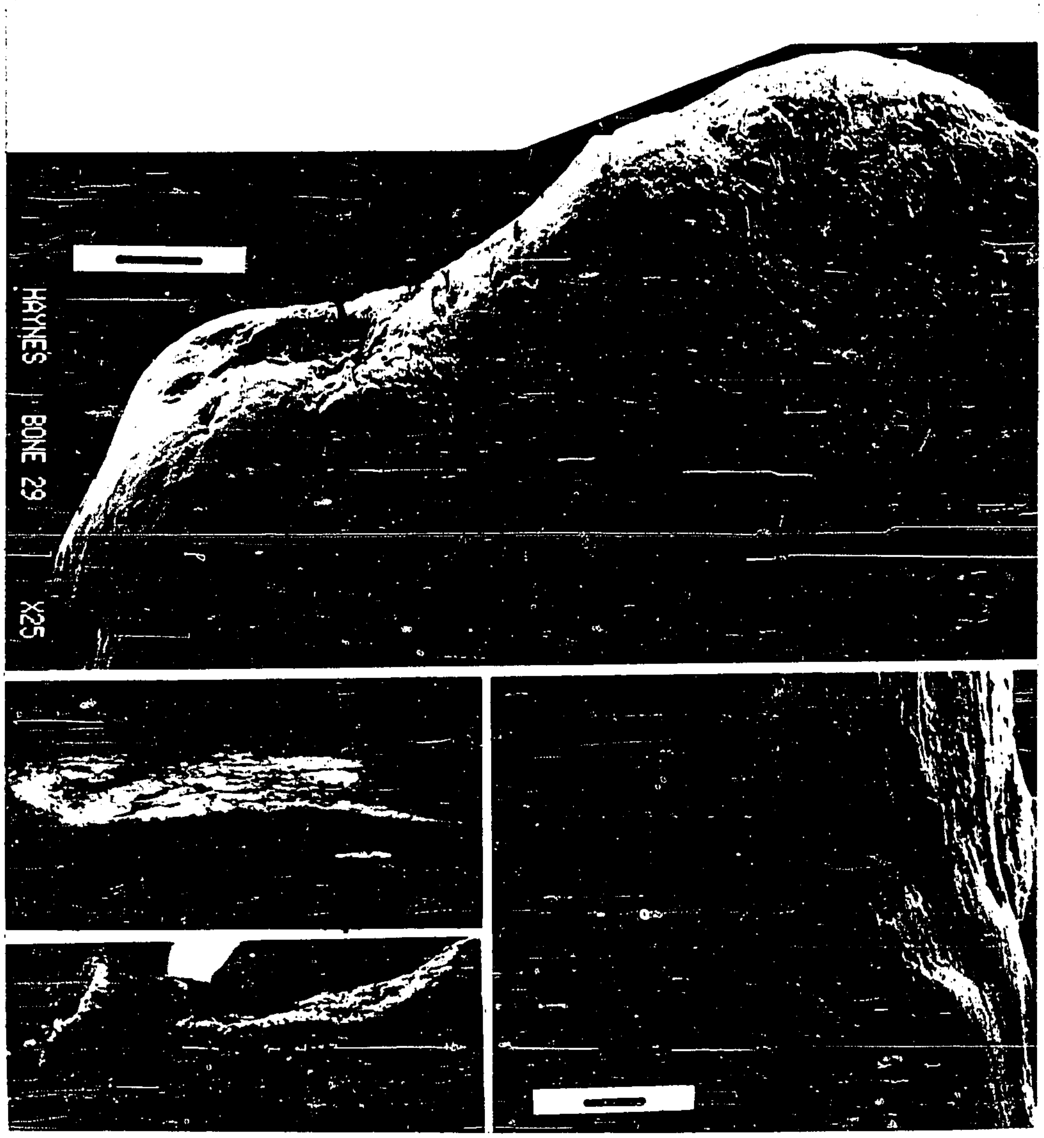

Figure 72. Edge rounding.
TOP: *Bos* tibia fracture edge, gnaw-rounded by captive wolves. Scale bar = 250 microns.
BOTTOM LEFT: (Two views) Trampling polish on fracture edges of Moose femur after over five years of weathering on Isle Royale.
BOTTOM RIGHT: *Bos* humerus (?) fragment fracture edge weathered to a rounded shape. Scale bar = 500 microns.

Figure 73. Edge rounding due to gnawing and trampling.

TOP LEFT: Proximal fracture edges of subadult *Bos* femur damaged by captive wolves, then subjected to occasional light trampling by wolves and rodents. Approx. actual size.
TOP RIGHT: End-on view of above specimen edge, enlarged x 3.
CENTER LEFT: SEM close-up of rounded edge. Scale bar = approx. 200 microns.
CENTER RIGHT: SEM photograph of rounded (gnawed and trampled) edge. Scale bar = 100 microns. Note small incisions.
BOTTOM: Extreme close-up SEM photograph of rounded edge, showing scratching. Scale bar = 27 microns.

The inferentially isolated processes of abrasive smoothing or polish include:

(1) Frost-heaving and solifluction. Objects buried in periodically-frozen soils (even to depths greater than two meters) are moved upwards perpendicular to the slope of the ground surface due to the formation of ice lenses in the sediments. These lenses form when frost penetration of soils is relatively slow, allowing unfrozen water in the lower sediments to move upward by capillary action as the upper sediments freeze. As the freezing front moves downward, the newly-created pressure moves upward (Johnson and Hansen 1974). Frost-heaving (actual and potential) is greatest where snow or vegetative cover is scant to absent, and where soils are saturated or poorly-drained immediately prior to freezing. Rod- or cylindrically-shaped objects move upwards much more than do spheres, especially if their long axes are vertically-oriented. Long bones or shaft fragments that are situated lengthwise in occasionally-frozen soils would be heaved upwards at each freezing. Such forced movement is obviously in opposition to soil cohesion which holds bones down, and would undoubtedly abrade delicate edges as well as bone surfaces, creating some smoothing or scratching, depending on the coarseness of the soil matrix. Even gravels can suffer frost-heave disturbances if enough moisture is available. In addition, when the sediments thaw, gravity may cause settling on slopes to be vertical whereas upward motion was perpendicular to the slope surface; thus, on slopes that frost-heave, the overall motion of heaved objects is upward and then (upon thawing) downslope, unless dense vegetation is present to retard downslope movement. Objects in frozen and thawed soils would be subject to

abrasive rubbing by soil particles in several directions (Benedict 1976). Even objects in a periodically-frozen soil that are not heaved upward (such as those objects that are horizontally-oriented) may be dragged along the harder frozen layers of subsoil lying below them if they are situated in thawed (and thus settling), saturated upper layers of sloping ground that had previously been frozen (Sigafoos and Hopkins 1952). This dragging would of course also produce abrasive rubbing on fracture edges or bone surfaces.

(2) Physical weathering. Periodic heating and cooling causes the different physical constituents of bone to expand and contract at slightly different rates or to different degrees. For example, the tissue of haversian systems would not expand isomorphically with adjacent non-haversian bone tissue. Fine cracks or separations between structural features might result; water enters these cracks and exerts pressure on the walls of structural components such as osteons or bundles of collagen, especially after freezing (when water may expand up to 9% in volume). Salts in solution may enter the cracks, then crystallize following evaporation of water (Gerasimov and Glazovskaya 1965:24). Crystallization exerts pressure on restraining walls, contributing to enlargement of the space, or to fragmentation. Over time these mechanical processes create fragmenting or splintering of once-integrated components. Sharp edges, because they undergo physical (<u>and</u> chemical) weathering from both intersecting surfaces, would tend to show deterioration much more quickly than would each flat surface.

(3) Trampling: Trampling by hoofed animals often times takes the form of inadvertent kicking rather than placement of the hoof directly <u>upon</u> a surface object, pushing it against the underlying

sediments or ground surfaces. Thus, there is scattering and impact loading on bones that are kicked. The impact loading would seldom be of sufficient force to fracture whole and fresh long bones of larger ungulate species such as bison; weathered and degreased long bones of such species, on the other hand, being much more brittle, often times do fracture upon being kicked or stepped on by big animals (Figure 63). If the bones were first fractured and then stepped on or kicked, it is probable that some abrasive action would occur on sharp edges and on surfaces. In high-traffic areas where animals often pass over bones that are lying atop ground surfaces or that are shallowly buried in sediments, the trampled pieces would be well-abraded, even polished (see Brain 1967). Fracture edges might be even more smoothed or polished than flat surfaces. Usually the side or edges of the bone that faces upward, because they are subject to more severe weathering than those edges and surfaces lying against the ground, are much more brittle and develop more micro- and macro-cracks. Thus, these up-side surfaces and edges, if they are only occasionally polished or smoothed by trampling, may also continue to roughen due to natural deterioration, whereas downside surfaces or edges which are abraded against the ground during trampling are protected from such rapid degeneration. However, if the upsides are regularly and often stepped on, these surfaces and edges develop a high degree of polish. After a time, the upsides actually become resistant to further weathering deterioration, because the heavy abrasion removes surface irregularities and topographic highs, eventually creating smooth, unbroken surfaces that lack weak zones or places where cracking can begin (such as in low points between surface ridges).

Even extremely low-energy trampling such as that done by rodents in burrows or caves probably is sufficient to explain advanced edge-rounding on fractured bone specimens (Figure 70, Figure 71). Soft-footed animals such as wolves or bears, when they habitually tread on fractured bones lying in lairs, dens, homesites, or home territory trails, would contribute to the abrasive smoothing of edges (first) and surfaces (later).

Polish or rounding on fractured bone edges is grossly alike regardless of causal agency. Dry bone usually abrades to a high gloss polish but weathers to a dull, exfoliating roundness, while greasy bone simply rounds and acquires a much lower gloss (Figure 72). The rounded surfaces on abraded buried bone quite often show striations (furrows or sleeks) due to rubbing by single particles of sediments or by aggregates of particles (Figure 73), whereas gnawing rounding rarely shows these tiny striae often visible only at magnifications above 50X. Occasionally gnaw rounding is marked by tooth scratching. It therefore appears that abrasive smoothing of bone surfaces is not formed by the accumulative creation of many small striations, but instead by the plastic flow of surfaces under pressure (see Del Bene 1979).

CONSIDERATIONS ABOUT EQUIVOCATION

When an excavator decides to call an item a tool and not a refuse bone, or to call a bone fragment an artifact as opposed to a naturally broken specimen, he has made a decision or an interpretation, and most often the decision is based on what he considers to be archeological convention. It is difficult to translate tacit convention into an explicit list of attributes, or criteria, without belaboring what most archeologists would consider to be obvious or common sense. Yet in the case of bone interpretation, when conventional criteria are explicated, the specifications used to weight evidence in favor of or against artifactual agencies explaining bone modification may be critically open to question. Below are listed a few possible criteria that might be in an archeologist's mind when interpreting bone assemblages; this list is not intended to be thorough or complete, but can be used to illustrate that certain conventional criteria may be equivocal or questionable;

How does an artifact stand out from an ecofact?

(1) It has an ethnographically documented shape ("This looks like one of those...")

(2) It has a practical (if not an ethnographic) form ("This might have been used for...")

(3) It occurs (whatever the form) in an unquestioned site.

(4) Such an item has already been found in many places, within other sites or within the same site (it has a patterned form).

(5) Such items have unusual ("unnatural") modifications, such as very localized edge rounding, scratches, or whatever.

When examined alone, the weakest points are numbers 3 and 4. Point number 2 is not especially strong, unless it occurs in combination with point 3. Thus, an excavator finding a bone that appears to be an artifact (such as a fragment of long bone that looks like it might have been smashed for marrow extraction) in a site also containing hearth rock, charcoal, and chipped stone implements, would most likely be confident that his interpretation of that bone as an artifact is unimpeachable. An excavator finding a tooth-edged metapodial in an unquestionable site area would be even more confident in his interpretation of the item as a *bona fide* artifact.

However, if gnawing animals can be shown to produce (no matter how rarely) toothed metapodial flesher-like items, then obviously archeological interpreters who closely subscribe to interpretive convention will be involved in a much riskier undertaking.

Of course, it seems absurd to expect gnawing animals to possess the capacity adventitiously to manufacture ethnographically documented forms such as toothed fleshers; however, it is perhaps not absurd at all to advance the idea that some natural processes can produce very localized edge rounding or polish. Yet, however strongly one believes that this latter premise may be supportable, one can still argue that no one can seriously advance the former premise, which is not dissimilar to the ancient saying about monkeys, typewriters, and all of Shakespeare's works (given enough time, paper, and carbon ribbons).

The point to be made is that we have not adequately documented what <u>could</u> happen to bones and bone assemblages in nature; for example, we don't know how scavengers may disturb bones at abandoned human sites, although we have some beginnings of an idea (see McKinney 1974; Gifford 1978; Crader 1974; Haynes 1980a,b); we don't know how carnivores and scavengers may break bones under different ecological conditions (such as privation versus abundance of prey); we know very little about how extensive freeze-thaw cycling (with frost heaving, cryoturbation, and solifluction) may affect bone surfaces or may even fracture bones, just as we know little about how the oftentimes violent process of northern ice breakup on rivers may fragment big bones.

Until we learn a great deal more about these processes and agencies in nature, the sorts of vague conventional guidelines used in bone interpretation should no longer be dutifully applied, even at the cost of requiring perhaps embarassing re-interpretations of earlier assemblages and bone items.

CONCLUSIONS: INTERPRETIVE PROBLEMS

Bonnichsen (1973) discusses the problems of distinguishing man-altered bones from animal-altered bones. He is probably correct in implying that most archeological interpretations of faunal assemblages are based on personal impressions and not on ethnographic data or replicable experimental work.

In the paper he and his associates attempted to establish criteria for distinguishing the end effects of butchering, marrow extraction, and carnivore damage. After some discussion of the mechanics and operational principles of bone fracture, Bonnichsen presents the five attributes which serve to distinguish bones "manipulated by animals" from those "produced by man":

(1) Tooth perforation marks.
(2) Gnawing and scooping out of cancellous tissue.
(3) Crunching and splintering.
(4) Spiral fracture directed from epiphyseal end.
(5) Partial digestion.

It is perhaps to be inferred that those bone assemblages produced by humans would lack all the above attributes. Of course, in assemblages produced by animals, only one or two attributes might be found on any single bone.

(1) First, pertaining to Bonnichsen's attribute 1, if whole or major parts or many bones are found by an investigator, then tooth marks will generally be somewhere visible on specimens that carnivores have altered.

However, many times, especially where carnivores such as timber wolves have partially eaten prey of cervid size or smaller, long bones are broken up into spirally-fractured fragments, many of which lack tooth marks or edge and surface scoring from gnawing. Even slightly gnawed animal assemblages may resemble some bone from weathered human butchering and processing assemblages.

Hence, investigators should interpret small assemblages or single bone finds with extreme caution, only after adequate consideration has been given to alternative hypothetical agencies of bone damage. This would require familiarity with weathering and other natural forces which can alter bone in specific environments.

I emphasize that many so-called distinctively human patterns of bone breakage cannot be matched by examples from assemblages produced by carnivores, but many patterns _can_ be matched; not enough discussion has been published on these problems of interpretation.

(2) Gnawing of cancellous tissue, when incompletely done by some carnivores, may be mistakeable for chopping damage inflicted by bone tools during dismemberment.

Frison (1978:311) illustrates damage done to the femora of two bison (_Bison bison_) during prehistoric butchering in a site in North America. The femora of bison and moose (_Alces alces_), bones which are as robust as bison femora, are damaged in similar ways by wolves during their first feeding on fresh carcasses. Lion (_Panthera leo leo_), spotted hyena (_Crocuta crocuta_), and even some bears (e.g., _Ursus maritimus_) also produce this same type of damage on bovid bones.

Fortunately, if nearly whole femora are found, other invariably accompanying damage to the shaft or major trochanter can serve to identify carnivore agency. Again, researchers should proceed cautiously when attributing epiphyseal damage to man or animal, especially with small assemblages or fragmentary remains. Frison's illustrated examples are from a large assemblage, and are thus more likely to have been correctly interpreted by an archeologist of his experience and judgement. However, other archeologists who see the photographs might be led to believe that such damage as illustrated is conventionally to be interpreted as artifactually produced.

(3) Carnivore crunching and splintering occurs for the most part on bones from medium to small animals, and does not often resemble the results of human processing of bone for marrow extraction or grease production. Carnivore crunching and splintering of ribs and vertebral processes is generally recognizable from tooth perforations near irregular edges.

Wolves, bears, and lions seldom (if ever) crunch and splinter long bones from prey the size of adult bovids, although these bones may become fragmented if they are hoarded at den sites or are gnawed heavily at socializing sites.

(4) Spiral fractures are difficult _not_ to produce on fresh bones; when carnivores gnaw elements from prey the size of moose or smaller, they sometimes break up whole long bones, especially those that end up in den or rendezvous sites, producing many fragments from the center of the shafts. It may therefore be impossible to tell that the bones were broken up beginning at an epiphyseal end, since the epiphyses may be consumed or destroyed during gnawing.

Carnivores will not always gnaw or consume shaft fragments, so that these bone pieces lack signs of crunching, tooth perforation, or gnawing, just as many human-produced fragments lack evidence of hammer impact or solid support impact. A single blow of a hard hammer onto a large long bone can often produce a half-dozen fragments, only a couple of which will show signs of the blow. Thus, unless an assemblage contains more than the pieces of a few or single bones, it is difficult to assign an agency of breakage. Even where artifacts occur near the bones, one should always bear in mind the possibility that carnivores and scavengers could have gnawed bones or otherwise altered the material.

(5) Partial digestion: Some animals such as hyenas and wolves will mouth and gnaw compact bone fragments for long periods of time, producing edge rounding and surface damage not dissimilar to partial digestion. I know of no human agency which will leave bones looking partially digested. Some weathering of bone, as for example in shallow water or in humic sediments, will etch bone surfaces and damage the outer layers, but this damage is seldom mistakeable for partial digestion by carnivores. Investigators should gain familiarity with the results of all such processes.

The greatest (but underestimated) cause of incomplete interpretation is the result of carnivore damage to bones in assemblages which were originally generated by man. When Quaternary scientists use a cookbook-with-recipe approach to their analyses, one or the other agency of damage may go unapprehended. Probably many Quaternary bone assemblages from North American sites contain elements on which butchering marks have been obscured by carnivores (or vice versa, as suggested by P. Shipman [1981 pers. comm.] in regards to Plio-Pleistocene age bones from African sites), and signs of human fracturing have been overlooked due to the presence of unmistakeable gnaw marks. I suspect that this double use of bone, by humans and carnivores, may be true for materials in the Geist collections at the University of Alaska and at the American Museum of Natural History in New York, for the Old Crow, Yukon, materials, some Rancho la Brea materials, and materials from many Late Pleistocene archeological bone beds in western United States.

It should also be emphasized that humans could have made tools from bones that were originally gnawed by carnivores, if the bones were not excessively aged. It has been found that long bones retain a capacity to fracture spirally even when months old under certain conditions, such as natural refrigeration or intermittent water-soaking.

The attributes which Bonnichsen discusses as criteria for distinguishing animal agency of damage are undoubtedly of great usefulness for the faunal analyst, but problems of interpretation remain.

XI. Summary

This chapter presents a summary of observations and conclusions that I made during the research; some observations which pertain to the second research goal, that of deriving ecologic information from analyses of naturally modified bones, will be treated as law-like principles during future research on fossil bone collections. The final conclusions in this section are concerned with my first research goal, the differentiating factors which set apart cultural bone modifications from natural modifications.

(1) Where present in the biotic community, rodents will expectably gnaw only dry bones, bones that have aged _ex vivo_ more than 24 hours and usually no less than a season, whether still articulated or not. Some aspects of the original environment of bone deposition may be inferred from the presence and the amount of rodent gnawing; that is, it may be possible to tell if the bone was deposited in a dry, seasonally dry, or wet environment. This is a commonly accepted notion, although it is intuitively accepted by many paleoecologists.

(2) Rodents gnaw burnished or cast antler, but not antler in velvet, which is derived from ungulates dying or killed only in specific times of the year, usually summer; carnivores gnaw fresh antler in velvet, but do not typically gnaw dried (cast) antler. The season of site creation (by predatory carnivores) or later use (by rodents) may be inferred from examination of antler at the site, since fresh antler in velvet is only occasionally available. North American cervids grow and cast antler in the same seasons in all parts of their natural range.

(3) The effects of rodent gnawing vary in appearance (width, length, and depth of tooth grooves). However, gross visual examinations of tooth marks usually show diagnostic characteristics that are useful in distinguishing carnivore tooth marks from rodent tooth marks, from stone or bone tool marks, and from gravity- or stream-caused abrasion marks.

(4) Species of carnivores may be distinguished by examination of widths and lengths of tooth marks, and by comparisons of relative damage done to specific bone elements. The effects of gnawing by smaller carnivores and larger carnivores are often self-evidently distinguishable from each other, but the distinctions among the effects of gnawing by bears, cats, and canids will be useful in environmental reconstructions using fossil bone assemblages.

(5) It has been observed with both wild and captive animals that a single sequence of gnawing activity will invariably occur on specific bones, even if several animals gnaw the same bones. Therefore, if an investigator finds only a part of a bone showing certain damage types, in many cases it will be possible to discuss the species responsible and the damage done to the other (missing) fragments, and in some cases it may even be possible to state: whether the carnivores were suffering privation; whether or not the site was a den or a rendezvous; and whether or not the carnivores were domesticated, semi-domesticated, or wild.

Gnawing damage done by captive animals can be distinguished from gnawing done by wild animals; I propose that the distinctions would be similar to those expectable between domesticated animals and wild animals. The distinctions are based on degree of gnaw damage done to specific elements, and parts of specific elements attacked. In the absence of other material evidence, it may be possible to infer the past existence of camp dogs or pet wolves, upon inspection of the relative gnaw damage types evident on fossil bone collections.

(6) It is possible to make distinctions between bones used by carnivores as play items, food items, and social gnawing items (which are the bones chewed by wolves, for example, in rendezvous sites, dens, or social gathering sites). The amount of damage and the overall relative alteration are the variables to be examined to allow these distinctions. This information may be useful to differentiate bones collected by carnivores out of their own kills from human refuse site bones which have been "raided" or scavenged after site abandonment.

(7) Knowledge of sequences of animal gnawing can be used to weight evidence for or against carnivore agency, as opposed to cultural agency involved in the marking or fragmentation of certain bone elements. Bone fragments that lack certain parts but that show unusual breakage or shaping may be interpreted as tools or carnivore-gnawed fragments on the basis of the information from Chapters 4 and 8. For example, a femur with possible chop marks on the distal end, damage that may be similar both to the effects of gnawing and to the effects of bone tool use-damage inflicted to separate the patella from the rest of the leg, may be more likely only a carnivore-gnawed bone if the rest of the elements shows typical carnivore damage areas that would have been affected before the possible chop/gnaw are in question; if the rest of the bone does not have the damage inflicted by carnivores before the area in question is usually damaged, then the bone may be likelier a tool or artifactually damaged bone.

(8) The bones of bison, moose, deer, elk, and caribou may be flaked and fragmented by large wolves and bears, and tooth marking may be minimal or nonexistent on some fragments. Some killsites produced by wild wolves may contain nothing but spirally fractured bones, especially at killsites of prey animals that weighed less than 270 kilograms. It is also plausible that the edges of fractured bones could be flaked bifacially by the teeth of gnawing animals, and to be so modified as to appear deliberately retouched, in a manner similar to artifactual tool items.

(9) Rounding of bone edges due to gnawing, trampling abrasion, or tool use can be distinguished only microscopically, and even then there may be no unquestionable features on the rounded edges which would permit firm judgements about the causal agencies of alteration. Some edge-rounding agencies such as trampling create fine scratches and furrowing on bone surfaces that is usually not visible except at magnifications about 50X. The use of bone tools as meat- or ligament-choppers would not necessarily produce these fine scratches unless the meat to be chopped was unusually dirty. Bones abraded from tooth-wear usually show few to no scratches at magnifications over 25X. Trampled bones are often extensively scratched (Figure 74) but to be visible the bone surface sometimes must be magnified well above the capacities of inspection microscopes used in many archeological laboratories.

Conclusions

Fracturing of megafaunal bone elements may be due to cultural modification of bones during meat procurement, butchering, marrow extraction, or bone tool manufacture. Use of fractured bones as chopping, digging, cutting, or scraping tools produces abrasive rounding of fracture edges. However, spiral fracturing and edge rounding may also occur occasionally during carnivore gnawing, and has also been observed in bone assemblages that undergo heavy or moderate trampling; fracturing may conceivably occur in bone assemblages that undergo violent tumbling in rivers, or ice break-up in northern streams. In regards to the fossil assemblages described in Chapter 3, it is concluded that many of the questionable bone modifications in the curated collections could have been created by carnivore gnawing, and not necessarily by human subsistence or economic activity. Other modifications, such as possible "whittling" marks and especially flaking of mammoth bone fragments, cannot be adequately explained as a result of carnivore gnawing.

Fragmenting of the very largest fresh bones has been very rarely recorded in the field observations. I recommend that such breakage be additionally documented under natural and unsimulated conditions before archeologists use the argument that weathering or other natural forces <u>commonly</u> produce spiral fractures, or <u>might</u> produce such fractures in nonnegligible numbers.

I consider it unrealistic to believe that lions, wolves, Dire wolves, or large bears flaked the mammoth bones found in some Pleistocene-age assemblages. Only in cases of extreme privation or boredom should wild adult carnivores gnaw unusually large bones so obsessively as to completely fragment them, and under such conditions many bone fragments would be mouthed and gnawed so heavily that a high proportion of surviving (uneaten) pieces would exhibit extensively ground, furrowed, and tooth-worn surfaces.

I must finally conclude that the operational definitions advanced by Stanford (1979a), Morlan (1980), and others for the Colorado and Yukon bone assemblages, that some bone specimens are more likely to have been modified by human behavior than by natural agencies, are not weakened by my research observations, although they are still positively supported only by their plausibility.

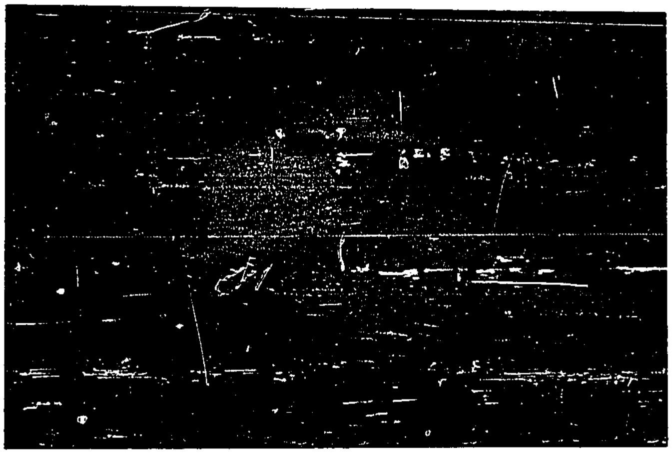

Figure 74. Fracture edge of part of innominate of Teleceras fossiger, a Pliocene age rhinoceros, recovered from near Long Island, Kansas (Smithsonian Institution specimen). Edge rounding and scratches possibly due to sediment churning and trampling by heavy animals.

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ADDENDA
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The Berezovka mammoth, a young male animal which died when it fell and became mired in mud at the edge of the Berezovka River during the Late Pleistocene period, is approached by wolves. Illustration from J. Augusta and Z. Burian, A Book of Mammoths. M. Schierl, translator. London: Paul Hamlyn. Translation copyright 1963.