

DEER REMAINS IN ARCHAEOLOGY WITH SPECIAL
REFERENCE TO THE MANDIBLE OF MATURE ROCKY
MOUNTAIN MULE DEER

by

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Abstract

This study is concerned with the estimation of a deer's absolute age, sex, weight and season of death from a single anatomical element. The value of these population parameters in zooarchaeological research is discussed and former methods for their derivation are reviewed. The results of an osteometric and histological analysis of the mandible in a modern sample of mature Rocky Mountain mule deer from the Cache la Poudre reserve, Colorado are then presented and discussed. From this analysis, more accurate approaches to the assessment of a deer's age, sex, weight and season of death are derived.

By means of simple regression analysis, significant correlations are shown to exist between various dimensions of the mandible and the bled carcass weight of mule deer. The strength of these associations increases substantially when seasonal fluctuations in weight are incorporated in the analysis. Significant correlations are also shown to exist between mandibular measurements and the skinned and eviscerated carcass weights of mature mule deer. The resultant regression equations are valuable predictive tools in the estimation of meat weights for prehistoric mule deer.

From the mandibular measurements, linear discriminant functions are also derived to segregate the sex of mature deer.

The resultant linear functions identify and classify the sex of an unknown with an accuracy of 88 percent or more. The accuracy of the functions in the analysis of prehistoric fauna, however, requires further testing.

Decalcified and stained longitudinal thin sections of the first mandibular molars are shown to be the most reliable for establishing the absolute age of prehistoric fauna. In the present study, ninety-one deer were aged independently from incremental growth lines of the central incisor and the first mandibular molar. There is perfect agreement between the age estimates for 80 of the deer. For the remaining 11 specimens, the disagreements in the age estimates do not exceed plus or minus one year. Possible explanations for these discrepancies are presented.

Incremental growth lines, as seen in decalcified and stained thin sections, are also shown to be reliable for inferences on a deer's season of death. This study presents a methodology for the derivation of a ratio of outer increment width over expected increment width. As shown, this ratio increases linearly from March until the end of December. Thereafter, there is no demonstrable increase in the outer increment until the succeeding March. The resultant annual growth curve for the cementum deposit of the first mandibular molar permits accurate assessments of a month of death for mature mule deer. Greater precision in the seasonality estimates, however, requires further research.

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Any work, such as the present thesis, exists only through the efforts of many individuals. I would like to take this opportunity to acknowledge and extend my gratitude to those who have contributed to the outcome of this research. The list here is not all inclusive, however, as I am indebted to many others for their support.

To Allen E. Anderson, Wildlife Researcher for the Division of Wildlife, Colorado, I cannot adequately express my gratitude and appreciation. It is no overstatement to say that without his interest, cooperation and encouragement, none of this would have been possible. I can only hope that my research and results have done justice to his perfect sample of mature mule deer mandibles.

To Kwai Lee, technician in the Department of Biology, Simon Fraser University, I owe a debt of gratitude for his willingness to train and assist a novice in applied histology. His cooperation and moral support were vital in the preparation of the decalcified thin sections.

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1. Introduction

As Kipling implies, scientific understanding does not advance from untruth to truth, but shifts from one viewpoint on a subject to another. Each viewpoint of the scientific "truth" has its place in the passage of history, and each viewpoint is conditioned by and has its utility in the economic, social, and technological milieu of its day (Spiess 1979:1).

The present thesis is not an analysis of faunal remains from an archaeological site nor is it a synthesis of zooarchaeological data from a number of sites. In fact, prehistoric faunal remains are peripheral to the present discussion, though the results of this analysis hopefully will benefit future zooarchaeological research in North America. Neither is this work a guide to the identification of Odocoileus remains nor is it a detailed account of deer biology, ecology and behaviour. Instead, this thesis is an introduction to the recent literature on the physiology and osteology of deer as it relates to some of the research goals of zooarchaeology. For that reason, the present work focuses on a detailed examination of selected skeletal elements in order to evaluate their potential as indicators of the animal's age, sex, weight and season of death. It presents a different approach to the analysis and interpretation of zooarchaeological data, an approach which hopefully will have more accurate predictive and explanatory power than its antecedents.

The selection of deer for intensive study herein reflects the substantive body of biological data relating to this genus and the relative importance of deer in North American prehistory.

The extensive distribution of deer makes it the favored big game of North American hunters today (Taylor 1956). This popularity extends into prehistory where deer also ranks as the primary prey species for most native American groups. Ethnographies throughout North and Central America document the importance of deer to the subsistence economy and material culture of aboriginal populations (Beaglehole 1936; Castetter and Bell 1942, 1951; Goddard 1913; Hill 1938; Nequatewa 1946; Parsons 1922; Steward 1938, 1955; Suttles 1951; Swanton 1946; Tietiev 1944, and Tooker 1964). In fact, intertribal wars at the time of contact often centered on the deer hunting rights of each group (Gramly 1977; Hickerson 1965, and Watrall 1968). In prehistoric sites, deer bones also form one of the major components in the faunal assemblages from 7000 years ago until the present (Cleland 1966; Flannery 1967; Gustafson 1972; Haury 1950, and O'Connell 1975). Even after the introduction of agriculture, deer meat persists as an important constituent of the aboriginal diet (Baker 1930; Cleland 1966; Flannery 1968; Greene and Mathews 1976; Harris 1977, and Smith 1974a, 1974b, 1975a). The bones of the genus Odocoileus thus represent a significant proportion of the faunal remains in many North American sites (Olsen 1971). The osteological remains of a species which occupies such an important place in prehistoric economies and adaptations are certainly worthy of detailed examination and analysis.

Though the relative importance of deer in North American sites may reflect recovery bias (Grayson 1981; Payne 1972a, 1975a and Thomas 1969), the presence of deer in the faunal assemblages

of many sites is unquestioned. Currently, faunal analysts note the relative proportion of deer bones in the assemblages but few exploit the potential interpretive value of these bones. While zooarchaeologists are often cognizant of the current biological research relating to the osteology of deer, few are willing to acquaint themselves with the pertinent techniques of biology and to apply these in their analyses of archaeological material. Instead, faunal analysts tend to analyze and interpret prehistoric faunal populations employing analytical procedures now known to be inaccurate in the study of modern populations. They rely on archaic methods (e.g. Severinghaus' 1949a method for aging deer and Taber's 1956, 1963, 1971 criteria for sex) to determine the age, sex, weight and season of death of the deer in their samples (see Emerson 1979; Smith 1975a, and Wilson 1974). If obtaining this information is one of the main objectives of the analysis, then zooarchaeologists should strive to secure the most accurate results possible. Such precision frequently requires time and money. As the present study indicates, the predictive potential of current biological techniques makes worthwhile the requisite expenditure of time and money.

Biological Techniques and Their Relevance in Zooarchaeology:

The direct application of biological techniques to estimate the age, sex, weight and season of death of prehistoric fauna is generally not practicable at present. Current research in wildlife biology, for example, incorporates the prediction of animal

weight from specific osteological and carcass measures. Here, wildlife biologists note a good correlation between the weight of an ungulate and the total length of some of its bones (Anderson, et al. 1974 and Lowe 1972). Further, researchers in the African savanna, in their attempt to discover a practical technique for determining the weight of the larger, bulky ungulates, document a comparable correlation between the weight of the animal and the weight of selected parts of its carcass (Ledger 1963). Wildlife biologists today also determine the sex of carcasses from osteometric attributes of certain skeletal elements. They measure various dimensions on complete bones and subject these data to statistical analyses to obtain a sex determination (Bergerud 1964 and Rees 1971a). In all cases, wildlife biologists measure only complete skeletal elements. The zooarchaeologist, on the other hand, bases his analysis almost exclusively on fragmentary bones. To use these techniques in zooarchaeology therefore, the analyst must demonstrate a correlation between the length of the fragment and the length of the complete element or between the length of the fragment and the weight of the animal. Furthermore, he must discover a relationship between the metric attributes of bone fragments and the sex of the animal. Establishing such relationships requires the collection and analysis of a modern sample using measurements and procedures conducive to the study of fragmentary faunal remains.

Current research in wildlife biology also focuses on the accuracy of age determination from incremental growth zones in the teeth and bones of mammals (Gasaway, et al. 1978; Keiss 1969;

Klevezal and Kleinenberg 1969; Morris 1972, and Spinage 1973, 1976). Wildlife management personnel select the incisor for thin sectioning because this tooth is easy to extract under field conditions (Hemming 1967; Kerwin and Mitchell 1971; Lockard 1972, and Turner 1977). For archaeological specimens, the ease with which single rooted teeth are lost post-mortem results in a lack of incisors (Benn 1974; Gilbert 1973, and Payne 1973). To employ this method of age determination in zooarchaeology therefore, the faunal analyst must examine those teeth occurring most frequently in the archaeological assemblages. He then must select the correct part of the tooth and use the appropriate type of section to obtain the most distinct annuli possible. Further, he must modify the histological procedures of wildlife biologists to accommodate prehistoric remains. The successful application of this method of age determination in zooarchaeology thus requires not only a familiarity with the technique but also an ability to modify the procedure to suit the nature of the archaeological material.

Wildlife biologists rarely address the question of seasonality since their collections usually consist of animals killed during the fall hunting season. They deal with natural deaths, poachings and road-killed animals throughout the year but they generally examine these carcasses within weeks of the animal's death. Conversely, the zooarchaeologist's main goal frequently is to determine an animal's season of death and, by inference, the season of site occupation. The current research on the incremental growth of tooth cementum offers a method for the

accurate assessment of seasonality. The appositional growth of cementum is a continual process marked by annual events in the growth of an animal (Klevezal and Kleinenberg 1969; Miller 1974b; Morris 1972, and Sauer 1973). Most wildlife management personnel report the formation of the wide, light-staining band during the summer months and the deposition of the narrow, dark-staining band during the winter months (Boozer 1970; Craighead, et al. 1970; Hemming 1969; Miller 1974b; Olson 1967; Reimers and Nordby 1968; Stoneberg and Jonkel 1966, and Thomas and Bandy 1973). These increments provide a basis for the assessment of a deer's season of death with a precision exceeding the present summer-winter dichotomy recorded in the biological literature (Miller 1974b; Olson 1967; Reimers and Nordby 1968, and Thomas and Bandy 1973). To attain this level of precision, the zooarchaeologist must attempt to quantify the rate of cementum growth throughout the year. In order to accomplish this, he must collect or obtain a sample of teeth from deer shot at successive intervals throughout one or, preferably, several consecutive years and quantify the extent of cementum growth in each.

The acceptance of biology's analytical procedures in faunal analysis also assumes an understanding of technique application and limitation. Hence, the zooarchaeologist, like the wildlife biologist, must establish the goals of his study and design his research to satisfy those objectives. He then can select and modify the analytical procedures of wildlife biologists to suit his specific requirements. Such attempts to use and modify the techniques of biology will enable faunal analysts to familiarize

themselves with the problems of technique application and provide them with the necessary experience to prepare their data and interpret the results.

Aims and Research Objectives of the Present Study:

The principle goal of the present research is to evaluate the potential of the deer mandible as an indicator of an animal's age, sex, weight and season of death. As such, it attempts to derive these four important population parameters from a single anatomical element. Here, the collection and analysis of a modern sample of deer is necessary to establish the relevance and reliability of the analytical techniques employed. This sample must include data on the age, sex and weight of each specimen collected. Further, the collection period of the sample must extend over one or several consecutive years to assess properly the potential of the incremental growth lines in the assessment of seasonality. Initially, an attempt was made to obtain such a sample using natural deaths, road-killed and hunter-killed deer from southwestern British Columbia. This failed due to a paucity of reported natural deaths and road-kills during the spring and summer of 1979. A request then was forwarded to Frank L. Miller of the Canadian Wildlife Service for the use of his caribou sample. He provided forty caribou molars which had been stored in 5 percent formalin for about 10 years. These teeth, when sectioned, failed to yield distinguishable lines in the outer part of the cementum layer, presumably as a result of prolonged

storage in formalin (Disbrey and Rack 1970, and Hill 1975a). A final plea for help then was addressed to Allen E. Anderson, Wildlife Researcher for the State of Colorado, Division of Wildlife. Within weeks, a gift package containing 102 mandible pairs was received. An invoice listing the age, sex, weight and date of death for the respective animals was included. I cannot adequately express my gratitude to Mr. Anderson for providing such a perfect sample. This sample is described in chapter two of the thesis, whereas the pertinent information for each deer in the sample is listed in Appendix I.

To facilitate statistical analysis of fragmentary archaeological material, eleven skeletal dimensions were quantified for each left mandible in the present sample. Appendix II provides descriptions for these dimensions while Appendix III lists the eleven measurements as well as the identification number, sex, age and four weight values for each specimen. Values of 000.0 in this table indicate missing data due to the fragmentary nature of some bones or missing weight data. During the actual analysis, the histological procedures of wildlife biology were modified to accommodate fragile archaeological materials. Chapter three of this study thus discusses the revised laboratory methods for age determination and seasonality assessment. Appendix VI outlines the proposed laboratory procedure while Appendix VII provides formulae and instructions for the preparation of the chemical solutions.

Chapter four discusses the approaches presently used to estimate the weight of those ungulates represented in archaeo-

logical assemblages. It also summarizes current research on weight estimation in wildlife biology and proposes regression analysis as a viable alternative for predicting the weight of mule deer from various mandibular measurements.

Chapter five evaluates the approaches of zooarchaeologists and wildlife biologists to sexing ungulates from their skeletal remains. This chapter then outlines a new method for sex determination in mature mule deer using skeletal measurements of the mandible. These data are subjected to discriminant function analysis to obtain weighted values allowing the faunal analyst to identify and classify an unknown with the least chance of error. The statistical techniques employed are outlined in Sneath and Sokal (1973) and are consistent with those presently used in numerical taxonomy.

Chapter six reviews the methods of age determination in zooarchaeology and summarizes those aging methods currently used by wildlife biologists. It then outlines the most viable method for determining the absolute ages of prehistoric fauna and justifies the use of this method in zooarchaeology.

Chapter seven, in turn, surveys zooarchaeological approaches to the assessment of seasonality from faunal remains. It also evaluates the potential use of incremental growth structures in such assessments and outlines a new approach capable of providing more accurate estimates of a deer's season of death.

Chapter eight summarizes the results of the present research and suggests new avenues for zooarchaeological research in North and Central America.

2. The Sample

It is suggested that archaeologists interested in the furtherance of osteoarchaeological analysis investigate the possibilities of osteometric research on modern animal populations (Emerson 1978:41).

The sample of deer mandibles used in the present research was collected by Allen E. Anderson and Dean E. Medin, researchers for the Division of Wildlife, Colorado. The sample, as provided by Anderson, comprises one hundred and two mandible pairs from wild Rocky Mountain mule deer, Odocoileus hemionus hemionus, collected at approximately weekly intervals over a 4-year period (Anderson, et al. 1974). Specifically, these mandibles derive from mature deer previously aged by Erickson (1967) using cementum annuli counts of the central incisor. All pertinent information for each specimen, including the identification number, sex, date of death, Erickson's age estimate from the incisor, and my age estimate based on cementum annuli counts of the first molar is tabulated in Appendix I of this study. Data relating to the collection area, the Cache la Poudre deer population and the methodology for the collection and analysis of the sample are summarized below. This information derives almost exclusively from the publications of Anderson, et al. (1970, 1971, 1972a, 1972b, 1972c, 1972d, 1972e and 1974). Data relating to the identification procedures, animal weights and the removal and cleaning of skeletal elements are the result of correspondence with Mr. Anderson.

The deer sample was collected on the eastern slope of the Front Range within a 1,368 km² portion of the Cache la Poudre drainage. The collection area, as shown in Figure 1, lies within and adjacent to the Roosevelt National Forest in Larimer County, northcentral Colorado. Lovering and Goddard (1950) discuss the geology of the range in this area whereas Costello (1954), Marr (1961) and Marr, et al. (1968) describe the climate and major ecosystems of the Front Range. Dietz, et al. (1962) and Loveless (1967) provide detailed analyses of the vegetation within the Cache la Poudre drainage. Specific data relating to the temperature, precipitation, snow depth, accessible forage and deer density within the study area during the period of collection are available in Anderson, et al. (1972a, 1972b, 1974), Medin and Anderson (1965) and Short, et al. (1966). Actual reports on this sample of the Cache la Poudre deer population include Anderson and Medin (1967, 1969, 1971); Anderson, et al. (1970, 1971, 1972a, 1972b, 1972c, 1972d, 1972e, 1974); Erickson (1967); Erickson and Seliger (1969); Erickson, et al. (1970); Farris, et al. (1967); Markwald, et al. (1971); Medin and Anderson (1979); Nicolls (1971); Rees, et al. (1966a, 1966b); Short (1970); Short, et al. (1965, 1966, 1966); Whicker (1964), and Whicker, et al. (1965, 1966a, 1966b, 1966c, 1967). This thesis is therefore an additional report in the series on the Cache la Poudre deer population.

As part of a broad ecological study of this deer population, Anderson and his co-workers shot mule deer at approximate weekly intervals from April 13, 1961 to April 27, 1965. For each month

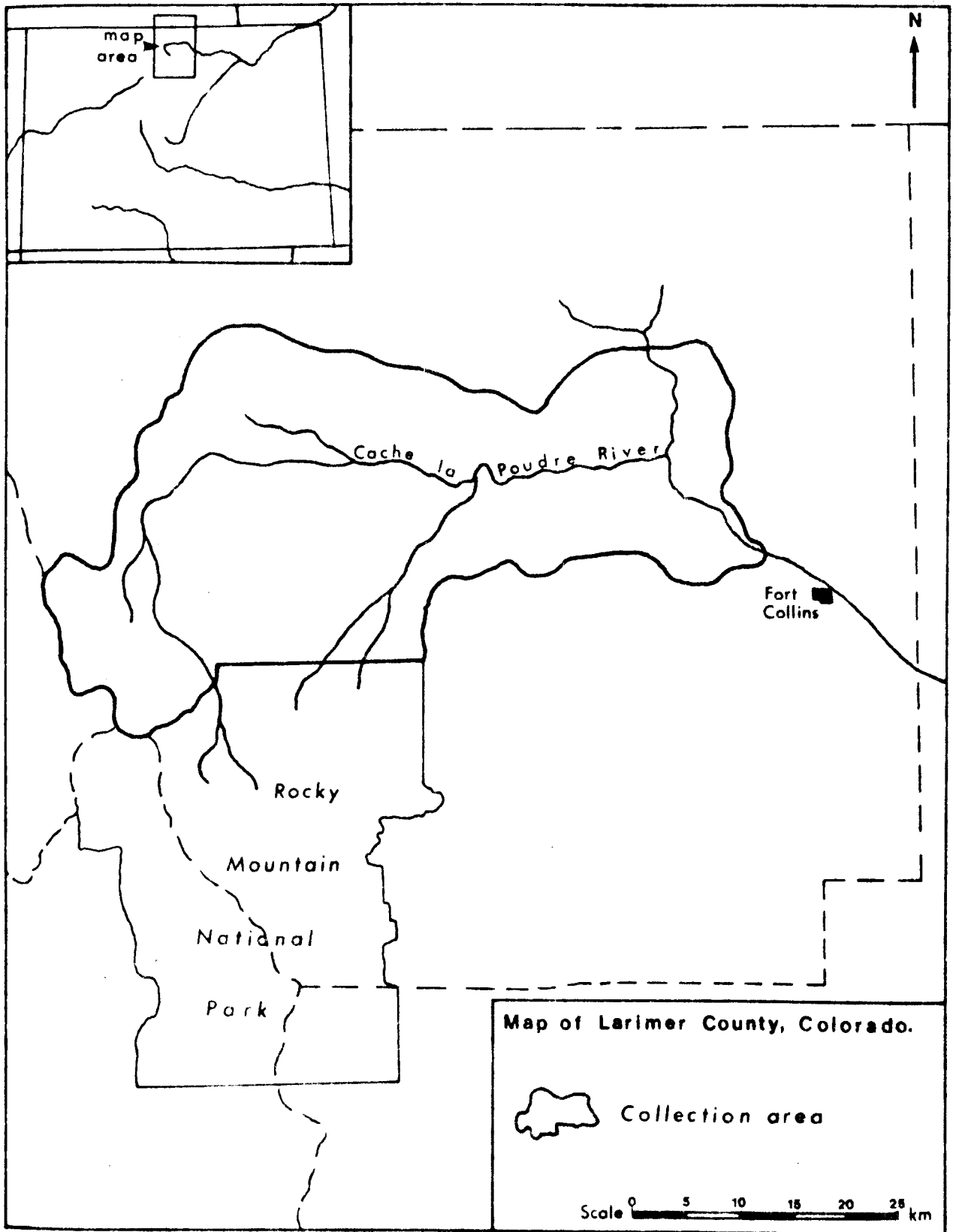


Figure 1: Map of Larimer County, northcentral Colorado, showing the location and approximate extent of the collection area.

of this 4-year period, they attempted to collect one immature (less than 18 months of age) and one mature animal of each sex from widely scattered portions of the deer's seasonal ranges. From June through September, the deer were shot in their 720 km² summer range above an altitude of 2,592 meters. During the remainder of the year, they were collected in their 648 km² winter range below the aforementioned elevation. In all, one hundred and ninety-two deer were shot at sites whose elevations ranged from 1,677 meters to 3,323 meters. A number of road-killed deer and natural deaths within the study area supplemented the above sample. The total sample collected for the ecological study thus included 200 Rocky Mountain mule deer of which 86 were males and 114 were females.

Most deer were shot through the spine in the thoracic or cervical region with mean times of death of 0915 ± 5.58 hours for males and 0832 ± 3.65 hours for females. After aspiration of the blood from the heart and mensuration of five carcass attributes, the intact deer carcasses were wrapped in tarpaulin and transported to the laboratory. The actual transport distances ranged from 16 to 113 kilometers. In the laboratory, several additional carcass, bone, organ and gland attributes were measured. Of interest to the present research are the carcass weights obtained for each animal in the sample. Within hours of death, the deer carcasses were weighed to the nearest 0.1 kilogram on a double beam balance. Four weight measures were recorded for each specimen as follows:

- Weight 1: Bled carcass weight - This is the weight of the intact deer carcass except for the loss of blood and tissue from the gunshot and, in some cases, the pelage lost during transit from the kill site to the laboratory.
- Weight 2: Eviscerated carcass weight - This is the bled carcass weight minus the weight of all thoracic and abdominal viscera (except the esophagus and trachea) and fat.
- Weight 3: Bled carcass weight excluding the intact stomach - This is the bled carcass weight minus the fresh weight of the intact stomach with fat and extraneous tissue removed.
- Weight 4: Skinned and eviscerated carcass weight - This is the bled carcass weight minus the weight of all thoracic and abdominal viscera (except esophagus and trachea), fat, hide and antler. The hide was removed without appreciable loss of subcutaneous fat and each antler beam was sawed off at the junction of the beam and pedicle.

The respective weights of each specimen are listed as W1, W2, W3 and W4 in Appendix III of this thesis. During the initial phase of the study, Anderson and his collaborators attempted to obtain densitometric estimates of carcass fat by weighing the unskinned carcass. Therefore, no skinned and eviscerated carcass weights were obtained for specimens 2 to 30 of the sample used in this study. Weights for specimens 001 and 180 were not obtained due to the physical condition of these road kills. Other missing values in this appendix indicate a lack of data resulting mainly from organ puncture by the bullet or bullet fragments.

In the laboratory, Anderson and Medin assigned ages to each specimen within 4 to 24 hours of death. All age estimates were made after removal of the lower jaw. To disarticulate the jaw,

they cut the appropriate muscles and forced the anterior portion of the mandible downward and backward. They then pulled the jaw forward to strip the hide, muscle and connective tissue from the mandible in one operation. To age deer with deciduous dentition, Anderson and Medin used the tooth replacement chronology of Robi-
nette, et al. (1957). To age the 110 deer with permanent teeth, they combined three criteria; namely the lingual crown heights, the molar tooth ratio and photographs of jaws from known-age mule deer (Erickson 1967). Subsequently, Erickson (1967) removed the incisiform teeth from 95 of these 110 mandibles and prepared 95 micron cross sections. These thin sections were decalcified and stained to provide accurate counts of the cementum annuli. A comparison of these independent age estimates then confirmed the accuracy of cementum annuli counts for absolute age determination in older animals. In the final report therefore, Anderson, et al. (1974) used the latter age estimates for deer with a permanent dentition. The sample used in the present research includes the 95 mandibles aged by Erickson (1967) and 7 additional jaws from mature deer aged by Anderson and Medin. Figure 2 illustrates the sex and age structure of the entire deer sample and the relative distribution of the 102 specimens used in this research.

To clean the elements, Anderson and his co-workers initially fitted an aluminum identification tag to the diastema and placed the jaw in a dermestid beetle colony. Later, they simply scraped the mandibles clean. To avoid subsequent misidentification, they then printed the specimen number on each mandible using India ink. They also prepared a cardboard tag bearing the specimen number,

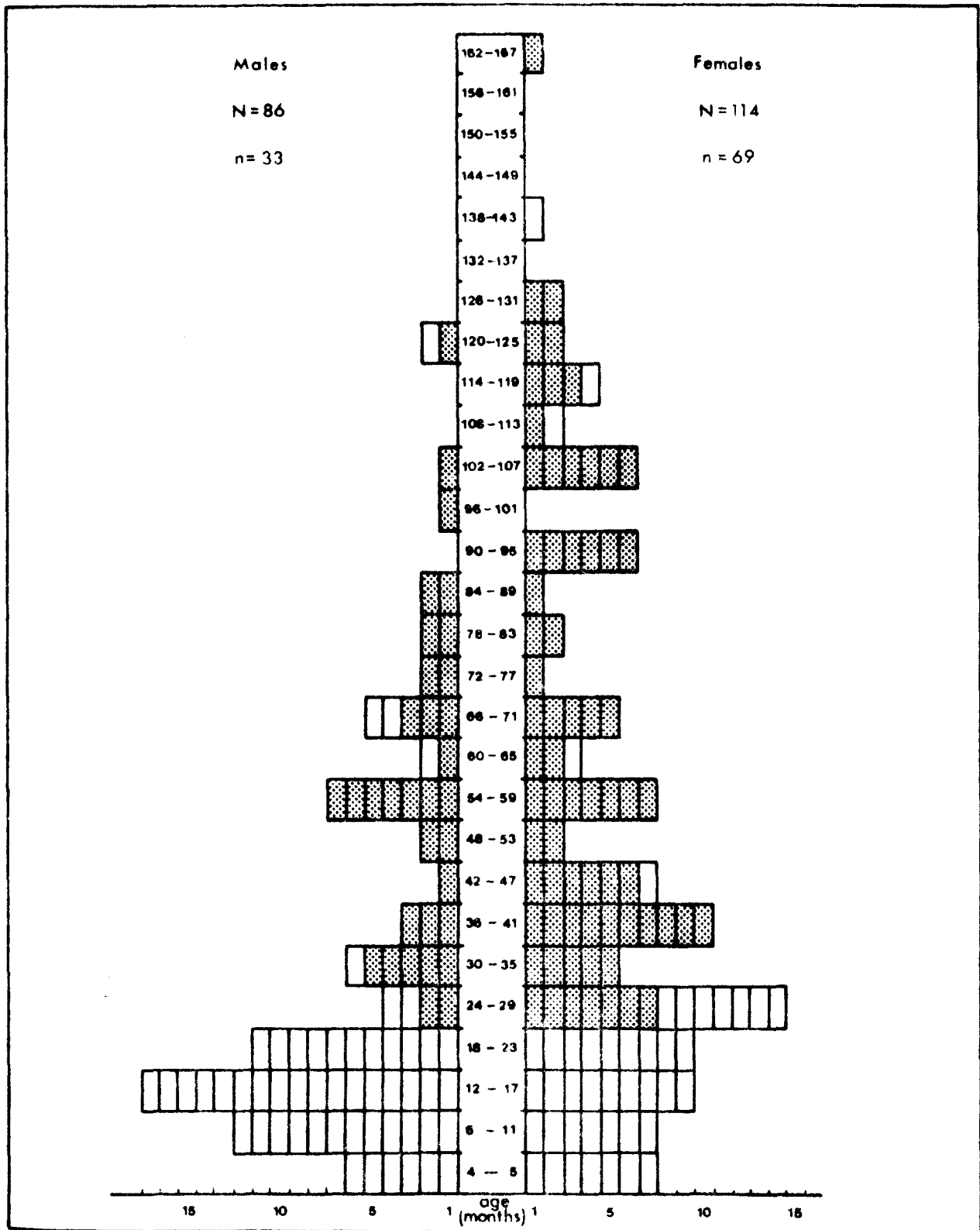


Figure 2: Graphic representation of the age and sex distribution of the deer sample relative to the 200 mule deer collected by Anderson, *et al.* (1974). Each rectangle represents one animal. Shaded rectangles indicate the deer used in the present research.

collection date and sex of the animal. These tags were bound to the respective mandibles with a string. Finally, they strapped numbered and dated aluminum bands to the diastema of each left mandible. After mensuration, they bound both mandibles together with an elastic band for storage. The mandibles were stored for only part of the 14 years since their collection. In the late 1960's, Erickson (1967), Erickson and Seliger (1969) and Rees, et al. (1966a, 1966b) used some of the mandibles for their research. Subsequently, various teaching assistants in the Department of Fishery and Wildlife Biology at Colorado State University, Fort Collins utilized the mandibles for instructional purposes.

In March 1979, I wrote Mr. Anderson requesting the use of his Rocky Mountain mule deer sample. In April 1979, I received a box containing the 102 mandible pairs and an invoice listing the identification number, sex, age and collection date for each deer in the sample. All specimens noted on the invoice were present and in good condition. Only 6 mandibles sustained damage during transport and these were glued prior to the laboratory analysis. Three identification tags accompanied each mandible pair. Cross-checks of these produced no incongruities. A comparison of these data with those listed in Erickson's (1967) thesis confirm the the authenticity of the sample. This sample is thus dependable and satisfies all the prerequisites for this research.

3. Laboratory Methods

It is best to prove things by actual experiment then you know; whereas if you depend on guessing and supposing and conjecturing, you will never get educated (Twain 1971:56).

Introduction:

In wildlife biology, absolute age determinations occur, for the most part, in a laboratory environment. A zooarchaeologist wishing to employ this method of age estimation must learn, and probably modify, the basic laboratory procedure for his research. This chapter outlines the laboratory methods of wildlife biology and specifies procedural modifications for the analysis of archaeological material. It also discusses the many problems encountered while fixing, decalcifying, sectioning and staining the mandibular molars of modern deer. Finally, Appendix VI proposes a laboratory routine for the analysis of archaeological deer mandibles.

The microscopic examination of any osseous material entails a certain amount of tissue destruction. Accordingly, the proper identification, description, photography, and mensuration of all elements designated for such examination must precede the basic histological work. The efficacy of any such macroscopic analysis depends on the cleanliness of the material. For this sample, the primary task then was to remove all of the dried flesh adhering to the mandibles. To facilitate this cleaning, the elements were

soaked in lukewarm water. The subsequent removal of the periosteal tissue was possible using a stiff brush. Concurrently, the mandibles were examined for obvious pathologies or abnormalities. These were recorded for future reference. To avoid any future misidentification of specimens, the appropriate identification numbers then were inscribed on each mandible. These were written in bold print on the lingual surfaces of the ascending rami using a black Staedler lumocolor permanent marker. No photographs were taken of these mandibles though the compilation of a photographic record for all archaeological bone is recommended. Once cleaned and catalogued, the mandible pairs were bound anew with a strong elastic band and stored until further processing.

Measurement for Weight Estimation and Sex Determination:

In this sample, 87 left mandibles and 2 right mandibles were intact. These complete elements and eleven incomplete mandibles (10 rights, 1 left) were measured according to the specifications of von den Driesch (1976) and Rees (1969). Selection of individual measurements reflected their appropriateness in the mensuration of archaeological materials. Throughout, dental variables were excluded since these apparently relate to the age and race of deer (Rees 1971b). A total of eleven skeletal variables were measured on each complete mandible. These are illustrated in Figure 3 and described in Appendix II of the thesis. Appendix II also provides instructions for each mensuration and lists the corresponding measures in Rees (1969) and von den Driesch (1976).

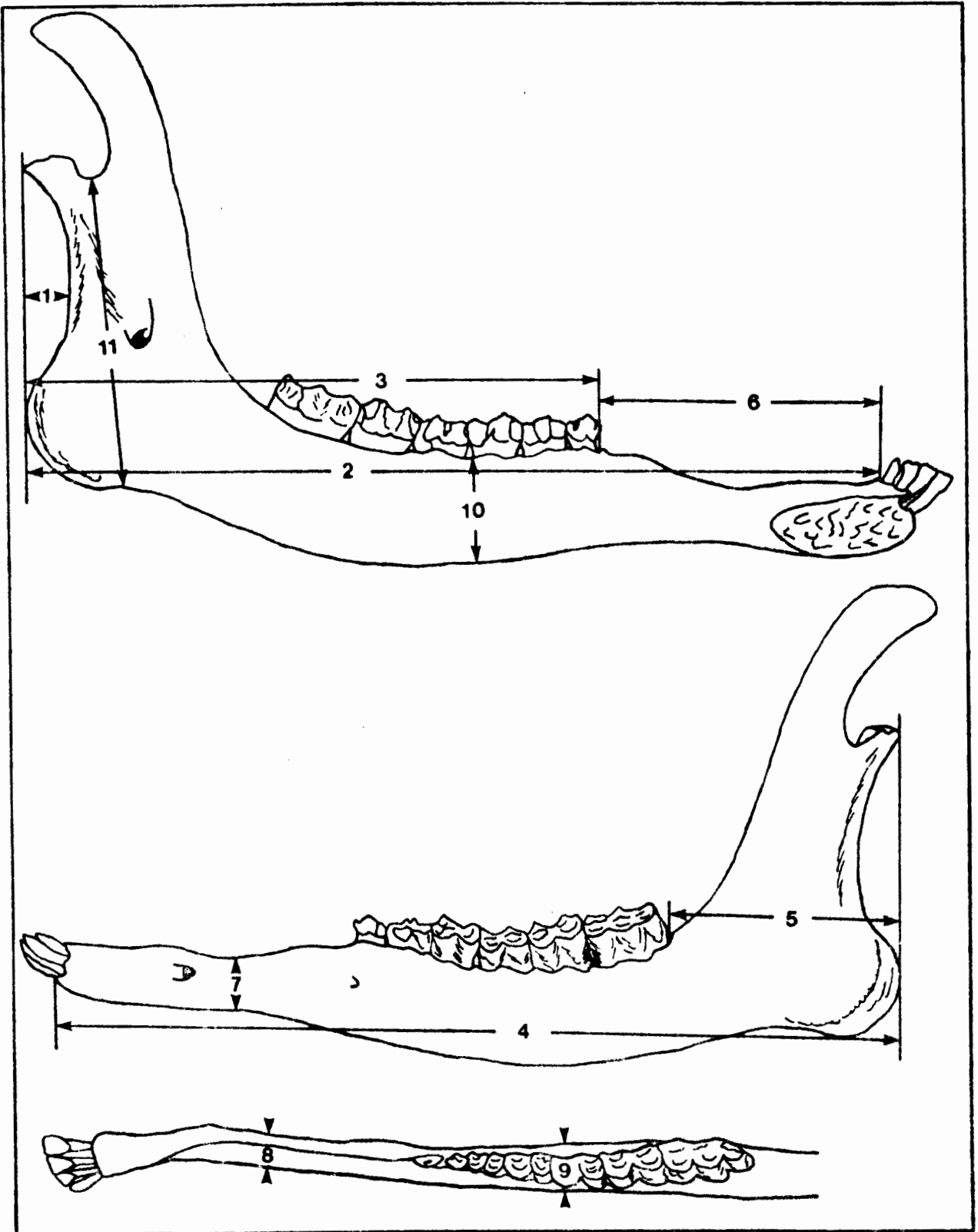


Figure 3: Diagram of a mule deer mandible illustrating the eleven mandibular measurements used in the osteometric analysis.

Appendix III then records the 11 measurements and the 4 weight measures for each specimen in the sample.

To minimize measurement error, a mandible board was designed and constructed. This board, as shown in Figure 4, consists of a 28 X 40 cm plywood base to which are fastened two 4 X 12 cm "side walls" and a 4 X 40 cm "base wall". Graph paper, calibrated in millimeters and glued to the plywood base, provided the scale. During mensuration, as illustrated in Figure 5, the gonion caudale and the mandibular condyle contacted the "side wall" while the ventral border of the mandibular corpus touched the "base wall". These three points of contact ensured uniform positioning and consistent mensuration of all mandibles. Measurements 1 to 5 were taken to the nearest millimeter using this board. Measures 6 to 11, on the other hand, were recorded to the nearest 0.1 mm using dial calipers.

The main objective of this osteometric analysis was to discover relationships between specific mandibular measurements and various attributes of the animal. In wildlife biology, for instance, researchers note an association between the total length of the mandible and the weight of the animal (Anderson, et al. 1974 and Lowe 1972). For archaeological remains, total mandible length is not always determinable. In this analysis therefore, it was important to discover other mandibular dimensions which related to the total length of the element and, by extension, to the weight of the animal. In fact, dimensions 2, 3, 5, 6 and 11 in Figure 3 correlate well with the total length of the mandible (measurement 4) and are measurable on most fragmented mandibles.

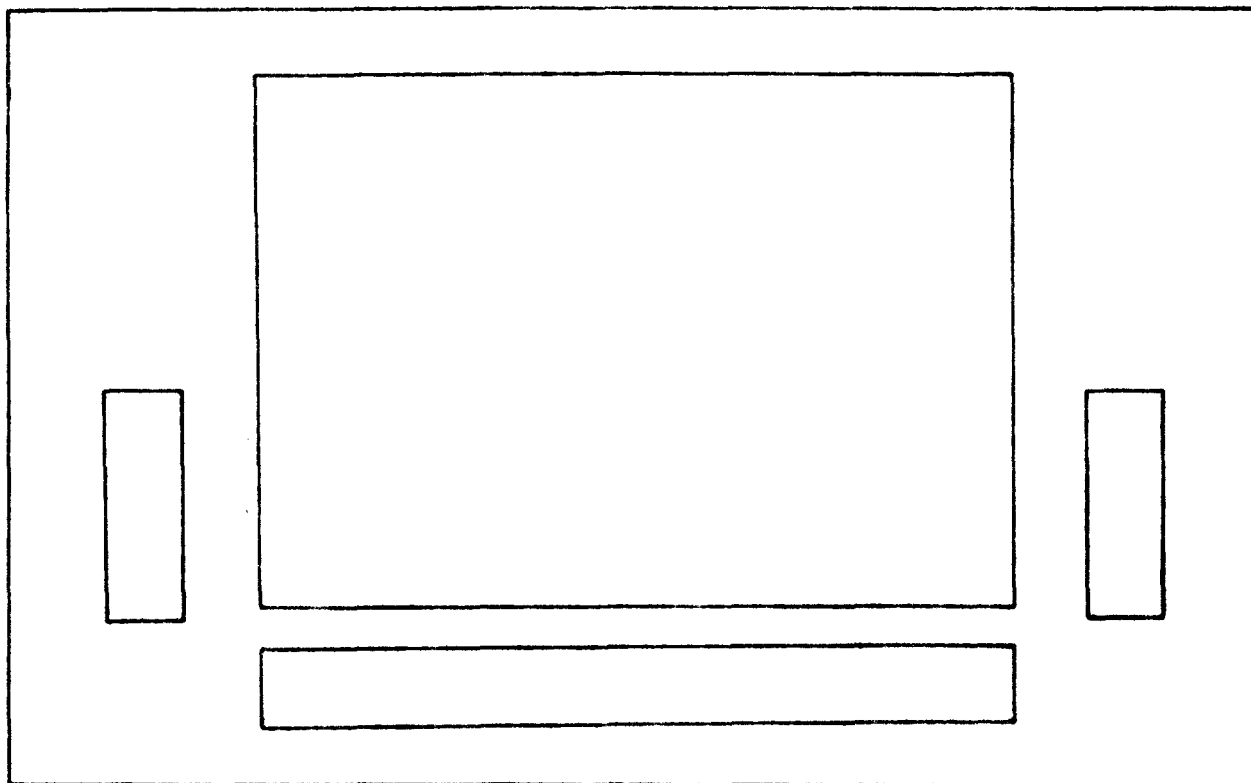


Figure 4: Plan of the mandible board.

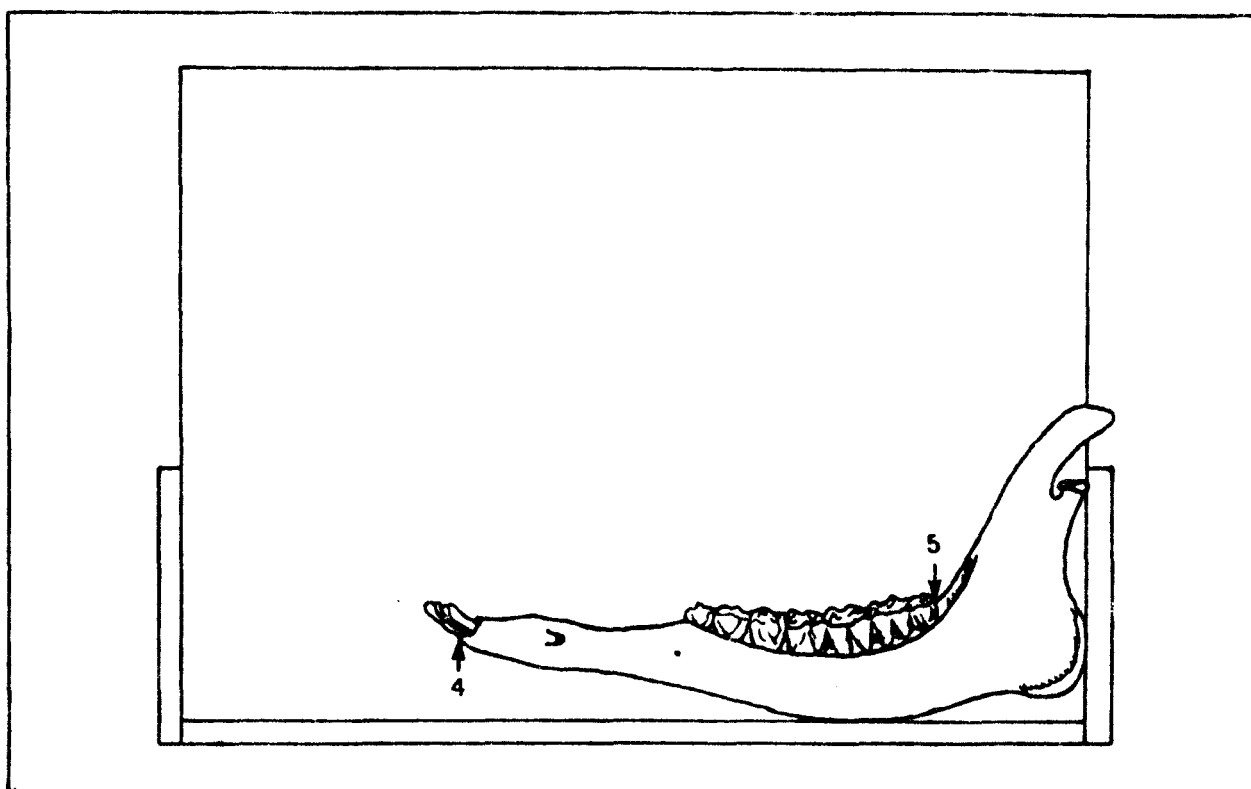


Figure 5: Diagram illustrating the use of the mandible board.

Further, as noted in chapter four of this thesis, these skeletal variables relate to the weight of the animal.

Biologists also use mandible measurements to determine the sex of a skeleton (Bergerud 1964; Miller 1974b, and Rees 1971a). Rees (1969) describes seven such measurements which differ significantly for male and female white-tailed deer. These include measurements 2, 6, 7, 8, 9, 10 and 11 of figure 3. The gonial angle or angulus of the mandible also varies according to sex. Measurement 1 is an attempt to quantify this skeletal variable. As shown in chapter 5 of this thesis, the mandibles of mature Rocky Mountain mule deer exhibit a pronounced sexual dimorphism. In fact, the above mandibular measurements discriminate the sex of modern mule deer with an accuracy of 88% or more.

Laboratory Methods for Age Estimation and Seasonality Assessment:

In his attempt to age the mature animals from the Cache la Poudre deer population, Erickson (1967) removed, decalcified and sectioned the first and second incisors from the right mandibles. In this histological analysis, the first molars from those same elements were removed, decalcified, sectioned and stained. This approach provides an independent check on Erickson's (1967) age estimates and evaluates my expertise in applied histology.

The selection of M_1 for age determination reflects a number of biological and practical considerations. In artiodactyls, M_1 is the first tooth of the permanent series to erupt. In most North American ungulates, this tooth erupts 4 months after birth

and is generally functional within the first 6 months postpartum (see Deming 1952; Dow and Wright 1962; Fuller 1959; Miller 1972; Passmore, et al. 1955; Quimby and Gaab 1957; Robinette, et al. 1957, and Severinghaus 1949a). Since cementum apposition begins before eruption, the first mandibular molar records every year of the animal's life. This tooth thus provides the most accurate age estimate. In addition, environmental and nutritional conditions do not affect tooth development as significantly in the fetus and newborn suckling as in the weaner (Cowan and Wood 1955, and Robinette et al. 1957). There is thus considerably less variation in the mean eruption dates of first molars (Saxen and Higham 1969). Further, the molariform teeth of most herbivores have bifurcate roots with relatively thick cementum deposits (Gottlieb 1943 and Sicher 1953). Such double roots provide more surface area for microscopic examination. The bifurcate root also anchors the tooth within the alveolus and prevents tooth loss resulting from cultural and taphonomic processes (Benn 1974). For archaeological mandibles, the retention of the molar within the socket protects the cementum deposit from mechanical and chemical alteration. Finally, the mandible, particularly the tooth-bearing part of the corpus, is a very durable skeletal element (Brain 1967, 1969; Clason 1972, 1974; Higham 1967, and Read 1971). In fact, Payne (1973) considers the mandible that part of the skeleton least affected, though not unaffected, by errors due to differential preservation and recovery. The mandible, specifically the tooth-bearing corpus, thus is the most common element in many archaeological and paleontological assemblages (see Bean

1974; Lyman 1976; Noe-Nygaard 1977; Read 1971; Voorhies 1969 and White 1952, 1953b, 1954, 1955 but see Emerson 1978 for opposing view). For these reasons, the first mandibular molar is the tooth of choice for age determination in prehistoric fauna.

i) Sample Preparation:

A well-preserved cementum layer is essential for accurate age determination. In the present study therefore, the first molar was cut out with a coping saw. This approach ensured the removal of intact roots within the alveoli (see Campbell 1967). In the process however, the roots of P₄ and M₂ were regularly damaged. The use of a radiograph is thus recommended to guide the cut. Lacking an x-ray unit, the analyst probably should cut out the entire alveolar region after mensuration and photography. The subsequent removal of a single tooth should be a relatively simple task.

Proper identification of specimens is necessary throughout the analysis. The respective identification numbers thus were inscribed on the buccal alveolar surface of each extracted molar. The specimen then was immersed in 150 ml of formol-saline for about 24 hours. Such preliminary fixation reduces the specimen's susceptibility to injury during manipulation (Brain 1966; McManus and Mowrey 1965; Page 1977; Wallington 1972, and Wolman 1955). For archaeological material, preliminary fixation of the entire mandible is advisable. Fixation of the bone's organic component at this time reduces the risk of injury during tooth extraction.

Fixation of the whole mandible, however, entails a cold water rinse before storage. The extracted tooth, on the other hand, requires additional primary fixation.

To fix and decalcify dense tissues such as teeth properly, histologists always use thin slabs (a maximum of 5 mm thick) in their analyses (Brain 1963; Disbrey and Rack 1970; Page 1977, and Wallington 1955). Fixation and decalcification of such slices ensures the production of high quality thin sections (Brain 1966; Clayden 1971; Preece 1965, and Wallington 1972). Only thin slabs of calcified tissue allow rapid penetration by the fixative. In fact, the thickness of a tissue block determines the rate and duration of both fixation and decalcification (Brain 1966; Morris and Benton 1956a, and Verdenius and Alma 1958). In general, thinner tissue blocks expedite penetration by fluids. Thinner slabs of bone thus decalcify more rapidly and need not undergo prolonged immersion in the acid. All thicker specimens unduly prolong the decalcification process and promote protein hydrolysis. Such excessive decalcification reduces the quality of the staining in the critical outer regions of the section (Brain 1966; Drury and Wallington 1967, and Preece 1965).

Thin pieces of decalcified tissue also enhance infiltration (Brain 1963 and Olson 1967) or freezing which, in turn, facilitates tissue sectioning (Disbrey and Rack 1970; Humason 1972, and Steedman 1960). Further, the flat surface of the tissue block enhances specimen orientation on the microtome mount. The presentation of a smooth surface to the microtome knife enables the removal of complete sections without cutting deeply into the tis-

sue block (Brain 1963 and Olson 1967). The consequent removal of fewer unwanted sections prolongs the cutting edge of the knife. Finally, the removal of thin slabs of teeth preserves part of the specimen in case of experimental error. For archaeological bone, where proper fixation and decalcification are critical, the use of thin slices is therefore essential.

The fixation and decalcification of dental slabs for age determination requires the selection of the appropriate tooth slice. For ungulate molars, Mitchell (1963) recommends the pad area, Miller (1974a, 1974b) prefers the entire root surface while Campbell (1967) specifies the region of the root which yields the most distinct lines. Armstrong (1965), Markgren (1969) and Wolfe (1969) note the presence of clearer annuli in the lingual half of the molar roots. In the present analysis therefore, a slab was removed from the lingual half of the tooth.

A decision to fix and decalcify tooth slabs also entails the selection of thin section type prior to subdivision. Obviously, the orientation of the cut determines the type of section. A sagittal cut through the molar necessitates the removal of longitudinal or sagittal thin sections. Conversely, a subdivision of the tooth along the transverse plane dictates the use of transverse or cross sections. In wildlife biology, both types of thin sections are used. Further, each type has its proponents and its critics (see Campbell 1967; Erickson 1967; Lockard 1972; Low and Cowan 1963; Miller 1974b; Olson 1967, and Thomas and Bandy 1973). In essence, transverse sectioning provides maximum numbers with minimal exposure per section. Sagittal sections of undecalcified

tissues, on the other hand, provide fewer sections per tooth but maximize the exposure of cementum in each section. Longitudinal sectioning of decalcified tissues increases the number of thin sections per tooth and provides maximum exposure per section. Such sections make it possible to follow the incremental lines along the entire root section. These are thus more reliable for seasonality assessment. As a result, all molars were subdivided along the sagittal plane.

Removing thin slabs of a uniform thickness from a deer molar necessitates grinding the alveolar bone to within a millimeter of the lingual root surface. In the present study, this grinding was done manually using a glass plate, coarse grit and water as a lubricant. Concurrently, petrographic slides were frosted using a finer grit. The ground specimens then were glued, lingual face down, onto the petrographic slides and mounted on a vacuum chuck for sectioning.

To remove a 3 mm slab from each ground specimen, an Isomet low speed diamond saw was used. This instrument, which employs the drag principle of lubrication to cool its thin wafering diamond blade, is ideal for sectioning even the most fragile specimen. To section an object, the operator mounts the specimen on the appropriate chuck, attaches the chuck to the specimen support arm and lowers the whole assembly onto a diamond blade which rotates at speeds ranging from 25 to 300 rpm. The operator regulates the cutting time by adjusting the blade speed or the weight of the support arm. High speeds and maximum weight reduce cutting time but increase damage to the specimen surface. Proper

support arm weight and blade speed produce low damage cuts with minimum kerf loss. In fact, correct adjustment of the Isomet saw results in polished surfaces and eliminates the bone dust problem noted by Galigher and Kozloff (1971), Lynch, et al. (1969) and Wallington (1972). In the present study, the blade rotated at a speed of 100 rpm while the gravity-fed specimen arm supported an additional 25 grams.

In the histological analysis of any calcified tissues, the weight of the tissue block dictates the volume of fixative and decalcifying fluid. The thickness of the specimen, on the other hand, determines the duration of the demineralization process. Hence, each tooth slab was measured and weighed before fixation and decalcification. These data are available in Appendix V.

ii) Primary Fixation:

Adequate fixation of calcified tissues is essential to ensure the production of properly stained sections. A good primary fixative minimizes tissue damage during manipulation, increases the refractive index of the material and renders the tissue receptive to most stains (Brain 1966; Wallington 1972, and Weesner 1960). For calcified tissues, fixation also renders the osteoid matrix resistant to the acids present in the decalcifying fluid (Preece 1965). As noted by the research of Cook and Ezra-Cohn (1962:563), "...fixation in formalin exerts a clear inhibitory effect upon the acid hydrolysis of the bone protein". Olson's (1967) comparative study of fixed and unfixed dental tissues

supports these results. His study confirms the importance of proper fixation for accurate age determination. In the analysis of archaeological bone, where partial degradation of the organic component is common, proper fixation is thus indispensable.

Formalin is unquestionably the best fixative for calcified tissues. This reagent penetrates well and inhibits hydrolysis of the bone protein during demineralization (Brain 1966; Cook and Ezra-Cohn 1962; Russell 1963, and Wallington 1955). The addition of sodium chloride increases the isotonicity of the fluid (Brain 1966). Formol-saline thus penetrates better than an ordinary solution of formalin and water.

Formalin solutions should never exceed 10 percent commercial formaldehyde (Clayden 1952, 1971; Drury and Wallington 1967, and Russell 1963). Higher concentrations cause overhardening and subsequent poor staining of the peripheral tissue (Brain 1966). Further, any formalin solution contains trace amounts of formic acid as a manufacturing impurity (Brain 1966) or as a result of oxidation of part of the formaldehyde (Disbrey and Rack 1970 and Lynch, et al. 1969). Acid concentration usually increases with storage. Consequently, prolonged storage of osseous tissues in unbuffered formalin results in inferior staining and eventual decalcification (Hill 1975a). Histologists generally neutralize such trace amounts of formic acid by adding calcium carbonate to their solutions (Brain 1966; Clayden 1952, 1971; Smith 1962a, and Wallington 1972). Thus, neutral or buffered 10% formol-saline is the fixative of choice for the zooarchaeologist.

Proper fixation of calcified tissues requires time. Several factors regulate the amount of time required for adequate fixation. These include: the action of the fixative; the volume, pH and temperature of the solution; the density of the tissue, and the thickness of the specimen (Thompson 1966). For thin slabs of bone 3-5 mm thick, thorough fixation in an ample volume of 10% formol-saline requires a minimum of 48 hours (Brain 1966; Clayden 1971, and Wallington 1972). Thicker specimens require much more time. In histological analysis, an ample volume of fixative constitutes 20 to 50 times the volume of the specimen. Placing the specimen on a plastic mesh at the bottom of the container or suspending the tissue in the solution ensures proper circulation by the fixative (Clayden 1952 and Wallington 1955). In this study, each lingual section and its respective identification tag was placed in a perforated plastic vial and immersed for 48 hours in 10% formol-saline at a rate of 100 ml per gram of tissue. The buccal portions of the molars, on the other hand, were fixed for a comparable time interval in an ample volume of fixative.

The perforated plastic vials and dymo tape identification tags were ideal for the task. Plastic is buoyant in water and does not deteriorate in either formol-saline or nitric acid. The perforations ensure adequate circulation by both the fixative and the acid. Further, the use of separate vials for each molar curtails direct handling of the specimen and reduces the risk of damage or misidentification during analysis. Finally, the buoyancy of these vials facilitates their removal from the decalcifying fluid for x-ray examination.

Perforated plastic vials are not available commercially. As a result, twenty ml nalgene vials were purchased and subsequently perforated using a red hot dissecting needle. Dymo guns and tape are available in most science stores.

iii) Decalcification:

Removal of the fixative necessitates an overnight rinse in cold tap water. After 48 hours of fixation therefore, the buccal sections were rinsed for approximately 12 hours and then stored in vials for future use. After a comparable rinse, the lingual portions of the molars were x-rayed and submerged in 1N nitric acid at a rate of 100 ml of solution per gram of tissue. After 6 hours of decalcification, the specimens were x-rayed again and every 2 hours thereafter until the completion of the process. Specifications for x-raying and film development are listed in Appendix IV.

The removal of a specimen from the decalcifying agent at the precise endpoint of decalcification is imperative when decalcifying in nitric acid. Excessive decalcification in such strong acids adversely affects the staining of peripheral tissue (Brain and Eastoe 1962; Clayden 1952; Page 1977, and Preece 1965) and causes intense, non-differential staining with eosin (Wallington 1972). Further, prolonged immersion in a strong decalcifying agent induces tissue distortion and eventual protein hydrolysis (Clayden 1952).

At present, radiography is the only reliable method for determining the endpoint of decalcification (Brain 1966; Galigher and Kozloff 1971 and Smith 1962a). The absence of an x-ray unit, however, entails a recourse to alternative tests. Mechanical techniques, as noted by Brain (1966), are unreliable and quite destructive. Probing, for example, perforates the tissue but frequently fails to detect calcium remnants within the specimen (Olson 1967). Such trace amounts of mineral in the decalcified matrix seriously damage the cutting edge of the microtome knife (Miller 1974b) and cause section lifting during staining (Gilbert 1964). Most chemical methods, on the other hand, are too sensitive and unduly prolong the process (Smith 1962a). As a result, the faunal analyst who is unable to locate a suitable x-ray unit should decalcify his material in a weaker acid. Formic acid, for example, does not impair tissue stainability even after prolonged immersion (Brain 1966).

Here, the selection of nitric acid as the decalcifying agent reflects financial restrictions. Formic acid is undeniably the better decalcifying agent for recent (Brain and Eastoe 1962; Gooding and Stewart 1932, and Lillie, et al. 1951) and archaeological bone (Andersen and Jorgensen 1960, and Ascenzi 1955). In the present research, however, the cost of decalcifying all 102 lingual sections in this acid would be excessive. Formic acid is very expensive and its optimum concentration is 4N. Complete decalcification of even a thin bone slab in 4N formic acid requires several days, a process which entails daily replacement of the acid solution (Brain 1966; Clayden 1971, and Wallington 1972).

Conversely, nitric acid, when used in much lower concentrations, decalcifies a 3 mm slice of dental tissue in less than 24 hours. This acid, which is very inexpensive (Olson 1967), also causes minimal distortion (Preece 1965), enhances sectioning (Clayden 1952), and yields good nuclear staining. Therefore, of all the strong acids, nitric acid produces the best results providing the decalcification time does not exceed 15 hours (Brain 1966).

Finances generally do not dictate the choice of the acid. Instead, the urgency of the analysis or the quality of the final preparations prescribe the suitable decalcifying agent. Strong acids decalcify rapidly but usually produce poorer sections. Weaker acids, on the other hand, demineralize slowly but yield higher quality stained preparations.

Though acid strength determines the general rate of demineralization (Brain and Eastoe 1962), each acid has an optimum concentration for efficient decalcification. For nitric and formic acid, the optimum concentrations are 1N and 4N respectively (Brain 1966). Acid concentrations, here, are presented in terms of normality since such expressions permit "... accurate assessment of the concentration of acidic solutions regardless of the strength of the acid" (Brain 1966:73).

Decalcification, like fixation, requires an ample volume of solution. Drury and Wallington (1967) and Wallington (1972) recommend a volume 30-50 times that of the tissue. Brain (1966) and Lillie, et al. (1951) prefer a volume of 100 ml of solution per gram of tissue. This volume of 1N nitric acid decalcifies a thin slice of bone within 24 hours.

In addition to volume and concentration, the working temperature of the decalcifying agent, replacement and agitation of the solution, and localisation of the specimen within the fluid affect the rate of the process (Brain 1966). Most histologists recommend working temperatures of 18°C to 20°C. Fortunately, this temperature range prevails in most histological laboratories (Brain 1966; Clayden 1952, 1971; Morris and Benton 1956a, 1956b, and Wallington 1972). Recommendations for agitation are contradictory. According to most histologists, agitation of the acid solution does not significantly affect the rate of the process (Brain 1966). Verdenius and Alma (1958), Morris and Benton (1956a) and Russell (1963), however, report a notable acceleration in the process as a result of agitation. Daily replacement of the solution, on the other hand, is essential. Finally, localisation of the specimen within the solution need only ensure free access of the acid to all surfaces of the tissue. In other words, the specimen surface should not contact the walls of the container. Of the above, only concentration, volume and working temperature of the solution markedly affect the rate of decalcification in a given acid.

Given optimal volume, concentration and temperature of the decalcifying agent, specimen thickness determines decalcification time. In general, the time required for the decalcifying fluid to penetrate a specimen increases with the dimensions of the latter. As shown in the sequence of radiographs in Figure 6, demineralization proceeds as the forward movement of a sharply delineated front from the periphery of the specimen toward the cen-

Figure 6: Sequence of radiographs showing the progress of the decalcification process.



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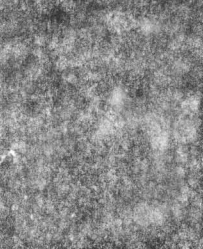
10



12



14



16



18

20

ter (Birkedal-Hansen 1974). Since the process advances at a uniform rate from all surfaces (Brain 1966; Morris and Benton 1956a, and Verdenius and Alma 1958), the smallest dimension of the tooth slice is critical in determining the duration of the process. A specimen measuring 100 X 10 X 1 mm, for example, will decalcify as rapidly as one measuring 3 X 2 X 1 mm. The absolute diffusing distance for the acid then is one half the smallest dimension. This distance, which Brain (1966:83) defines as the minimum diffusing distance, determines the duration of the decalcification process.

To test this hypothesis, all one hundred and two lingual sections were measured and weighed. Here, maximum thickness was measured to the nearest 0.05 mm using dial calipers. Weight was recorded to the nearest 0.1 gram using an Ohaus Autogram scale. All specimens, except for the 12 first molars, were fixed and decalcified at room temperature in solutions as specified above. The initial 12 specimens were decalcified in 4N formic acid and do not concern us here. Here, no attempt was made to standardize the temperature of the solution as suggested by Smith (1962a). Agitation of the acid solution to disperse the decalcification products occurred after each x-ray examination. The specimens were x-rayed after 6 hours of decalcification and every 2 hours thereafter until completely decalcified. For individual teeth, the process was complete within 30 hours. There was thus no need to replace the solution. The duration of the process, expressed in hours, was recorded for each specimen. Appendix V lists each of the 90 specimens and records its respective thickness, weight

and decalcification time.

To determine the nature of the relationship between specimen thickness and decalcification time, the data were plotted on a system of Cartesian coordinates with time as the dependent variable (Y) and thickness as the independent variable (X). The result, as illustrated in Figure 7, is a curvilinear plot of the general form $Y = kX^b$. This is consistent with the observations of Brain (1963), Morris and Benton (1956a), Birkedal-Hansen (1974) and Verdenius and Alma (1958) who note a decrease in the rate of decalcification as the amount of demineralized matrix increases.

Transforming both the X and Y values using common logarithms rectifies the data and yields the linear plot shown in Figure 8. The correlation coefficient for this relationship is $r = 0.94$. Specimen thickness thus accounts for 88% of the observed variance in decalcification time. This variance estimate, in my opinion, represents a minimum value. Given rigidly controlled experimental conditions with careful mensuration of the absolute specimen thickness, hourly x-rays and uniform solution temperatures, this association of specimen thickness and decalcification time would exhibit a higher correlation. Thickness measurements of molars with large pulp cavities do not represent adequately the minimum diffusing distance of the specimen. Also, laboratory temperatures fluctuate on a daily and annual basis (Smith 1962a). Such "room temperature" fluctuations affect the working temperature of the decalcifying agent and the resultant decalcification rate (Brain 1966; Morris and Benton 1956b, and Wallington 1972).

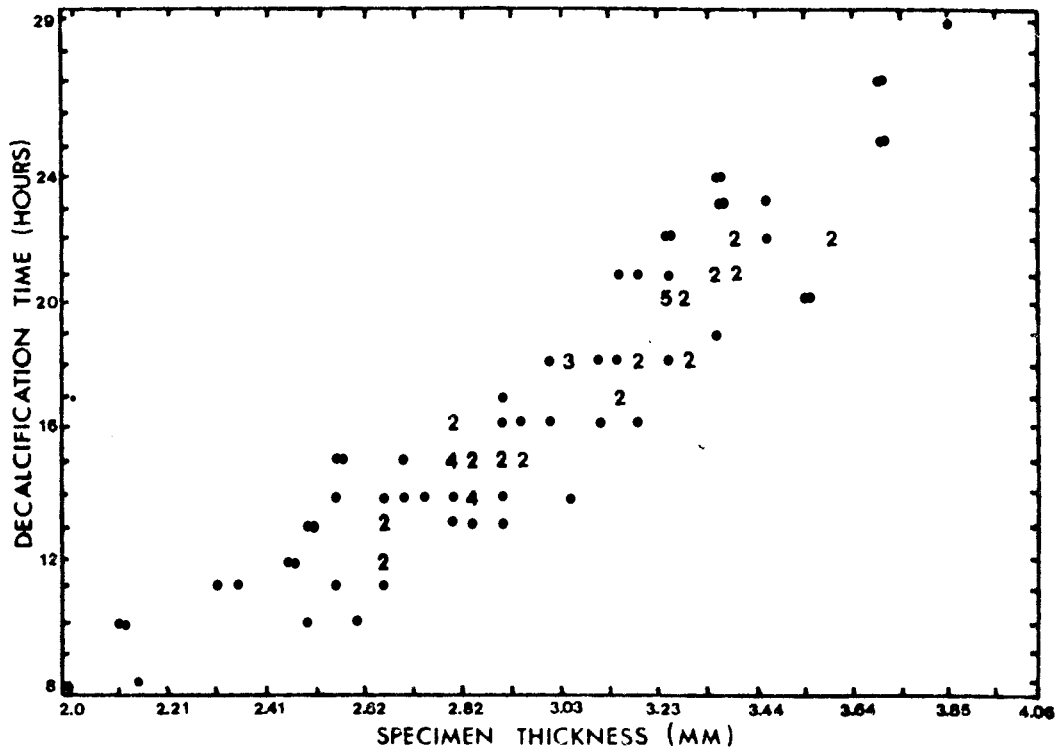


Figure 7: Relationship between specimen thickness in mm and decalcification time in hours.

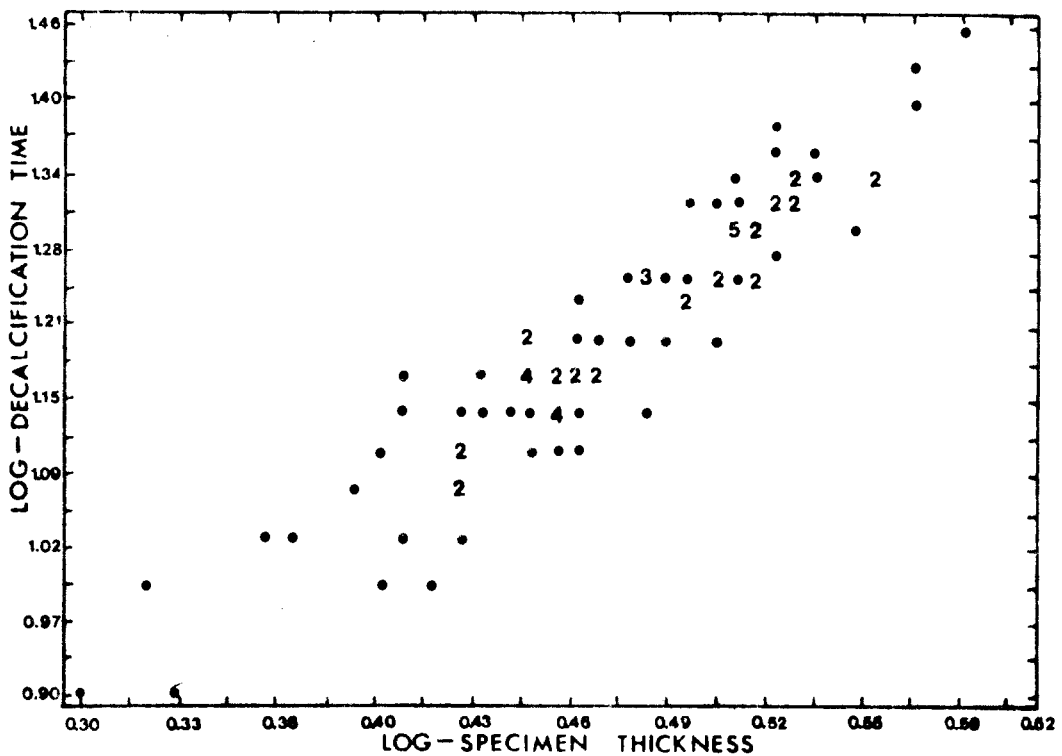


Figure 8: Relationship between log-specimen thickness and log-decalcification time.

The least-squares regression equation for the log-log plot is:

$$\log \hat{Y} = \log 2.06 + 1.90(\log X) \quad (1)$$

where X is specimen thickness and Y is the decalcification time. This relationship allows the histologist to predict the endpoint of decalcification with some reliability. More important, equation 1 now permits the computation of a maximum specimen thickness for decalcification in 1N nitric acid. Wildlife biologists must avoid immersing entire teeth into strong acid solutions for 36 to 72 hours (see Miller 1974a and Olson 1967). Such excessive decalcification explains, in part, the poor quality of several preparations. Similarly, faunal analysts dealing with degraded tissues must use weaker acids to guarantee the production of high quality stained preparations. Here, determining the appropriate specimen thickness and decalcification time for weak acids necessitates the calculation of a similar regression equation for acids such as 4N formic.

To remove the acid after decalcification, overnight rinsing of the tissue in cold tap water is necessary. Some histologists prefer to neutralize the acid by soaking the decalcified teeth in aqueous solutions of lithium carbonate (see Low and Cowan 1963, and McCutchen 1966). Neutralization with lithium carbonate apparently reduces section curling (Lockard 1972) and prevents excessive general staining of the cementum (Thomas 1977). After the rinse or neutralization, decalcified tissues are stored in distilled water or a secondary fixative to await further processing. The secondary fixative, usually a buffered formalin solution,

enhances tissue preservation, sectioning and staining (Wallington 1955, 1972). Secondary fixation of decalcified archaeological tissues is thus advisable. Use of a secondary fixative, however, entails a tissue rinse before staining (Smith 1962a). In the present study, the decalcified molars were stored in distilled water prior to sectioning.

iv) Microslide Preparation:

One day before sectioning, microslides require cleaning and coating. Most wildlife biologists coat their slides with Mayer's albumen (Morris 1972). Many then discuss problems with section curling, section loss (Miller 1974a; Thomas and Bandy 1973, and Winterton and Strickland n.d.) and annuli clouding (Miller 1974a, 1974b). Section curling results from inadequate decalcification, insufficient washing, improper sectioning or poor selection of an affixative. Section loss, on the other hand, reflects a poor choice of affixative. To overcome such problems, Page (1977) coats his microslides with gelatin. In the present study, the use of gelatin-coated slides, prepared as described in Appendix VII, resulted in minimal curling and no section loss.

v) Thin Sectioning of Ungulate Molars:

The removal of thin sections from decalcified teeth entails the preparation of embedded or frozen tissue mounts. Adequate dehydration, clearing and impregnation of dense tissues for wax

embedding requires several days (Brain 1966). This process also causes distortion of tissue structure (Gooding and Stewart 1932 and Smith 1962a) and sloughing of the cementum layer (Miller 1974b). The removal of frozen thin sections, on the other hand, requires little time and the resultant sections lack the shrinkage and distortion characteristic of embedded tissues (Clayden 1971 and Page 1977). Furthermore, use of the freezing microtome enhances proper orientation of the specimen (Miller 1974b). In the present study therefore, frozen thin sections, twelve microns thick, were removed from all decalcified molars.

Two types of freezing microtomes are available to section decalcified dental tissues. In general, the surface area of the tissue block dictates the choice of microtome (Smith 1962a). To section an ungulate molar and its associated alveolar bone, the base sledge microtome is the apparatus of choice. Only this instrument has the proper stage dimensions and provides adequate rigidity of the knife and stage during sectioning (Smith 1962a). Similarly, only on this microtome is the travel distance of the knife sufficiently great to accommodate such larger specimens (Brain 1966). Unfortunately, no suitable base sledge microtome was available for the present analysis. As a result, the decalcified teeth were subdivided and then sectioned on a standard freezing microtome.

The frozen sectioning of decalcified tissues on a standard microtome requires maximum rigidity of the knife and freezing stage. To achieve such stability, proper adjustments of the microtome are necessary. Smith (1962a), for example, lubricates

all slides, tracks and runners of the microtome with grease. In this research, a well-oiled microtome with a sharp knife firmly clamped in position provided the necessary rigidity. Insecure clamping of either the knife or the block holder invariably resulted in corrugated or uneven sections.

Selection of the appropriate, well-sharpened microtome knife is also essential for efficient sectioning of decalcified teeth. Only heavy wedge-shaped (D-profile) knives are sufficiently rigid for such sectioning (Clayden 1971; Drury and Wallington 1967, and Wallington 1972). Slender knives tend to vibrate while cutting and produce corrugated sections (Page 1977 and Steedman 1960). Conversely, a vibrating D-profile knife indicates an inferior cutting edge. Such dull microtome knives produce corrugated or alternate thin and thick sections which curl when mounted and frequently fall off during staining (Brain 1966; Miller 1974a; Morris 1972, and Steedman 1960). Inferior cutting edges also produce sections with a "moth-eaten" appearance and sloughed cementum layers (Miller 1974b).

The maintenance of a sharp cutting edge requires frequent sharpening of the knife using manual (Smith 1962a) or mechanical (Brain 1966) sharpeners. In the present research, the microtome knives dulled very quickly. Once dull, the knife was shifted to expose a fresh cutting surface. After four such shifts, the knife was removed and resharpened using the available automatic sharpener. To avoid delays, two knives were used and alternated between the microtome and the sharpener. These sharp D-profile knives permitted the removal of 12 micron serial sections. Most

attempts to remove sections thinner than 10 microns resulted in failure.

Frequent removal and replacement of knives during sectioning necessitates repeated adjustments of the knife's inclination and tilt. Proper placement of the anti-roll plate after each change is also essential. Improper adjustment of either results in corrugated sections. To section decalcified tissue, Page (1977) increases the tilt. Smith (1962a), on the other hand, recommends minimum inclination of the knife. Correct adjustments vary from microtome to microtome and knife to knife. Considerable practice is thus necessary to adjust properly the microtome and its knife during sectioning. As a result, the faunal analyst must acquire this experience using modern tissues before attempting to section fragile archaeological tissues.

Sectioning with the standard freezing microtome requires the use of small tissue blocks. Accordingly, each decalcified molar was quartered before freezing. This subdivision involved the removal of the crown followed by three bucco-lingual cuts through the mesial root, the bifurcation and the distal root. Aside from the discarded crown, this division yielded 4 subrectangular root fractions for each tooth. Each such root fraction contained a continuous cementum layer adjacent to the alveolar bone. The reduction of the tissue block at this time facilitated tissue sectioning and ensured rapid freezing (see also Humason 1972). Furthermore, this subdivision confirmed the completion of the decalcification process (see also Olson 1967).

Each root fraction was mounted, lingual face down, in Cryoform on a portable freezing stage and transferred to the microtome chamber for rapid freezing. When frozen, the block was trimmed and positioned in the specimen holder of the microtome. At this time, the orientation of the specimen relative to the knife edge is critical. To section decalcified tissue, Page (1977) and Smith (1962a) place the long axis of the specimen perpendicular to the knife edge. Wallington (1972) prefers to set the long axis oblique to the knife. In the present study, each root fraction was oriented parallel to the knife with the dentine closest to the cutting edge. This orientation minimized distortion or damage to the cementum layer. Given a comparable placement, the sectioning of decalcified deer molars requires only patience and plenty of practice.

When sectioning the root fractions, the initial 30 sections were discarded. In general, these were incomplete or otherwise unsatisfactory for microscopic examination. Subsequent sections usually were acceptable for mounting and staining. At this time, the microtome knife was brushed clean and then six to ten serial sections were removed. These came to rest on the knife beneath the anti-roll plate. The transfer of sections to the slides then was accomplished by lowering the gelatin-coated slide over the cut sections. In general, the cold sections adhered to the warm slide. Transferring the slide to a black surface at this time enhanced section visibility and eased subsequent manipulation (see Brain 1966 and Weesner 1960). The addition of a few drops of water induced section flattening and facilitated the final

positioning of the section on the slide. Removal of the excess water, as proposed by Weesner (1960), expedited initial drying and ensured the adhesion of flat sections. The final drying, however, required a slidewarmer. In this manner, four slides, each containing 6-10 serial sections, were prepared from each molar. In other words, six to ten sections were removed from each root fraction and mounted onto microslides.

Once dried, the prepared slides were stored in dust-free containers to await staining. The actual staining, as outlined in Appendix VI, usually occurred shortly after drying. However, slides can remain in storage for weeks without noticeable impairment in the quality of the staining.

vi) Staining of the Thin Sections:

To accentuate annuli present in the decalcified cementum, wildlife biologists use various hematoxylin stains (see Boozer 1970; Low and Cowan 1963; MCEwan 1963, and Reimers and Nordby 1968). According to Thomas (1977) however, metachromatic dyes are much more effective in delineating cementum annuli. In his comparative study of cationic dye solutions, he ranks toluidine blue as the most rapid, effective and efficient stain for mammalian age determination. Further, this metachromatic dye is less expensive, easier to prepare, more consistent and more stable than hematoxylin (Thomas 1977:209). Finally, toluidine blue has been proven effective in the histological analysis of archaeological bone (Andersen and Jorgensen 1960). Given such

results, all sections were stained with toluidine blue O.

The quality of the staining depends on section thickness, dye concentration and staining time. In general, staining time decreases as dye concentration and section thickness increase (Lee, personal communication). Given a standard section thickness, dye concentration regulates staining time. For sections twelve microns or more, Thomas (1977) recommends a staining period of 20-40 minutes in a dye solution of less than 0.02 percent. He also recommends destaining in slightly acidic water to accentuate the annuli. In the present study, all sections were stained for approximately 20 seconds in a 0.05 percent dye solution. Here, destaining was not necessary. When staining archaeological tissues however, the longer staining period and lower dye concentrations are preferable.

Periodic examination of the slides to evaluate the quality of staining is necessary to ensure the production of good preparations. At this time, all understained sections are returned to the dye for additional treatment. Overstained sections, on the other hand, are destained in distilled or acidified water. Some overstaining is necessary for the production of permanent mounts (Lee, personal communication). Occasionally, certain sections do not stain properly due to excessive decalcification. Resolution of this problem necessitates overnight staining in a dilute dye solution (Page 1977; Smith 1962b, and Wallington 1972).

Proper examination of stained sections for age determination and seasonality assessment requires the production of permanent mounts. In this analysis therefore, all sections were dehydrated

cleared and mounted in Permount after proper staining. Numerous biologists report difficulties with this phase of the staining procedure (Lockard 1972; Miller 1974a, 1974b, and Thomas 1977). In general, dehydration eliminates the metachromatism in toluidine blue. The resultant sections are light blue with dark blue annuli. Unlike Thomas (1977), however, I noted an increase in color contrast between the annuli and the background cementum as a result of dehydration. In his analysis, Miller (1974a:50) also notes considerable tissue distortion during the preparation of permanent mounts. Shrinkage of formalin fixed tissues is common during dehydration (see Disbrey and Rack 1970). Such shrinkage amplifies section curling and influences the quality of the final preparation. Only sections, properly affixed to gelatin-coated slides, do not curl during dehydration. Thus, correct sectioning and mounting of the thin sections, not dehydration, affect the quality of the permanent mount. In the present study, all good permanent mounts were flat and easy to read.

After the application of coverglasses the slides were dried for 3 days on a slide warmer at 45°C. Subsequently, the excess Permount was scraped off using a razor blade. Particularly untidy slides were cleaned with a Q-tip soaked in xylene. Microslides and coverglasses then were polished using a commercial glass cleaner. The cleaned slides then were stored in dust-free containers to await microscopic examination.

vii) Microscopic Examination of the Stained Thin Sections:

In the present study, all slides were examined with a Nikon Sk-T binocular microscope at magnifications ranging from 40X to 400X. The light source on this microscope was an adjustable tungsten bulb. Filters, condensers and polarizers were available but did not appear to enhance annuli visibility. Light filters, however, did alleviate eye fatigue during examination and were necessary for photography.

During the microscopic examination, each section was scanned initially to locate an area with suitably distinct annuli. Any such cementum deposit then was examined at higher magnifications to obtain an accurate count of the annuli present. In general, magnifications of 40X or 100X were satisfactory for thicker deposits with diffuse annuli such as the pad area and the root apices. Higher magnifications, including oil immersion (1000X), were necessary to substantiate counts in areas of compact, evenly spaced annuli such as the coronal third of the root. Every thin section on every slide was examined in this manner to obtain a reliable annuli count for each specimen. The observations and actual results of the microscopic examination for age determination are discussed in chapter six of this thesis.

During the microscopic scan for age estimation, the clarity of annuli throughout the cementum layer was noted. Concurrently, the overall appearance of the outer annulus in each thin section was examined and evaluated. Such extensive and intensive examination of the sections was necessary to locate a suitable area

for seasonality assessment. A suitable locale for assessing the deer's season of death is one with distinct, evenly spaced annuli and an accurate representation of the outer layer. Given such a deposit, the magnification was increased to oil immersion or 1000X. Using an ocular micrometer, the cumulative thickness of the layer after each year of cementum growth then was recorded. In other words, the distance from the dentino-cementum interface to the outer edge of the first and all subsequent annuli was noted. Finally, the total thickness of the cementum deposit at this spot was measured. Similar measurements were obtained, if possible, for at least 4 locales on each specimen. The logistics and results for this phase of the research are presented in chapter seven of the present study.

Summary:

In summary, chapter three and the associated appendices outline the laboratory procedure for the macroscopic and microscopic analysis of modern and archaeological deer mandibles. The macroscopic study consists of quantifying selected dimensions on each mandible. Appendix II describes eleven such measurements which provide basic data for weight estimation and sex determination in mature Rocky Mountain mule deer. The microscopic analysis of the mandible, on the other hand, includes the preparation and examination of decalcified thin sections from the first molars. The microscopic examination of such sections provides an accurate assessment of the animal's absolute age and season of death.

4. Weight estimation

The principal aim (of the Bone Research Scheme) has been to put life and flesh into the bones, to think in terms of animals, of flocks and herds, and not of their mortal remains. To be of real value this bone material must be made to tell everything it possibly can... (Chaplin 1965:205).

Introduction:

In zooarchaeology, one of the primary research objectives is to establish the relative economic and dietary importance of each species. In general, this is done by determining the relative frequency of a species within the assemblage or by calculating the relative meat weights of taxa constituting such assemblages. Here, the observed representation of the various faunal resources furnishes additional data concerning past environments (Chaplin 1971) or selective patterns of predation (Klein 1978, 1979) and herd management (Flannery 1969). The quantification of faunal remains in archaeological assemblages also enhances intersite comparisons (Chaplin 1971). Such comparisons apparently indicate the nature, direction and rate of change in man's manipulation of wild and domestic stock. The transformation from bone to meat to caloric data forms the basis for inferences on the duration of site occupation (Smith 1978), the size of the population (Spiess 1978) and the overall energy expenditure (Reed 1963). In faunal studies therefore, the relative contribution of a species constitutes an important body of secondary data.

At present, there are two basic approaches to estimating taxon frequency: the "fragments" method and the minimum number of individuals (MNI) approach. The former compares the numbers or weights of identified fragments attributable to each species (see Chaplin 1971; Clason 1972, 1973; Payne 1972b, 1975b; Perkins 1973 and Uerpmann 1973). The latter determines the minimum number of individuals (MNI) for a species from the elements occurring most frequently in the assemblage (White 1953a). Refinements for the computation of the MNI value abound in the literature. Bokonyi (1970), Chaplin (1971), Flannery (1967), Smith (1975a, 1975b) and Stewart (1974), for example, advocate the segregation of elements according to age, sex and size. Grayson (1973) recommends the subdivision of an archaeological assemblage into distinct spatial and temporal aggregates and the determination of a MNI for each. Watson (1979), in his faunal studies, refers to diagnostic zones. His approach to the quantification of faunal remains based on the frequency of diagnostic zones provides one set of data for the derivation of MNI, fragment counts or fragment weights.

Of the above, each approach has its proponents and its critics, its relative merits and its shortcomings. These are discussed in detail by Casteel (1978), Chaplin (1965, 1971), Grayson (1973, 1978, 1979), Payne (1972b), Perkins (1973) and Ziegler (1973). In essence, these discussions pertain to the recovery and sampling of archaeological assemblages and do not concern us here. Of particular interest to the present research is the derivation of meat weights from the osteological remains of prehistoric fauna.

Weight Estimation in Zooarchaeology:

In economic prehistory, only specific meat weights provide reliable assessments of the relative dietary contribution of a species. At present, there exist three methods for making the apparent logical transfer from excavated bones to kilograms of meat. The first, known as the Wiegemethode or weight method, assumes a constant relationship between the bone and meat weight in a given taxon and thus derives meat weights directly from the bone weights (see Cook and Treganza 1950; Reed 1963, and Ziegler 1973). Here, the analyst weighs the osteological remains of a taxon and multiplies this value by a factor presumed to represent the proportion of bone to meat weight for that taxon. The Wiegemethode thus provides meat weight estimates unaffected by the degree of fragmentation within the faunal assemblage. As noted by Casteel (1978), however, the multiplicative factors vary from author to author and do not reflect the true relationship of bone to meat weight within a taxon. In fact, modern domesticates are known to exhibit considerable variation in the ratio of bone to meat weight as a result of selective breeding (Uerpmann 1973). The association also does not hold empirically for mineralized, leached or dry bone (Reed 1963). This problem is compounded by variations within and between sites. Such intra- and intersite differences curtail any attempt to calculate the appropriate correction factors for bones in individual or multiple assemblages (see Noe-Nygaard 1977). Finally, the relationship of bone weight to meat weight does not hold where certain skeletal elements are

abnormally numerous or rare (Reed 1963). In brief, the Wiege-methode, as presently defined, offers limited promise as a viable method for weight estimation in zooarchaeology.

The second approach, known as White's method, uses MNI to determine the relative dietary importance of a species. As proposed by White (1953a), this approach derives an average meat weight by multiplying MNI and the average live weight for an individual of the species. Cleland (1966), in a paleoecological study of the Upper Great Lakes, employs White's basic methodology but uses different live weights for the species of this region. Smith (1975a, 1975b), to obtain more accurate weight estimates for his deer sample, subdivides the assemblage into distinct age and sex classes. He then calculates a MNI for each class and multiplies this estimate by an average weight for individuals in each group. Aside from the restrictions on MNI (see Casteel 1976/77 and Grayson 1973, 1978, 1979), White's method of weight estimation, by definition, provides only average weights. This method does not account for individual variation relating to the animal's diet, sex, age or season of death. Hence, it is of limited value to the zooarchaeologist studying prehistoric faunal populations.

The third approach or the regression method predicts the weight or size of an animal directly from the size of its bones by means of one or more regression formulae (Casteel 1976). The constants for the regression equations derive from a large sample of observations on the relationship between bone size and animal weight in a particular taxon. In essence, the sample of data

points relating the two variables must be sufficiently large and varied to indicate accurately the nature of the curve or regression formula. A correlation coefficient, r , calculated for the sample then indicates the strength of the relationship between the variables under consideration.

The empirical derivation of these constants requires the collection, preparation and measurement of a large number of animals. The resultant values for the constants α and β are, however, only estimates of some parameters and, as such, vary slightly from sample to sample. The values of α and β also change from bone to bone in a species or for the same element between species. Furthermore, the constants and the regression equation are tenable only for the size range specified by the sample. Given the proper constants however, the regression equation is a valuable statistical tool for predicting animal weight directly from some measure of bone size. As such, the regression approach, unlike other methods, provides body weight estimates for individual animals rather than average weights for specified taxa.

Regression analysis assumes the existence of a size-weight relationship for the species under study. Such associations are known to exist for many ungulates. The relationship of heart or girth measurement to live weight in wild and domestic ruminants is well-documented in the biological literature (Anderson, et al. 1974; Franzmann, et al. 1978; Manning and Williams 1950; McEwan and Wood 1966; Mullick 1950; Smart, et al. 1973; Talbot and McCulloch 1965, and Wanderstock and Salisbury 1946). Linear

carcass measurements such as total length, shoulder height and hind foot length are also good estimators of body weight in ungulate populations (see Anderson, et al. 1974; Bandy, et al. 1956; Franzmann, et al. 1978; Hall-Martin 1977, and McEwan and Wood 1966). For these animals therefore, the size of the body relates to the weight of the animal.

Similar associations exist between metric attributes of the major weight-bearing bones and the live weight of the animal. In an osteometric analysis of bovine long bones, Noddle (1973) notes a straight line relationship between specific dimensions of these elements and the fat free carcass weight of cattle. Anderson, et al. (1974) also report significant correlations ($r=0.75$ for males and 0.77 for females) between metacarpal length and bled carcass weight in Cache la Poudre mule deer. For this population, metacarpal width is also a good predictor of the bled carcass weight ($r=0.84$ for males and 0.86 for females). In white-tailed deer, various dimensions of the astragalus relate to the live weight of the animal. For a sample of 71 deer, Emerson (1978) reports correlation coefficients of $r=0.934$ for length of the astragalus versus live weight, $r=0.869$ for width of the astragalus versus live weight and $r=0.923$ for length plus width versus live weight. Hence, the size of the major weight-bearing bones relates to the weight of the ungulate. These bones, however, furnish no data on the deer's age or sex (Emerson 1978). Such population parameters must derive from other skeletal elements.

To study the dynamics of a prehistoric deer population, the zooarchaeologist must determine the proportion of animals in the

various age, sex and weight classes. These population parameters must be derived from the skeletal remains of such animals. At present, the faunal analyst determines the age of a deer from the dentition, its sex from the pelvis or cranium and its weight from weight-bearing bones such as the astragalus, metacarpal or metatarsal. He then integrates the respective proportions to assess the status of the population (see Smith 1974a, 1974b). Any such age:sex:weight ratios are, of course, somewhat tenuous. Ideally, all population parameters should derive from the same skeletal element. With respect to cervids, the mandible provides the most reliable age estimate. This chapter discusses the potential of this element as an indicator of the live and dressed carcass weight in mature mule deer.

Weight Estimation from Mandible Length in Mature Mule Deer:

In mammals, the growth of the cranium is proportional to that of the body (see Mystkowska 1966). With very few exceptions (see Ryel 1963), the larger animals support the longer mandibles. Mandible length thus relates to body size and should be a good estimator of live weight in mammals.

In cervids at least, mandible length relates to body weight. The strength of the association, however, varies from sample to sample. For instance, Lowe (1972), in his analysis of three red deer (Cervus elaphus) populations, presents five correlation coefficients for mandible length versus body weight. These range from $r=0.76$ to $r=0.95$ for males and $r=0.67$ to $r=0.94$ for females.

The significant variation in r , in my opinion, reflects seasonal differences in the collection periods and discrepancies in the computation of weights and mandible lengths for two of the three populations. The lowest correlation coefficients derive from the Rhum sample which was collected at regular intervals over several years (see Lowe 1967). Further, both the mandible lengths and body weights in this sample were predicted from recorded values. The highest correlation coefficients, on the other hand, obtain for the Oksbol sample. Here, no corrections were necessary and the sample, though not documented, probably was collected during a restricted fall hunting season. Anderson, et al. (1974) also obtain a strong correlation between mandible length and carcass weight in Colorado mule deer. Their correlation coefficients for samples of 86 males and 114 females are respectively $r=0.89$ and $r=0.86$. In cervids therefore, mandible length relates to body weight.

In order to assess this relationship and to determine more accurately the sources of variation, mandible length and live weight were correlated for my subsample of the Cache la Poudre deer. In the original study, Anderson, et al. (1974:10) define mandible length as the maximum length of the element, excluding the incisors. This mandibular dimension represents measurement four in the present research. In archaeological specimens, the infradentale generally is missing due to the fragility of the anterior alveoli. A more appropriate measure of mandible length for such specimens is the maximum length of the mandible as measured from the angulus to the aboral border of the canine

alveolus. This is measurement two in Figure 3 and represents mandible length in this thesis. Weight in this analysis, like that of Anderson, et al. (1974), is the bled carcass weight or weight 1 as defined above.

Of the 100 measured mandibles, twelve were fragmented and lacked the anterior reference point. An additional two elements were from deer whose weights were not recorded. These fourteen animals were excluded from the analysis. The sample used in the derivation of the constants therefore comprised eighty-six mandibles, of which 27 were from males and 59 were from females. The respective mandibular measurements and weights for these deer are listed in Appendix III of this thesis.

To determine the nature of the relationship between these two variables, the data were plotted on a system of Cartesian coordinates with bled carcass weight as the dependent variable (Y) and mandible length as the independent variable (X). The result, as illustrated in Figure 9, is a slightly curvilinear relationship of the general form $Y = \alpha(X)^\beta$. This distribution is consistent with the results of Lowe (1972) and Anderson, et al. (1974). Transforming the X and Y values using common logarithms produces the linear plot shown in Figure 10. The strength of this association is $r=0.77$ while the least-squares regression equation for this distribution is:

$$\log \hat{Y} = 3.27(\log X) - 5.81 \quad (2)$$

To predict the weight of a deer using this regression equation, the analyst inserts a value for X (mandible length) and solves for log Y. The antilog of Y then provides the predicted weight,

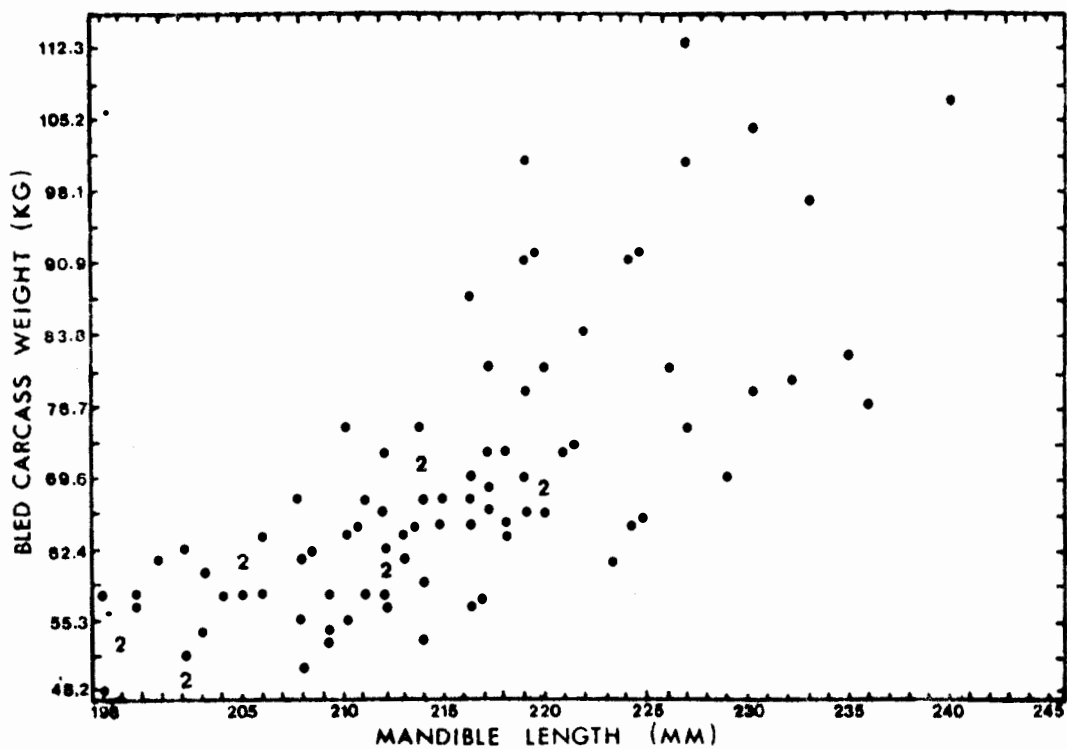


Figure 9: Relationship between mandible length in mm and bled carcass weight in kg for mature mule deer.

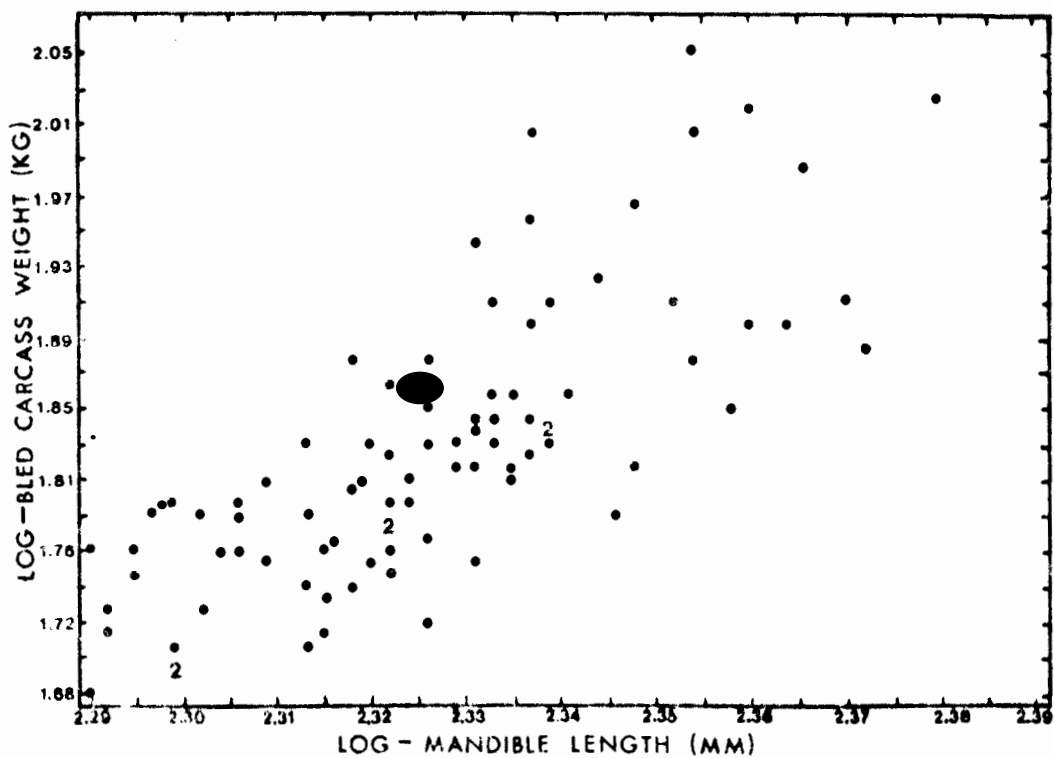


Figure 10: Relationship between log-mandible length and log-bled carcass weight for mature mule deer.

in kilograms, of the animal.

In the above association, mandible length accounts for 59% of the observed variance in the bled carcass weight. For white-tailed deer, at least, live weight depends on the genetics of the deer population, the quality of the forage and the age, sex and season of death of the animal (see Smith 1975b). For the present sample, population genetics and available forage are assumed to be identical. Variations in age are significant only in as much as they relate to the skeletal maturity of the animal. In other words, the skeletons of immature animals more accurately reflect variations in body size than that of skeletally mature deer. In the total sample, for instance, mandible length accounts for approximately 79% of the variance in males and 74% of the variance in females (Anderson, et al. 1974). Of the 200 animals in this original sample, 58 are less than 18 months old and 78 are less than 2 years of age. In my opinion, the higher correlation coefficients reported by Anderson and his collaborators reflect the greater proportion of younger growing deer in their sample. The 86 animals used in the present research are 2 years old or older. In such mature deer, mandible length does not represent, as accurately, the weight of the animal. Furthermore, older deer undergo greater seasonal fluctuations in weight than their younger counterparts (see Anderson, et al. 1974). As a result, mandible length accounts for a lower percentage of the variance in this sample.

Variations in live weight relating to the sex of the animal reflect the sexual dimorphism within a species. The effect of

such sexual differences on the relationship between bone length and body weight is undetermined at present. In his study, Lowe (1972) presents separate regression formulae for the stags and hinds in each population. He then notes a significant sexual difference for the population in Denmark whereas he reports no significant difference between the sexes for the Rhum population. Anderson, et al. (1974) also present separate coefficients for males and females but offer no explanation for this subdivision. In the present analysis, the variation due to sex apparently does not warrant the computation of separate regression formulae. In fact, the strength of the association decreases when mature males and females are considered separately ($r=0.43$ for the 27 males and $r=0.68$ for the 59 females). In the scatter of data points, the larger males with the correspondingly longer mandibles form a cluster in the upper right corner of Figure 9. The smaller females, on the other hand, occur in another cluster nearer the junction of the two axes. A single regression formula best fits the distribution and provides reliable weight estimates for both sexes. These results and observations are consistent with those of Talbot and McCulloch (1965) who report a similar distribution for male and female ungulates in Africa.

The Effects of Seasonal Fluctuations in Weight Estimation:

Seasonal fluctuations in weight, on the other hand, are well documented for several ungulates (Wood, et al. 1962) and account for much of the observed variance in live weight. In moose, for

example, seasonal weight losses amount to as much as 50% of the total live weight (Franzmann, et al. 1978). In Cache la Poudre mule deer, the magnitude of seasonal gains and losses ranges from 15 to 23 percent of the peak weight with a more pronounced seasonal fluctuation in the older animals. In this population, the mature animals generally attain their peak weight in October and their minimum weight in March-April (Anderson, et al. 1974).

In an attempt to account for this variation, the sample was subdivided into 2 categories and a separate regression analysis was performed on each set of data. The first group consists of fifty-one deer shot from June to January. In this group, the correlation coefficient of log-weight on log-mandible length is $r=0.85$ and the corresponding least-squares regression equation is:

$$\log \hat{Y} = 3.92(\log X) - 7.29 \quad (3)$$

The second category consists of thirty-five animals shot from February to May. For mature Rocky Mountain mule deer, this time of year represents the period of maximum weight loss (Anderson, et al. 1974). The correlation coefficient for this group is $r=0.86$ while the regression formula is:

$$\log \hat{Y} = 2.56(\log X) - 4.18. \quad (4)$$

The incorporation of seasonal fluctuations in live weight thus enhances the strength of the relationship such that mandible length now accounts for 72% or 74% of the observed variance in body weight.

An additional source of variation for deer shot throughout the year constitutes the presence or absence of fetuses in the

females of the species. To eliminate this source of bias in weight estimation, mandible length was correlated with weight 2 or the eviscerated weight of the deer. In the first group, the strength of the relationship is $r=0.81$ while the least-squares regression equation is:

$$\log \hat{Y} = 4.25(\log X) - 8.20 \quad (5)$$

In the second group, the correlation coefficient becomes $r=0.91$. Mandible length now accounts for 83% of the observed variance in weight. The best-fit regression equation for group 2 is:

$$\log \hat{Y} = 3.04(\log X) - 5.44 \quad (6)$$

These results again are intuitively consistent with the observations of wildlife biologists. Mating in migratory Rocky Mountain mule deer generally occurs from late November to early December (Anderson and Medin 1967). Pregnant does therefore drop their calves in early June. Consequently, the fetuses contribute significantly to the live weight of the female from late January to early June.

The stronger association of bone length and animal weight for animals shot in late winter is also consistent with the noted variability in the autumnal weight gain. For Rocky Mountain mule deer, this weight gain represents energy storage predominantly in the form of subcutaneous fat. Here, the weight gain is variable and reflects the ability of individual deer to store fat. Hence, a weaker association between bone length and body weight should hold for this time of year. The lower coefficient for group one is consistent with this observation though the weaker association

may reflect the larger sample size or the greater time interval involved.

In sum, the length of the mandible is a useful estimator of the bled carcass weight in mature Rocky Mountain mule deer. The precision of the weight estimate, however, depends primarily on the accuracy of the seasonality assessment. In deer at least, the season of weight gain is concurrent with the period of rapid cementum apposition whereas the season of weight loss corresponds to the period of minimal cementum growth (see Sauer 1973). Given a seasonality determination from the cementum annuli (Benn 1974), mandible length is then as reliable as any other measure of bone size in predicting the live weight of mature mule deer.

The above regression equations apply only for those archaeological mandibles where measurement 2 is quantifiable. In most assemblages, such intact mandibles are rare due primarily to the fragmentation inherent in taphonomic and cultural degradation. Poor recovery techniques also contribute to the fragmented nature of the assemblage. As a consequence, the zooarchaeologist must establish the nature and strength of the relationship between quantifiable dimensions of the fragment and the live weight of the deer. In this study, ten additional skeletal variables were quantified on each mandible and correlated with measurement 2. Of these, measurements 3 ($r=0.85$), 4 ($r=0.94$), 5 ($r=0.86$), 6 ($r=0.83$) and 11 ($r=0.75$) correlate well with measurement two. Given the appropriate α and β values, it then becomes possible to estimate live weight from mandible fragments using two regression equations; one to estimate the total length of the mandible and a

second to determine the animal's carcass weight from the length estimate. Alternatively, it is possible to predict live weight directly from specific dimensions of the fragment by means of a single regression formula. In this research, single regression equations were computed for each of the five measurements listed above. These and their respective correlation coefficients are tabulated in Appendix VIII of this thesis.

The Prediction of Edible Meat Weight in Mature Mule Deer:

In zooarchaeological analysis, the ability to calculate the live weight of an ungulate from the osteological remains is only an initial step toward assessing the relative dietary importance of a species. Obviously, the dietary contribution of a species constitutes only the edible portion of the live weight. Hence, only the edible or useable meat weight of an animal is of interest to the economic prehistorian. To enhance the computation of such meat weights, White (1953a) provides a table of useable meat weights for several North American mammals. For "...wild game animals of the cattle-sheep type..." the useable pounds of meat represent 50% of the average live weight whereas for animals like "...the heavy-bodied, short-legged pigs..." the ratio increases to 70% of the live weight (White 1953a:397). Unlike White, Smith (1975a) assumes 57% of the deer's live weight to be useable meat. Hunter (1947), on the other hand, estimates 80% of the deer to be edible. In a cautionary note on edible meat weights, Stewart and Stahl (1977) discourage the use of any such constant proportions.

In their analysis of twelve mammals, they report no consistent pattern for edible meat percentages. In fact, their ratios of edible muscle tissue are consistently lower than those of White while their proportions for all edible tissues and organs approximate those of White.

Wildlife biologists, in general, concur with these observations. They recommend the use of regression equations to estimate a dressed carcass weight from the live weight of the animal (see Hamerstrom and Camburn 1950, and Severinghaus 1949b). Emerson (1978) uses such regression formulae to calculate the dietary contribution of archaeological deer. He proposes a double regression approach for estimating edible meat weights from the osteological remains of prehistoric deer. In essence, he provides one regression equation for predicting live weight from various astragalus measurements and then advocates the use of Severinghaus' (1949b) equation to derive edible meat weights from the predicted carcass weight. This approach, though more accurate than the standard proportions discussed previously, is neither as efficient nor as reliable as the single regression method described below. The double regression approach entails the derivation and solution of two regression equations. Each estimate in such analysis has an associated error. The calculations, of necessity, incorporate these cumulative errors into the final prediction. As a result, it is preferable to predict dressed carcass weight directly from the size of the mandible by means of a single regression formula.

To obtain the constants for such a predictive equation,

mandible length (measurement 2) was correlated with the skinned and eviscerated carcass weight of the deer. This weight measure (weight 4) lacks the weight of the skin and antlers and, thus, more accurately reflects the amount of edible tissue in a deer carcass. Unfortunately, skinned and eviscerated weights were missing for the first eighteen deer in the sample. Hence, the sample size for the first group (those deer shot from June to January) was reduced to 39 animals whereas that of the second group comprised only 28 deer. The correlation coefficient for group one is $r=0.82$ while the regression equation is:

$$\log \hat{Y} = 3.96(\log X) - 7.57 \quad (7)$$

For the second group, these are respectively $r=0.92$ and

$$\log \hat{Y} = 3.11(\log X) - 5.65 \quad (8)$$

Using these formulae, it is thus possible to predict the skinned and eviscerated carcass weight of mature mule deer directly from the length of the mandible.

Problems in the Estimation of Edible Meat Weights:

Reliable estimates of the useable meat in a taxon are a prerequisite for the study of prehistoric diets. Defining and quantifying the true amount of edible or consumed meat, however, is problematical. Some authors assume the dressed carcass weight to be the more reliable estimate of the edible meat weight (see Casteel 1978 and Emerson 1978). In most instances however, the dressed carcass excludes important organs such as the stomach, heart and liver while at the same time including such inedible

portions as the skin, bone and antler. Furthermore, a dressed carcass may or may not include the brains, tongue or fetus. This carcass weight therefore does not represent adequately the actual amount of edible meat. The skinned and eviscerated carcass, as used in the present study, includes muscle tissue, subcutaneous fat, brains, tongue and bone but excludes antler, skin and many organs. Again, this representation of the useable meat, though reliable, does not approximate the edible tissue available on a deer carcass. According to Lyman (1979:536), the available meat for a species includes "...all parts of an animal exclusive of bone and hide,..." or the "...live weight minus bone and hide weight". To derive this carcass weight during the preparation of the comparative collection is relatively simple once a weight for the skeletal mass is derived. Given a large sample of such values, the calculation of the appropriate regression constants is a matter of simple arithmetic. The resultant equations, however, enable the prediction of available meat weights directly from the size of a bone.

Any estimate of the available meat does not necessarily reflect the actual amount of consumable meat. As defined by Lyman (1979:536), the consumable meat incorporates "...those portions of the available meat of a species that are/were consumed by the group of people under study". Obviously, the utilization of an animal carcass varies from group to group. Different groups consider different portions of the carcass edible. Such variations in carcass consumption require meat weight estimates for the various tissues and organs available

in the animal carcass. Therefore, the analyst must weigh separately all muscle tissue, subcutaneous fat, edible organs and other selected viscera, brains and fetus during the preparation of comparative specimens (see Stewart and Stahl 1977 for a procedure). Given such consumable meat weights, the empirical derivation of single regression formulae for the prediction of any consumable meat weight becomes practicable. In fact, given the appropriate tables, the faunal analyst can predict, by means of regression analysis, the edible meat weight which he assumes best represents the prehistoric utilization of a species.

The regression approach, like all other methods of meat weight estimation, assumes full utilization of, at least, the muscle tissue in an animal carcass. This is implicit in the derivation and utilization of the formulae. In archaeological assemblages therefore, one deer mandible represents one animal in terms of consumed muscle tissue. In dietary or food energy studies (see Cook 1975 and Shawcross 1972), such predicted meat weights are often inapplicable. Prehistoric populations, like their modern counterparts, rarely consume the entire carcass of the animal (Stewart and Stahl 1977). Instead, the consumption of a carcass reflects the dietary preferences of the group, the size of the prey and the relative abundance of the catch. Meat weight estimates thus must represent, as accurately as possible, the degree of carcass consumption.

Evaluating the degree of carcass utilization requires the explicit delineation of butchering techniques and the definition of butchering units from the bones in the faunal assemblage. A

butchering unit, according to Lyman (1979:539), is "...a piece of the animal that results from the act of butchering". It is the cultural entity which most accurately reflects the actual amount of consumed meat. In situations where butchering units cannot be defined, Lyman (1979:539) advocates the use of skeletal portions which he defines "...as some arbitrarily defined part of the body..." such as the forelimbs, hindlimbs, cranium, rib cage and vertebral column. Predicting weights for such butchering units or skeletal portions would provide meat weight estimates which approximate the amount of consumed meat.

Determining the weights of skeletal portions or butchering units directly from the appropriate bones is also practicable using regression analysis. Ledger (1963) and Smith and Ledger (1965) describe a number of skeletal portions or modern butchering units which relate to the weight of African ungulates. There is thus a good correlation between the weight of skeletal portions and the live or dressed carcass weight of African ungulates. Comparable associations are probably tenable for most North American ungulates. Given this relationship, the dimensions of the skeletal elements within each butchering unit may well relate to the weight of the portion. Predicting the weight of a skeletal portion or butchering unit directly from the bone by means of a single regression formula thus becomes practicable.

To obtain the constants for such regression equations, the faunal analyst again must record the weights of selected skeletal portions and butchering units during the preparation of compa-

rative collections. Here, reference to regional ethnographies, faunal studies (Brumley 1973; Guilday, et al. 1962; Lyman 1976, 1979, 1980 and Wheat 1972), and modern butchering practices may aid in delimiting the constitution of skeletal portions or butchering units for specific regions. Given comprehensive tables of such meat weights, the computation of the appropriate regression formulae is relatively straightforward. The resultant regression equations then would provide meat weights for the consumed portions of the animal carcass.

Summary:

In brief, this chapter demonstrates the potential utility of regression analysis as a statistical technique for predicting the live, dressed, or skinned and eviscerated weights of mature deer directly from some measure of bone size. As noted, bone size need not derive exclusively from the major weight-bearing elements. In fact, several skeletal dimensions of the mule deer mandible are accurate estimators of the animal's live, dressed or skinned and eviscerated carcass weight. Regression analysis also appears to be a viable technique for estimating the weight of the available, consumable or consumed meat in the mule deer carcass.

5. Sex determination

The application of methods of sex estimation to bones from excavations presupposes a knowledge of the variation in a known modern population of that species, or alternatively upon a subjective interpretation of the variation observed in the archaeological population (Chaplin 1971:100-101).

Introduction:

Deriving the sex of modern artiodactyls from their osteological remains is difficult in the absence of unique secondary sexual characteristics such as antler pedicles. Sex identification of an archaeological specimen from the fragmentary bone in an assemblage is thus tenuous at best. Nevertheless, many zooarchaeologists measure innumerable skeletal elements to derive the relative sex structure of faunal populations (Chaplin 1971). Some faunal analysts attempt to use sex estimation in prehistoric populations to infer early domestication and subsequent methods of herd management (Boessneck and von den Driesch 1978; Clason 1972, and Higham 1969). Variations in the sex and age structure of such populations through time also argue for a fundamental transition from animal exploitation to animal domestication (Chaplin 1971).

In the study of prehistoric hunting and gathering societies, the sex and age structure of archaeological kill samples reveals "...the nature and evolution of human predation on populations of large mammals" (Klein 1978:195). Here, the population parameters indicate whether stalking or drives predominated as prehistoric

hunting strategies (see Cleland 1966 and Klein 1978, 1979). The sex and age composition of the kill sample also may indicate the seasonality of communal hunts or aboriginal control over herd composition in a drive (see Bedord 1974).

Age and sex determinations are also essential in the establishment of life tables and survivorship curves. These data then reveal the cultural and ecological stress on prehistoric faunal populations (see Reher 1970). In fact, any study of the morphological variation in a species assumes the segregation of a sample relative to sex (see Bedord 1974).

Finally, a knowledge of the sex and age distribution in a faunal assemblage enhances the estimates of MNI (Bokonyi 1970) and meat yield (Smith 1975b). These data also reveal sex-related patterns of butchering. In zooarchaeological research therefore, reliable sex determinations are as important as accurate age estimates. Both are necessary to reconstruct the structure of prehistoric herds.

To infer speciation, domestication or exploitation of prehistoric fauna from the above population parameters assumes the recovery, aging and sexing of a representative sample. This chapter does not attempt to solve the problems of sample bias. Instead, the present discussion focuses on the problem of sex estimation from osteological remains. As such, it advocates discriminant function analysis as a viable statistical tool for sex determination using various skeletal measurements of the mule deer mandible.

Sex Determination in Zooarchaeology -- Postcranial Elements:

For artiodactyls, reliable sex determinations from the postcranial skeleton derive exclusively from the pelvic girdle. In most ungulates, morphological differences in the form and anatomy of the pelvis relate to the sex of the animal (Taber 1956, 1971). The presence of this diagnostic element in a faunal assemblage thus permits a sex determination. In most prehistoric contexts however, innominates are absent as these elements are often left at kill sites. If present, they generally are fragmented due to cultural and taphonomic processes (Smith 1975b). As noted by Lie (1973) however, it is possible to sex fragmented pelvises. Using a modern sample of ten male and fifteen female reindeer (Rangifer tarandus), he quantified various dimensions of the pubis and subjected the data to discriminant function analysis. The resultant discriminant scores enabled him to classify correctly 98% of the modern animals on the basis of these three measurements. He then calculated a similar function with a comparable reliability for his archaeological material.

In the absence of innominates, sexing from the postcranial remains involves a subjective or objective evaluation of visible differences in the robusticity of the skeleton relating to the dimorphism in a species. Sexually dimorphic species normally exhibit qualitative differences in the anatomical features of their skeletal elements (Chaplin 1971). Given comparable age, nutritional status and level of activity, the male skeleton usually supports larger processes, muscle ridges and muscle scars.

Here, the faunal analyst classifies all large and robust elements as male and all slender and smooth bones as female. At present however, the zooarchaeologist cannot ascertain reliably the age or physiological status of an animal from the postcranial bones. As a result, there is a tendency to classify incorrectly many of the old females and young males. Observer bias and experience also influence the accuracy of the determinations. In addition, subjective estimates are difficult to communicate and offer no opportunity for the assessment of classificatory reliability (see Chaplin 1971). Hence, sex determinations which rely exclusively on qualitative differences in the anatomical features of bones are suspect.

Bone dimensions, on the other hand, reflect the average size or weight of the animal (Chaplin 1971). In sexually dimorphic species therefore, quantitative differences in the osteometric attributes of mature animals provide a relatively objective means for sex determination. Such osteometric data are also easy to present and offer the reader of the report an opportunity to evaluate the validity of the sex estimate.

In certain sexually dimorphic species, few osteological measurements are necessary to ascertain the sex of mature animals. In fallow deer, for example, metacarpal length is an efficient criterion of sex (Chaplin 1971). For red deer, there exists a similar sexual dimorphism in the dimensions of the atlas, epistropheus and pelvic bones (Jequier 1963 cited in Clason 1972). In most sexually dimorphic species however, there is considerable overlap in the osteological dimensions of both sexes. Here, only

extremes are separable with certainty. Consequently, researchers quantify several dimensions and then compute indices for specific elements. The latter are purported to separate the sexes and are independent of variations in animal size (Bedord 1974; Duffield 1973; Higham 1969 and Lorrain 1968). The plot of the indices and measurements produces clusters which supposedly are indicative of sex. Frequently however, the identification and delineation of clusters within the point scatter is subjective (Cornwall 1956). Further, the line which subdivides the scatter for one population is not valid for another of different geographical and temporal provenance (Cornwall 1956). Interpretation of these clusters is also problematical due to a lack of normative standards. Here, the clusters are assumed to be sex-related. The correct interpretation of the plots, however, requires an understanding of the character and direction of osteometric variation in modern animals of known sex. At present, few studies record the osteometric differences in the bones of animals of known sex. Only Duffield (1973) and Higham (1969) use modern samples to test the validity of their measurements and indices.

In most faunal assemblages, the paucity of intact elements precludes the use of indices for sex determination. As a result, many researchers plot the dimensions of specific bones to obtain a sex estimation (Chaplin 1971 and Higham and Message 1969). The data normally yield histograms with unimodal, bimodal or trimodal distributions. Presumably, the distributions represent one, two or three sexes respectively. Subsequent application of a proper statistical test indicates whether or not the distributions dif-

fer significantly. Again, normative standards for the interpretation of such histograms are lacking.

In brief then, osteometric data reveal the dimorphism in the postcranial skeleton of prehistoric fauna. The reliability of the sex estimate, however, depends on a prior knowledge of the osteometric variation in modern animals of known sex.

Sex Determination in Zooarchaeology -- Cranial Elements:

Sex identification from cranial features is unambiguous in the presence of certain unique secondary sexual characteristics. In most cervids, for example, antlers and the associated bony pedicles occur only on the frontal bones of males (Chaplin 1971 and Smith 1975a, 1975b). Rarely are these present in females (Ryel 1963). In the genus Rangifer where both sexes support antlers, differences in antler size apparently relate to the sex of the animal (Kjos-Hanssen 1973). For Polish red deer (Cervus elaphus), differences in certain cranial dimensions also relate to the sex of the animal (Mystkowska 1966). In elk, the permanent maxillary canines differ morphologically between the sexes (Greer and Yeager 1967). In bovids, cranial breadth and various horn core dimensions discriminate the sexes given a reliable age estimate (Howard 1963; Skinner and Kaisen 1947, and Wilson 1974). For some bovids however, growth variability, age differences and cultural practices such as castration obscure sexual differences in horn core dimensions (Verpmann 1973). In suids, the maxillary and mandibular canines are very efficient criteria of sex (Clason

1972). Reliable sex identifications are thus practicable in zooarchaeology given intact crania. Establishing the relative frequency of males and females in such assemblages, though, is unreliable due to sex-related differential preservation of the skull (see Mystkowska 1966 and Uerpmann 1973).

In bison, the lingual width of the mandible below the center of M_3 supposedly relates to the sex of the animal (Reher 1974). Reher, however, does not validate his approach using animals of known sex. For red deer of known sex, dimorphism is evident in the length of the mandible, the length of the diastema and other mandibular indices (Mystkowska 1966). Dentary bone length and diastema length also segregate the sexes of mature caribou (see Bergerud 1964 and Miller 1974b). For white-tailed deer, seven skeletal dimensions of the mandible, including mandible length and diastema length, differ significantly for mature males and females (Rees 1971a). In modern cervids therefore, osteometric attributes of the mandible discriminate the sex of the mature animals.

Sexing Mature Mule Deer from Mandibular Measurements:

As noted in the previous chapter, specific dimensions of the mandible relate to the weight of mature Rocky Mountain mule deer. For this species, mandibular measurements, comparable to those of Rees (1971a), identify the sex of mature animals. To evaluate properly the discriminatory value of such measurements, eleven skeletal dimensions were quantified on each complete mandible in

the sample. These dimensions are illustrated in Figure 3, described in Appendix II and listed in Appendix III of this thesis. Of the 100 mandibles, five male and seven female specimens were too fragmented for mensuration. These twelve mandibles thus were excluded from the present statistical analysis. In addition, three complete specimens, namely mandibles 46, 47, and 88, were withheld. These specimens subsequently served as a check on the reliability of the function. The sample for the derivation of the appropriate function thus included twenty-eight male and fifty-seven female mandibles. Here, sample size restrictions precluded the incorporation of age differences during the computation of the function.

To determine the statistical significance of these variables in sex estimation, the data were subjected to a one-way analysis of variance (Simpson, et al. 1960). Here, probability levels of 0.05 or greater were considered to be statistically significant. Means, variance estimates and levels of probability for each measurement are listed in Table I. A perusal of the table indicates that the probabilities for variation between the sexes are highly significant for all skeletal variables. Here, the means of all eleven mandibular measurements are consistently and significantly greater in males than in females.

Although the means are consistently greater in males than in females, the individual measurements show considerable variation about the means. In fact, a perusal of the variables in Appendix III and an examination of Table I reveals a significant overlap in a number of measurements. No single measure or combination

Table I: Means (in mm) of eleven mandibular measurements for mature males and females from the Cache la Poudre deer population. Statistical probabilities of sex variation for each variable are indicated.

Measurements	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11
Males											
N	28	28	28	28	28	28	28	28	28	28	28
Mean	11.11	223.86	150.54	233.36	61.43	72.81	15.11	7.68	13.95	25.31	76.45
Variance	1.06	56.28	19.15	57.94	19.07	21.24	1.29	0.436	0.917	6.30	13.81
Females											
N	57	57	57	57	57	57	57	57	57	57	57
Mean	8.79	209.93	143.04	219.11	55.32	65.84	13.31	6.75	13.50	23.11	71.57
Variance	1.20	40.03	16.28	43.99	18.76	14.28	0.92	0.250	0.746	3.04	10.34
Probability of Variation	>0.99	>0.99	>0.09	>0.99	>0.99	>0.99	>0.99	>0.99	>0.96	>0.99	>0.99

thereof allows the correct identification and classification of an unknown specimen. A further examination of Table I indicates a variability in the degree of overlap for the eleven mandibular measurements. Measurement 2, for instance, shows considerably less overlap than measurement 9. For sex estimation, it is thus preferable to use a combination of measurements and to weight the characters so as to emphasize the better discriminators or those measurements with the least overlap. In numerical taxonomy, the statistical technique of choice for the classification of animals into one or more overlapping groups is discriminant function analysis (Sneath and Sokal 1973).

The linear discriminant function is a linear function which weights the characters describing taxonomic units so as to maximize the probability of correctly classifying an unknown. Discriminant function analysis thus ascribes an unknown to one of two or more predetermined classes with the least chance of error (Kendall 1972). Variables describing these classes generally include measurements such as those listed above. In the populations from which the classes are drawn, the variables must have a common multivariate normal distribution (Hope 1969). Further, the dispersion matrices of the various groups must be identical (Hope 1969). Discriminant function analysis thus assumes equality of variances and covariances.

In the present study, the 2 predetermined classes or groups are the respective mandibles of mature male and female mule deer. Since the number of members in each group need not be equal (Hope 1969), 28 male mandibles and 57 female mandibles were used in the

derivation of the discriminant function. The characters or variables for these groups include the eleven mandibular measurements described above.

Each group of mandibular measurements is assumed to be a random sample from a population. In the present analysis, the statistical population includes the values for the same eleven measurements on all the mandibles of deer extant in the Cache la Poudre area during the collection period. These data are assumed to have a common multivariate normal distribution. Application of the F-test (Sokal and Rohlf 1969) to the variances in Table I confirms the equality of variances. The Midas statistical package for discriminant function analysis provides a statistic for testing the equality of covariance matrices (Fox and Guire 1976). The results indicate that although the covariance matrices are not identical, they do not vary significantly. Reyment's (1962) study on homogeneity of covariance matrices in paleontological biometry confirms moderate insensitivity of the test to minimal heterogeneity. The classes of mandibular measurements therefore satisfy all of the above assumptions and are amenable to discriminant function analysis.

To obtain the weighting vectors for these measurements, the data were subjected to discriminant function analysis (Fox and Guire 1976). The data then were subjected to canonical analysis of discriminance to standardize the variables and transform the original test space from ellipsoids to spheres with radii equal to unity (Hope 1969). The results of the canonical analysis include standardized canonical vectors which are better vectors

of weights than the original weights provided by the discriminant function analysis. These standardized weights combine to form a linear discriminant function for a specified set of variables. Using measurements 2, 5, 6, 7, 8, 9, 10 and 11, for example, the standardized canonical vectors and the resultant discriminant function take the form:

$$\begin{aligned}
 a = & 0.094 \text{ (measurement 2)} - 0.030 \text{ (measurement 5)} \\
 & + 0.041 \text{ (measurement 6)} + 0.535 \text{ (measurement 7)} \\
 & + 0.933 \text{ (measurement 8)} - 0.248 \text{ (measurement 9)} \\
 & - 0.299 \text{ (measurement 10)} + 0.019 \text{ (measurement 11)} \quad (9)
 \end{aligned}$$

where a is the discriminant score. The within group variance and standard deviation for these discriminant scores is unity. Using this equation, the discriminant function scores and respective means for each group can be calculated. Alternatively, the means or centroids for each group of scores can be obtained using the respective means for each measurement. Using the appropriate means from Table I, the weighted mean for males becomes

$$\begin{aligned}
 & 0.094 (223.86) - 0.030 (61.43) + 0.041 (72.81) \\
 & + 0.535 (15.11) + 0.933 (7.68) - 0.248 (13.95) \\
 & - 0.299 (25.31) + 0.019 (76.45) \\
 & = 27.86
 \end{aligned}$$

while that of females is:

$$\begin{aligned}
 & 0.094 (209.93) - 0.030 (55.32) + 0.041 (65.84) \\
 & + 0.535 (13.31) + 0.933 (6.75) - 0.248 (13.50) \\
 & - 0.299 (23.10) + 0.019 (71.57) \\
 & = 25.29
 \end{aligned}$$

The difference or distance between the group centroids is equal to Mahalanobis D . In this case, D equals $27.86 - 25.29$ or 2.57 . The midpoint between the group means is the discriminant score for males minus $D/2$ or $27.86 - 1.29 = 26.57$. Using the above measurements, this value (26.57) represents the critical value in

the division between males and females. Individuals with scores greater than 26.57 are males while those with scores less than this critical value are classified as females.

The critical value also provides an estimate of function reliability. This point ($D/2$) is 1.29 standard deviation from the mean for males and equally distant from the centroid for females. Consultation of a Table of the Cumulative Normal Distributions (Thomas 1976, Table A.3) indicates that 1.29 standard deviation from the mean includes over ninety percent of the population. Consequently, the above discriminant function should classify correctly the sex of 90% of the mature Rocky Mountain mule deer in the Cache la Poudre reserve.

To test the reliability of the discriminant function, the measurements for specimens 46, 47 and 88 were inserted into the equation. Specimen 46 is a 94 month old female; 47, a 34 month old female, and 88, a 56 month old female. The discriminant scores for specimens 46, 47 and 88 were respectively 22.61, 25.38 and 24.65. All scores fall well below the critical value and, therefore, all three specimen were classified correctly by their discriminant scores. The discriminant function thus appears to be a viable tool for sex estimation.

In discriminant function analysis, the same characters must be used in the description of the classes, the derivation of the function and the classification of an unknown (Doran and Hodson 1975). In others words, equation nine identifies and classifies only those mandibles where measurements 2, 5, 6, 7, 8, 9, 10 and 11 are quantifiable. If measurements 2 or 6 are lacking, a dif-

ferent function is necessary. Appendix IX of this thesis lists seven additional discriminant functions for the classification of mandible fragments. The selection of individual measurements for inclusion into these functions reflects their appropriateness in the classification of archaeological fragments. Here, only those dimensions which are measurable on typical mandible fragments were combined for the derivation of the discriminant functions. Appendix IX also lists the critical value and relative accuracy of each linear equation.

Discretion in the Application of the Function in Zooarchaeology:

The results of the present analysis conclusively demonstrate a sexual dimorphism in the complete and fragmented mandibles of mature mule deer from the Cache la Poudre area. The application of discriminant function analysis in the study of archaeological fauna, however, requires further testing. Discriminant functions assign an unknown to one of two predetermined groups. It does not create such groups. As a result, it is effective only for a given population (Kendall 1972). Technically, the above function is valid only for the 1961-1965 Cache la Poudre deer population. It may be invalid for deer inhabiting the Cache la Poudre reserve from 1861 to 1865 or for contemporaneous mule deer populations in differing geographical regions. Here, further testing with mandibles of known-sex is necessary to establish the relevance of the function in the analysis of deer populations from different geographical and temporal proveniences.

Proper testing of the function requires mandibles of known sex. In archaeological assemblages, articulated skeletons and skulls are frequently sexable on the basis of specific secondary sexual characteristics. The mandibles of these animals are thus of known sex and fitting to test the suitability of the function. As a result, proper recovery, identification and storage of such elements is essential.

Secular trends in temporally disparate populations also may influence the centroids and critical values for the function. If such is the case, it then becomes necessary to calculate separate discriminant functions for prehistoric fauna. Here, articulated skeletons or intact skulls which derive from catastrophic events such as drives or mudslides are necessary. Only such assemblages provide a series of mandibles of known sex from a restricted time period. The excavation of any such site thus requires special attention (see Wheat 1972 for recommendations). Given a sufficiently large collection of such elements, it is then possible to establish sex classes and to compute discriminant scores for the respective mandibular measurements. The resultant functions are then invaluable in the identification and classification of mandibles from assemblages of similar temporal provenience.

In sum, only future research in numerical taxonomy, in the osteology of contemporaneous mule deer populations, in taphonomy, paleontology, and zooarchaeology can demonstrate the general applicability of this statistical technique for sex estimation. Nevertheless, because the results of this study are so encou-

raging, the application of the discriminant function in wildlife biology and zooarchaeology merits further study and testing.

Summary:

In summary, discriminant function analysis is an effective statistical technique for sex determination of mature mule deer. The results of this study conclusively demonstrate an observable sexual difference in the mandibles and mandible fragments of mature Rocky Mountain mule deer from the Cache la Poudre deer population. The application of this method of sex determination in the analysis of prehistoric faunal remains, however, requires further study.

6. Age determination

The ageing of animals from skeletal remains of any antiquity cannot be an exact science, and calls for the exercise of considerable judgement (Silver 1969:300).

Introduction:

In zooarchaeology, determining the age of an animal from its skeletal remains is a fundamental step in any analysis. Reliable age estimates are essential for adequate quantification of the remains (Bokonyi 1970; Chaplin 1971; Clason 1972, and Flannery 1967). They also provide the secondary data for establishing the relative age structure of fauna within the assemblage. This information then forms the basis for subsequent interpretations and inferences.

For studies on domestication, the proportions within the various age groups represent mortality frequencies which, when compared, segregate wild and domesticated animals (Bokonyi 1973 and Flannery 1969). Presumably, age at death differs for wild and domestic stock (see Collier and White (1976) for a rebuttal). Comparisons of such assemblages through time then permit the detection and elucidation of stages in the domestication process.

For assemblages from stock-rearing societies, age structure reveals specific aims and methods of animal husbandry (see Bowen 1975; Chaplin 1971; Higham 1968, and Payne 1973). Presumably, distinct activities such as wool, meat and milk production entail distinct patterns of herd utilization (Saxon and Higham 1969).

Age estimates for the younger animals within the assemblage also disclose their date of death and thus indicate the seasonality of slaughter practices (Higgs and White 1963) and hunting activities (Emerson 1979; Latady 1978, and Smith 1974a, 1974b).

Age structure and mortality frequencies are also essential in the study of prehistoric population dynamics. Mortality frequencies in paleontological and archaeological assemblages represent either catastrophic or attritional mortality rates (Nimmo 1971 and Voorhies 1969). These mortality rates then reveal the characteristic balances between natality and mortality, essential life-death relationships and basic predation patterns (Voorhies 1969). In most archaeological assemblages, mortality frequencies reflect selective patterns of human predation such as stalking or drives (see Cleland 1966; Elder 1965; Emerson 1979; Guilday 1962; Klein 1979 and Read 1971). Comparing mortality rates in heterochronic assemblages then reveals shifts in hunting practices through time (Klein 1978 and Waselkov 1978).

Finally, age estimates furnish insights into the longevity of prehistoric fauna (Guilday 1962; Klein 1978, and Nimmo 1971). A comparison of longevity in modern and prehistoric fauna then indicates the relative merit of modern management practices (see Elder 1965, and McGinnes and Reeves 1957). In brief, accurate age estimation is an integral part of any faunal analysis.

Any discussion of the age structure in a faunal assemblage assumes the recovery of a representative sample. Further, such studies presuppose accurate aging of all recovered materials. Whether or not the recovered samples are representative of the

exploited populations is not an issue here. The following discussion recognizes but does not attempt to resolve the problems of differential preservation, recovery and identification. Nor does this section of the thesis provide an accurate method for aging all the recovered skeletal elements. Instead, this chapter reviews the many problems of ungulate age estimation and proposes cementum annuli counts of the first molar as a viable approach to estimating the absolute age of prehistoric deer.

Age Determination in Zooarchaeology:

At present, faunal analysts examine the degree of epiphyseal fusion (see Bowen 1975; Duffield 1973; Gilbert 1973; Noe-Nygaard 1977, and Williams 1978) or the robusticity of skeletal elements (Chaplin 1971 and Gilmore 1949) to determine age from the post-cranial skeleton. Radiographs of such elements usually enhance estimate reliability. According to Reed (1963), the general sequence of fusion is comparable in most mammals. Chaplin (1971) argues for a specific regularity in the sequence of epiphyseal fusion but acknowledges variability in the age at which fusion occurs. In domestic stock, for example, the timing of epiphyseal fusion depends on the breed, diet, shelter and age at castration (Silver 1969 and Uerpmann 1973). In deer, on the other hand, the sequence and timing of epiphyseal closure is sex related (Lewall and Cowan 1963). The distal end of the radius and the proximal ends of the tibia and humerus fuse one year later in females than in males. Conversely, the distal end of the femur

fuses 18 months earlier in the female than in the male. Lewall and Cowan (1963) also acknowledge the effects of nutrition on the rate of epiphyseal fusion. In their opinion, inanition delays epiphyseal closure by as much as 12 months. The robusticity of skeletal elements is equally unreliable as it reflects the sex, age and activity patterns of the animal (Chaplin 1971).

In view of the above limitations, faunal analysts prefer to examine age related features of the crania. Specific characters examined include cranial suture closure, relative development of horns and antlers, and macroscopic or microscopic attributes of the dentition (Chaplin 1971). As with the postcranial skeleton, cranial development and suture closure relates to the age and nutritional status of the animal (Chaplin 1971). Further, in red deer, the sequence and rate of suture closure is sex-related (see Mystkowska 1966).

Antler development is equally unreliable as a criterion of age for male cervids (but see Bouchud 1966). Antler growth and development varies from year to year and reflects the environmental and dietary factors extant during antlerogenesis (Ryel, et al. 1961; Severinghaus and Cheatum 1956, and Severinghaus, et al. 1950). Age and heredity contribute only minimally to the final appearance of the antler. Only the diameter or circumference of the antler base seems to increase consistently with advancing age (Anderson and Medin 1971). Here, however, individual variation severely limits the utility of this dimension in the establishment of age classes.

Unlike antlers, the horn sheaths of bovids exhibit major

corrugations or horn rings which relate to the annual growth patterns of the animal. Horn ring counts, in bighorn sheep at least, are reliable indicators of age until the eighth year (Geist 1966). Thereafter, the actual rings are difficult to distinguish from other minor corrugations. As a result, age estimates for the older animals are often inaccurate. For such animals, Armstrong (1965) and Hemming (1967) recommend longitudinal bisection and polishing of the horn sheath to count the internal growth layers.

Horn sheaths rarely preserve in archaeological sites. Zooarchaeologists therefore use horn core dimensions to estimate the ages of bovids in their sample. In bighorn sheep, horn core size relates to sex, nutrition and, to a lesser extent, age (Hemming 1967). The faunal analyst thus should confirm the validity of this approach using a sample of known-age animals.

To many researchers, only an analysis of tooth eruption and replacement provides accurate age estimates (see Chaplin 1971; Cleland 1966; Emerson 1979; Frison and Reher 1970; Guilday 1962, 1970; Latady 1978; Read 1971 and Smith 1975a). Here, radiography again enhances estimate reliability since radiographs reveal the developmental stage of unerupted teeth and the relative degree of pulp cavity closure in the erupted dentition (see Williams 1978). Though relatively accurate, the sequence of tooth eruption and replacement cannot provide an age estimate to the nearest month as reported by Bouchud (1966), Carter (1975), Emerson (1979), Smith (1975a) and others. Like Brumley (1973), Higgs and White (1963), Silver (1969) and Spiess (1979), I regard such assertions

with skepticism. Within any given population, there is too much individual variation in tooth development and eruption to justify such claims.

According to Chaplin (1971:78), the order of tooth eruption for a given species is largely constant "... though minor variations may occur in local populations". In heterochronic fauna, this variation is occasionally quite significant as documented by Ewbank, et al. (1964). In their comparative study of modern and Iron Age sheep, these authors note significant differences in the relative order of tooth eruption. Though selective breeding may contribute to the above variation, only diet and evolution can explain the divergent eruption schedules evident in the various species of wild sheep (see Hemming 1967). Similar anomalies may occur in modern and prehistoric populations but these will remain undetected as long as wildlife biologists and zooarchaeologists rely on tooth eruption as the sole criterion for aging all the younger animals in their samples.

Though the sequence of tooth eruption is largely constant, the age at which a tooth erupts varies from individual to individual within a species (Chaplin 1971 and Morris 1972). In caribou populations, for example, age spans during which individual teeth are erupting range from 3 to 15 months (Spiess 1979). Here, only the first mandibular molar is consistent and predictable in its development and eruption. Studies with known-age animals clearly demonstrate the effect of diet on tooth eruption. Poor nutrition delays tooth replacement from 6 months to 1 year (Hamerstrom and Camburn 1950; Severinghaus and Cheatum 1956; Robinette, et al.

1957, and Ryel, et al. 1961). Heredity also controls the timing of tooth eruption in certain species (see Ludwig 1967, and Wiener and Purser 1957).

Wildlife biologists recognize the latitude in tooth replacement but, for their purposes, "... this variation does not affect the hunting season age determination" (Ryel, et al. 1961:311). In wildlife management also, age estimates derive from the examination of complete mandibles. In zooarchaeology, on the other hand, age determinations often are based on fragmentary remains (see Klein 1978; Klein, et al. 1981, and Spiess 1979). Further, unlike the wildlife biologist, the zooarchaeologist does not age animals whose seasons of death are known or delimited. In fact, he uses tooth eruption and replacement to determine the season of death (Emerson 1979 and Smith 1975a). At no time can he assume, as a biologist can, a restricted hunting season of a few months. Some prehistoric faunal samples derive from site occupations of unknown duration. Others reflect a recurrent occupation of a particular site area. This heterochrony in the zooarchaeological material prohibits the segregation of an assemblage into annual or seasonal kills. Further, the zooarchaeologist cannot evaluate or reconstruct the nutritional status of archaeological fauna. Tooth eruption sequences thus provide relative age estimates for the delineation of age classes within an assemblage (Chaplin 1971 and Morris 1972). Such age classes vary from site to site and provide only a general estimate of the animals' absolute age.

To determine the ages of mature mammals, faunal analysts assess the degree of wear on the molariform teeth (see Payne 1973

for an elaborate scheme of wear pattern analysis). In wildlife management studies, biologists use tooth wear as a criterion of age but recognize its inherent drawbacks. Although teeth wear with increasing age, this degradation is not uniform. Regional variations in the degree of wear occur and seem to reflect the quality of forage (Ryel et al. 1961, and Szabik 1973), the relative amount of grit in the food (Severinghaus and Cheatum 1956), the actual timing of tooth eruption (Hamerstrom and Camburn 1950) and local differences in tooth hardness (Morris 1972; Robinette, et al. 1957, and Szabik 1973). Variations in the rate of wear are also apparent between sexes (Flook 1970; Miller 1974a, and Thomas and Bandy 1975). Abnormal tooth wear also occurs and generally results from malocclusion and dental anomalies (Miller 1974a; Morris 1972, and Robinette, et al. 1957).

To account for the regional differences, biologists have established the typical tooth wear patterns for many of the major wildlife regions (refer to Lueth 1963 for an example). In faunal studies, establishing the representative tooth wear patterns for specific regions is often impracticable. Too many authors report temporal variations in the attrition rates for prehistoric fauna. According to Bouchud (1953), for example, tooth wear relative to dental eruption age is more rapid in Paleolithic caribou than in their modern counterparts. Witter (1971) also documents a similar difference for the modern and prehistoric caribou of Alaska. Further, certain geologic events such as volcanic eruptions are known to alter significantly the attrition rates in ungulates (see Burt 1961).

The analysis of tooth wear is also plagued by human error. Determining the degree of attrition on molariform teeth is very subjective. Brown (1961) and Ryel, et al. (1961), using known-age samples, conclusively demonstrate the variability in such age estimates. To curtail this source of error, Robinette, et al. (1957) developed a molar tooth ratio based on a number of crown measurements. Carter (1975), Klein (1978, 1979), Klein, et al. (1981) and Reher (1973) adopted this quantitative approach to determine the relative ages of species in their archaeological assemblages. In fact, Carter (1975:231) estimates "...the rate of wear in mm per month..." and ages mature prehistoric sheep to within a month.

For mule deer age estimation, such accuracy is never obtained. In a comparative study of cementum annuli counts and three methods of wear pattern analysis, including the molar tooth ratio, Erickson (1967) clearly demonstrates the inconsistencies and inaccuracies of tooth wear as a criterion of age. In the present study, seven additional specimens from the Cache la Poudre population were available for such a comparative study. Specimens 13, 57, 65, 83, 84, 91 and 09 were aged from the molar ratio and from cementum annuli counts of the first mandibular molar. Here, the respective age estimates of only the youngest specimen (09) were in agreement. For the remaining 6 specimens, the molar ratio overaged two deer by 1 year and underaged four animals by as much as two years. These results are consistent with the conclusions of the comparative studies listed in Table II. The majority of the researchers listed report significant

Table II: List of studies* which compare age estimates from cementum annuli counts and tooth replacement and wear patterns. Their conclusions are also presented.

Source	Species	Results
Aitken (1975)	Roe deer from Thetford Chase, Norfolk	in 63 animals, there was complete agreement in 63.5% of the cases and agreement to within one year in 90.5%
Boozer (1970)	white-tailed deer from Alabama	in his total sample, both aging methods agree in 72% of the cases. Here, there is a tendency for tooth-wear to underage the older animals.
Campbell (1967)	white-tailed deer from Illinois	tooth development and wear is 95% accurate for animals 4½ years old or younger. For animals older than 4½, this method of aging is unreliable.
Erickson (1967) & Erickson, et al. (1970)	mule deer from Colorado	37% of the deer were aged incorrectly by visual examination of the tooth wear. Here, also, there is a tendency to underestimate ages by this method.
Gilbert & Stolt (1970)	white-tailed deer from Maine	tooth wear patterns tend to overage the younger animals and underage the older animals.
Keiss (1969)	elk from Colorado	there is only 50% agreement between aging methods. In older animals, eruption and wear estimates were in error by as much as 7 years.
Kerwin & Mitchell (1971)	pronghorns from Alberta	there was a slight tendency for younger animals to be underaged by development and wear while older animals were overaged.
Lockard (1972)	white-tailed deer from 15 states and 1 province	there is a 26% error with a tendency for eruption and wear to overage animals. discrepancies between aging methods were more common in older animals. differences were as much as 3 years.
Low & Cowan (1963)	black-tailed deer from British Columbia	record several discrepancies both in over-aging and underaging animals 18 months or older.

Table II: (cont'd)

Source	Species	Results
Lowe (1967)	red deer from Rhum	using a known-age sample, ages derived from an analysis of tooth replacement and wear were 88% accurate while those derived from cementum annuli counts were only 50% accurate.
McCutchen (1966)	pronghorn antelope from Montana	there is significant disagreement between the two techniques, especially in the older age classes.
Olson (1967)	white-tailed deer from Indiana	no significant difference in the age estimates though tooth wear was in error more frequently in the older age classes.
Sergeant & Pimlott (1959)	moose from Newfoundland	several animals 2 years of age and older were aged incorrectly by tooth wear. the divergences increase for older animals.
Simkin (1965)	moose from Ontario	considers tooth wear the most inaccurate of the methods tested. from Table 7, wear-class aging appears to underage older animals.
Thomas & Bandy (1975)	black-tailed deer from British Columbia	tendency for tooth wear to under-estimate the ages of deer in older age classes.
Winterton & Strick- land n.d.	white-tailed deer from Ontario	great deal of individual error in wear class aging with a tendency to underage, particularly in the older age classes.

*Most studies assume cementum annuli counts to be accurate indicators of absolute age.

discrepancies in the age estimates based on tooth wear. In their opinion, the tooth wear patterns in ungulates generally underestimate the age of older animals.

Tooth wear analysis is thus an unreliable criterion of age for modern and prehistoric faunal populations. The observed individual and regional variations in wear patterns and the human error inherent in the evaluation of attrition severely limit the accuracy of the technique in the study of modern populations. In the analysis of prehistoric tooth wear, temporal variations in attrition rates and the heterochronic nature of the assemblages constitute additional sources of error. Further, the limited experience of the analyst and his reliance on mandible fragments for age determination impose additional restrictions on the reliability of such age estimates. At best, wear patterns provide relative age estimates for the fauna in individual sites. The relationship of such wear stages with the absolute ages of animals remains speculative (Payne 1973).

Incremental Growth Structures and Age Determination:

Presently, only incremental growth structures provide reliable estimates of absolute age in prehistoric faunal populations (Chaplin 1971:84). The successful application of this method of age determination in zooarchaeology is clearly documented in the literature (see Benn 1974; Bourque, et al. 1978; Kay 1971; Saxon and Higham 1969, and Spiess 1976, 1978, 1979). With very few exceptions, the above researchers examined polished half-tooth

sections or undecalcified thin sections to make the annuli count. Such preparations, as noted below, are usually unsatisfactory and unreliable for accurate age estimation.

In wildlife biology today, counting the annuli in the dental cementum is the only reliable method for estimating the absolute age of artiodactyls. The twenty-three studies with known-age animals listed in Table III confirm the accuracy and overall reliability of the method. There is not, however, perfect agreement between the cementum annuli counts and the known-ages of all animals. Several significant disagreements are evident in this chart. Gasaway, et al. (1978) discuss some of the errors which contribute to the inaccuracy of the age estimates. In their opinion, these relate to the legibility of tooth sections, the subjectivity in identifying annuli and the presence of multiple lines in some sections. Obviously, the quality of a preparation influences section readability and, by extension, the ease of annulus identification. Innate factors of the organism, on the other hand, affect the actual complexity of the cementum deposit.

In their research, Gasaway, et al. (1978) examined longitudinal and cross sections of undecalcified teeth. Few of these tooth sections were easy to read. Numerous other biologists encountered similar problems in the examination of both half-tooth and undecalcified thin sections (see Campbell 1967; Douglas 1970; Erickson 1967; Lockard 1972; Low and Cowan 1963; McEwan 1963 and Stephenson 1977). To improve the clarity of their thin sections, these researchers opted for decalcified, sectioned and stained preparations. The studies listed in Table III indicate the value

Table III: Chart listing studies with known-age animals. This table lists the species involved, the teeth and histological procedures employed and the choice of section. The chart also indicates the size and age range of the known-age sample as well as the number of agreements and disagreements between annuli counts and the chronological ages of the animals.

Source	Species	Tooth	Histological Procedures	Type of Section	Sample Size	Age Range	Agree	Dis-agree
Aitken (1975)	Roe deer	first molar	sawing, grinding and polishing of half tooth sections	half tooth sections	9	4-7	8	1
Armstrong (1965)	Bison	all teeth	for half tooth sections-- fixation in 70% alcohol followed by repeated grinding and polishing for undecalcified thin sections-- fixation in 70% alcohol, removal of 177 micron longitudinal and transverse sections followed by grinding and polishing	half tooth sections longitudinal & transverse sections	19	4½-17½	16	3
Armstrong (1965)	cow	all teeth	same as above	same as above	2	7½-8½	0	2
Boozer (1970)	white-tailed deer	first molar	decalcification in 20% formic acid, paraffin embedding, micro-tome sectioning and staining in Harris' hematoxylin	8 micron serial transverse sections	9	2-17	8	1
Campbell (1967)	white-tailed deer	first molar	decalcification in 30% formic acid, paraffin embedding, micro-tome sectioning and staining in Delafield's hematoxylin	10 micron longitudinal sections	76	½-5½	75	1

Table III: (cont'd)

Source	Species	Tooth	Histological Procedures	Type of Section	Sample Size	Age Range	Dis-agree
Erickson (1967), Erickson & Seliger (1969)	mule deer	central incisor	fixation in 10% formalin, removal of 100 micron sections, grinding and polishing of specimens, decalcification in 5% formic acid and staining in hematoxylin	95 micron transverse sections	16	1½-7	16 0
Gasaway, et al. (1978)	moose	central incisor	removal of cross-sections followed by grinding and polishing to attain desired thickness	0.3 mm transverse sections	68	1-11	46/78* 32/78*
Gasaway, et al. (1978)	moose	central incisor	removal of longitudinal sections followed by grinding and polishing to attain desired thickness	0.3 mm longitudinal sections	68	1-11	57/97* 40/97*
Gilbert (1966)	white-tailed deer	central incisor	decalcification in 30% formic acid, paraffin embedding, microtome sectioning and staining in Delafield's hematoxylin	10 micron longitudinal sections	10	1½-11	10 0
Hemming (1967), (1969)	Dall sheep	central incisor	removal of sections, washing in detergent, rinsing, dehydration, clearing and mounting in Permount	50-75 micron longitudinal sections	1	1½	1 0
Keiss (1969)	elk	central incisor	same histological procedure as Erickson (1967) and Erickson and Seliger (1969)	95 micron transverse sections	18	2½-15½	18 0

Table III: (cont'd)

Source	Species	Tooth	Histological Procedures	Type of Section	Sample Size	Age Range	Agree	Dis-agree
Lockard (1972)	white-tailed deer	central incisor	decalcification in formic acid, embedding in Paraplast, microtome sectioning and staining in Harris' hematoxylin	6 micron transverse sections	46	not stated	46	0
Low & Cowan (1963)	black-tailed deer	central incisor	decalcification in 5% formic acid, double embedding, microtome sectioning and staining in Erlich's hematoxylin	10 micron longitudinal sections	20	1½-6	20	0
Low (1967)	red deer	first molar	same histological procedure as Mitchell (1967)	half tooth sections	28	1-8	15** 13***	13** 15***
McCutchen (1966), (1969)	antelope	central incisor	removal of 150-200 micron longitudinal and transverse sections, grinding of sections to 16 microns, washing in detergent, decalcification in 2.5% nitric acid and staining in Erlich's or Delafield's hematoxylin	16 micron longitudinal & transverse sections	10	1½-6½	10	0
Mitchell (1963), (1967)	red deer	first molar	cutting, grinding and polishing of half tooth sections	half tooth sections	22	1½-19½	18	4
Olson (1967)	white-tailed deer	central incisor	fixation in 10% formalin, decalcification in 5% nitric acid, double embedding,	10 micron longitudinal sections	4	N/A	4	0

Table III: (cont'd)

Source	Species	Tooth	Histological Procedures	Type of Section	Sample Size	Age Range	Disagree	Agree
Ransom (1966)	white-tailed deer	first molar	microtome sectioning and staining in Harris' hematoxylin repeated grinding and polishing of half tooth sections	half tooth sections	16	1-12	variation is not more than plus or minus 1 layer for any of the 16 deer	
Reimers & Nordby (1968)	reindeer	central incisor	decalcification in 0.8N nitric acid, sectioning on freezing microtome and staining in Mayer's acid haemalum	30 micron longitudinal sections	37	14-94		37 0
Sauer (1973)	white-tailed deer	central incisor, first premolar & first molar	decalcification in 20% formic acid, sectioning on freezing microtome and staining in Harris' hematoxylin	10 micron longitudinal sections	69	1-7		58 11
Sergeant & Pimlott (1959)	moose	central incisor	for undecalcified thin sections, removal, grinding and polishing of thin sections to attain desired thickness for half tooth sections, cutting, grinding and polishing of the specimen	half tooth sections & longitudinal thin sections	1	34		1 0

Table III: (cont'd)

Source	Species	Tooth	Histological Procedures	Type of Section	Sample Size	Age Range	Agree	Disagree
Thomas & Bandy (1973)	black-tailed deer	central incisor	decalcification in 10-30% formic acid, paraffin embedding and staining in Delafield's hematoxylin	10-16 micron transverse sections	37	4-7½	37	0
Turner (1977)	bighorn sheep	central incisor	decalcification in formic acid, sectioning on freezing microtome and staining in Paragon stain	8 micron longitudinal sections	12	3½-9½	12	0
Wolfe (1969)	moose	first molar	cutting, grinding and polishing of half tooth sections	half tooth sections	18	1-2	18	0

*Here, annuli counts in 46 of 78 transverse sections are in agreement with the known age of the animal while 32 of 78 transverse sections disagree. For longitudinal sections, agreements occur in 57 of the 97 sections while disagreements are evident in 40 of 97 sections.

**Age estimates based on minimum count of annuli present.

***Age estimates based on maximum count of annuli present.

of their option. Most of the disagreements between the cementum annuli counts and the known-ages of the animals occur in studies where researchers use undecalcified tooth sections.

Decalcified, sectioned and stained preparations of ungulate teeth also result in considerably less wastage (Page 1977). For each undecalcified thin section, there are, at least, ten decalcified sections. The subsequent examination of more sections improves the accuracy of the final age estimate (Miller 1974a). In the analysis of prehistoric faunal remains therefore, the preparation of decalcified thin sections is not only feasible (see Andersen and Jorgensen 1960; Saxon and Higham 1969, and Stout 1978) but strongly recommended for age determination. According to Spiess (1979) however, decalcification and staining have a poor success rate with imperfectly preserved teeth. In my opinion, given the proper histological procedure, much of the archaeological faunal material can be successfully decalcified and stained.

Counting annuli in stained preparations requires experience as well as a good histological preparation (see Craighead, et al. 1970; Erickson and Seliger 1969; Jensen and Nielsen 1968, and Thomas and Bandy 1973). Even high quality histological work does not guarantee the production of thin sections with very distinct annuli. For some animals the patterns of the incremental growth lines are innately indistinct or complex (Erickson and Seliger 1969; Gasaway, et al. 1978, and Grue and Jensen 1979). Further, the general appearance and clarity of the annuli vary throughout the cementum deposit of individual teeth. As a result, thin

section examination and interpretation entails a certain degree of subjectivity and, like thin section preparation, requires considerable practice. With experience however, the observer formulates, though usually not explicitly, an acceptance level for the quality of the preparation required for accurate age determination (Miller 1974a).

Age Determination from the Cementum Annuli of Mule Deer Molars:

In the present study, the first mandibular molars of one hundred and two mule deer formerly aged by Erickson (1967) were decalcified, sectioned and stained. A total of four hundred and eight slides containing some four thousand sections were prepared and examined as specified in chapter three and Appendix VI of the present thesis. Of these, only the last one hundred slides, in my opinion, contained good histological preparations. The remainder of the microslides had several corrugated, "moth-eaten", poorly affixed or inadequately stained thin sections. Such are obviously the consequences of limited practice and experience in the preparation of histological material.

Microscopic examination of all stained sections revealed the presence of alternating light and dark blue increments in both the cementum and dentine of mule deer molars. Here, the bands present in the cementum were more consistent and more distinct than those in the dentine. The former thus were selected for age determination.

In Cache la Poudre deer, the period of rapid cementum growth

coincident with the apposition of the light staining zone occurs from April to December. The deposition of the dark staining band coincides with the episode of slow cementum growth from January to early April (Erickson 1967). One light staining band and one dark band constitute one annulus and represent 1 year of cementum growth. Counting the annual bands or annuli from, but excluding, the dentino-cementum interface to the periodontal border of the cementum deposit provides an estimate of the deer's absolute age. Theoretically, the annuli count corresponds to the chronological age, in years, of the animal. In practice however, counting the cementum annuli is never so simple.

In their analyses, wildlife biologists always examine the entire cementum deposit of each thin section to ensure the proper annuli count (see Grue and Jensen 1979; Miller 1974a, 1974b, and Morris 1972). This approach facilitates the distinction of true annuli from the secondary or accessory growth increments. It also aids in delineating areas of annuli splitting and merging. Thus, although annuli occur throughout most of the deposit, only a thorough examination of the entire cementum layer ensures the location of those areas best suited for reliable annuli counts.

Selecting the appropriate area for counting the incremental growth lines is then the first important practical consideration. For ungulate molars, Aitken (1975), Douglas (1970), Lowe (1967), Markgren (1969), Mitchell (1963, 1967), Ransom (1966) and Wolfe (1969) recommend the pad area. In all cases, these investigators examined polished half-tooth sections. In most decalcified and stained thin sections, the pad area generally displays diffuse

layers with numerous accessory lines which tend to confuse the count (see Grue and Jensen 1979, and Miller 1974b). As a result, Boozer (1970), Campbell (1967), Grue and Jensen (1979) and Miller (1974b) prefer to examine the thinner coronal deposits of the root. They, however, do not restrict their counts to this region of the tooth. Frequently, these researchers examine the thicker deposits to substantiate their counts.

In the present analysis, the entire cementum deposit of each section was scanned at a low magnification (40X) to evaluate the nature of the cementum and to locate areas with distinct annuli. In longitudinal sections of mule deer molars, cementum covered the entire root surface from the crown to the root apex. There was however considerable variation in the nature and thickness of the deposit throughout. In general, the deposit was thinnest in the cervical region near the cemento-enamel interface and thicker in the bifurcation and the apical region. The cementum was also relatively thick on the distal surface of the mesial root and on the mesial surface of the distal root. The thicker layers generally were cellular and convoluted. They also had irregular borders with numerous resorptive surfaces. Here, growth increments were diffuse, irregular and of uneven thickness. In addition, secondary or accessory lines were abundant. The thinner layers, on the other hand, were relatively acellular and had straight borders with few or no resorptive cavities. Within these deposits, the annuli were usually distinct and evenly spaced.

Areas best suited for annuli counts varied somewhat from specimen to specimen. In general however, the growth increments

within the coronal third of either root were more consistent and more distinct, hence easier to count. Here, secondary lines were absent though higher magnifications were necessary for the tally. As a result, most of the age estimates tabulated in Appendix I derive from annuli counts within the areas illustrated in Figure 11. At no time, however, were the counts restricted to these deposits. Annuli counts were also made in the pad area, the root apices and other areas of the root. In fact, any deposit deemed acceptable for an annuli count was included in the age estimate. A minimum of ten readings from differing areas within the deposit and from different thin sections was made on each specimen. The age estimates listed in Appendix I thus represent the mode of all annuli counts for each tooth.

Proper identification of the dentino-cementum interface is a necessary first step in any annuli count. In the decalcified sections of mule deer molars, there usually was a band of lightly stained matrix between the darkly stained dentine and the first annulus. The dentino-cementum interface lay within this band. Frequently, a slight stain concentration within this part of the deposit identified the interface. Occasionally however, the detection and recognition of the interface required careful viewing at higher magnifications. According to Gilbert (1964), Erickson (1967), Low and Cowan (1963) and Sergeant and Pimlott (1959), at higher magnifications, the cementum adjacent to the dentine layer appears to be cellular. The term "fibrous" is probably a better descriptor for this deposit in mule deer. This fibrous cementum contrasted markedly from the compact dentinal matrix. As a

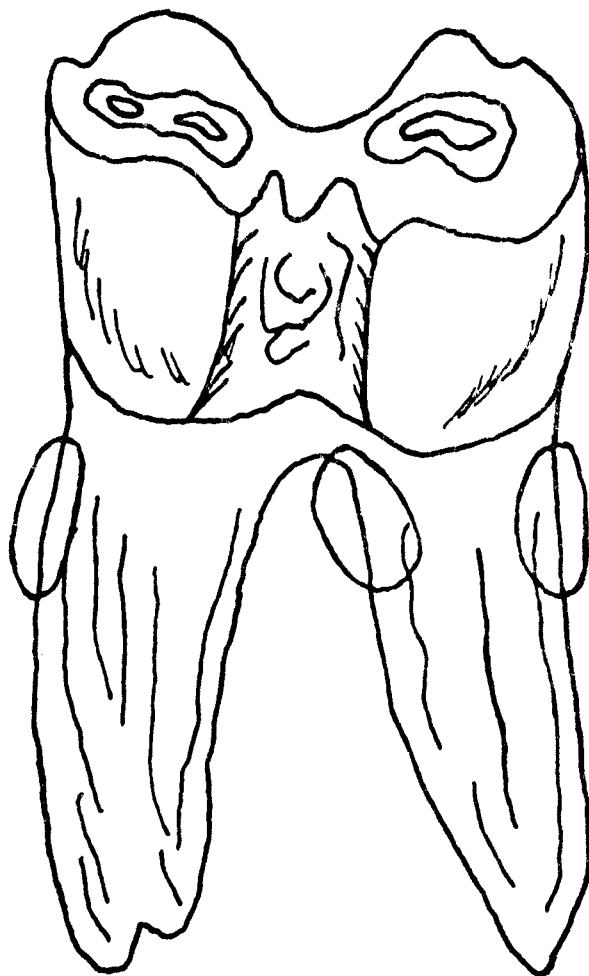


Figure 11: Diagram of a mule deer molar showing areas best suited for annuli counts and quantification.

result, even a poorly stained interface was easy to detect at higher magnifications.

When using cementum structures for age determination, it is imperative to establish the nature of initial cementum deposition and the time of first annulus formation. In mule deer, the crown of the first mandibular molar is in the process of formation at the time of birth (see Rees, et al. 1966b). This tooth erupts at about four months postpartum and is generally functional within the first six months although, at this age, the roots are still forming. Of all the permanent teeth, the first molar is also the least variable in its development and eruption (see Spiess 1979). Since cementum apposition precedes eruption (Campbell 1967; Grue and Jensen 1979; Miller 1974b, and Rees, et al 1966a), the first annulus in this tooth forms during the first year. Assuming no substantial delays in calving or tooth eruption, the first mandibular molars of mule deer thus record every year of the deer's life. In theory therefore, the annuli count for this tooth represents the chronological age of the animal.

In longitudinal thin sections which expose the root foramen, the first annulus is quite distinctive. Only this annulus fades out near the root apex. This reflects the partial development of the root at the time of annulus formation. In mule deer molars, the first annulus also appears to stain more darkly than all subsequent annuli. The absence of this annual layer then implies a delayed birth or retarded tooth development. For such animals, it would be necessary to add 1 year to the annuli count. In the present study, all sections examined contained a typical first

annulus. All age estimates listed in Appendix I thus correspond to the actual annuli counts.

The ease in identifying and counting annuli varies with the nature and complexity of the cementum deposit and the quality of the histological preparation. In general, the growth increments within the coronal region decreased in width with increasing age. In older animals therefore, the annuli were difficult to delineate and count (see also Gilbert 1966; Lockard 1972; McCutchen 1966; Miller 1974a, 1974b, and Thomas and Bandy 1973). Here, higher magnifications, including oil immersion, were necessary. In a few instances, only an examination of the thicker deposits provided a reliable age estimate.

In the thicker deposits, accessory lines were generally present and variable in number. In properly stained sections, such supernumerary lines were not easily confused with annuli. Conversely, in poorly stained preparations, the lamellae often were rather difficult to differentiate. Split annuli were also common in the diffuse cementum and, in older animals, tended to confuse the count. In the thicker deposits, the growth layers also were of variable thickness. Here, the tendency was towards wider growth increments with advancing age making these deposits of considerable value in aging some of the older animals.

The cementum deposits of some animals innately produce more legible annuli with fewer accessory lines and split annuli. For Cache la Poudre mule deer, the first mandibular molar of males generally contained more distinct annuli than those of females.

The reason for this observed sexual difference, however, is unknown at present.

False annuli or rut lines were also present in a number of thin sections. A false annulus is a thin, darkly stained band occurring near the dark band of the annual layer but separated from the latter by a narrow, light staining zone. Low and Cowan (1963:469) associated this band with the period of starvation in males during the rut and labelled it the "rut line". Reimers and Nordby (1968) reported a higher incidence of such lines in male reindeer on poorer range and suggested a nutritional basis for its presence in only certain males. Subsequently, several biologists noted the occurrence of such false annuli in both sexes and, on this basis, disputed its association with the rut (see Lockard 1972, and Miller 1974b). In the present analysis, such double rest lines were observed in the thin sections of both the males and females. When present, false annuli occurred for the second and all subsequent annuli. In all cases however, they were easy to identify and did not confuse the annuli count.

Resorption of the cementum resulting from mesial drift or dental trauma was evident in a number of the thin sections. In longitudinal thin sections, the areas of resorption were easy to identify by their characteristic irregular or scalloped borders (see Enlow 1963; Jowsey 1963, and Little 1973). In all cases, the resorption cavities were localized within the cementum layer (see Grue and Jensen 1979). In general, they crosscut several annuli, occasionally extending well into the dentine. At no time was there any evidence for the selective resorption of individual

annuli as suggested by Hemming (1969). As a result, cementum resorption is a potential source of error in the examination of transverse sections but in longitudinal thin sections, the areas of resorption are easy to identify and, hence, should not affect the reliability of the final age estimate.

Results of the Present Research:

In the present study, annuli were present in the cementum deposits of most specimens. Of the 102 molars sectioned, only four produced illegible thin sections. For specimens 38 and 75, the patterns of the incremental growth lines were too indistinct or too complex for reliable counts. Specimens 120 and 178, on the other hand, exhibited extensive resorption of the cementum and dentine. In fact, the mesial root of deer 120 was totally resorbed. The remaining 98 specimens were aged from cementum annuli counts of the first mandibular molar. Their respective age estimates are listed in Appendix I. Of these 98 deer, ninety one, ranging from 2 to 13 years old, were aged independently from cementum annuli counts of the central incisor (Erickson 1967) and the first mandibular molar (present study). As shown in Appendix I, there is perfect agreement in the age estimates of 80 deer or 88 per cent of the sample. For the remaining 11 deer or 12 per cent of the sample, there is a disagreement of only plus or minus 1 year. The disagreements incorporate all age groups and, thus, do not appear to reflect difficulties in delineating and counting the annuli in older animals. There is, however, a tendency for

higher age estimates when examining longitudinal thin sections of the molar. For the 11 animals with differing annuli counts, the molar thin sections yielded the lower age estimates in only two deer (specimens 5 and 95). In the remaining nine deer, the molar thin sections displayed one more annulus than the cross sections of the central incisor.

It is tempting to attribute the errors to variations in the eruption dates of the respective teeth. For the first molars, delayed eruption was not indicated as distinct first annuli were present in all sections. In the case of the central incisors, on the other hand, the eruption dates cannot be determined from the thin sections since Erickson (1967) removed transverse sections. Delayed eruption of the incisors thus may account for some of the lower age estimates in Erickson's study.

As noted above, the legibility of the tooth sections, the subjectivity in identifying annuli and the presence of multiple lines influence the accuracy of any age estimate based on growth increments. In this particular study, the experience of the researcher constituted an additional source of error. For the 11 specimens under consideration however, all thin sections were clearly legible and devoid of multiple lines as illustrated in the photomicrographs of Figure 12. With the exception of specimen 98, all the respective thin sections are easy to interpret. The complexity of the thin section thus cannot account for the observed differences in the age estimates.

The choice of histological procedure and thin section type probably also contributed to the observed differences in the age

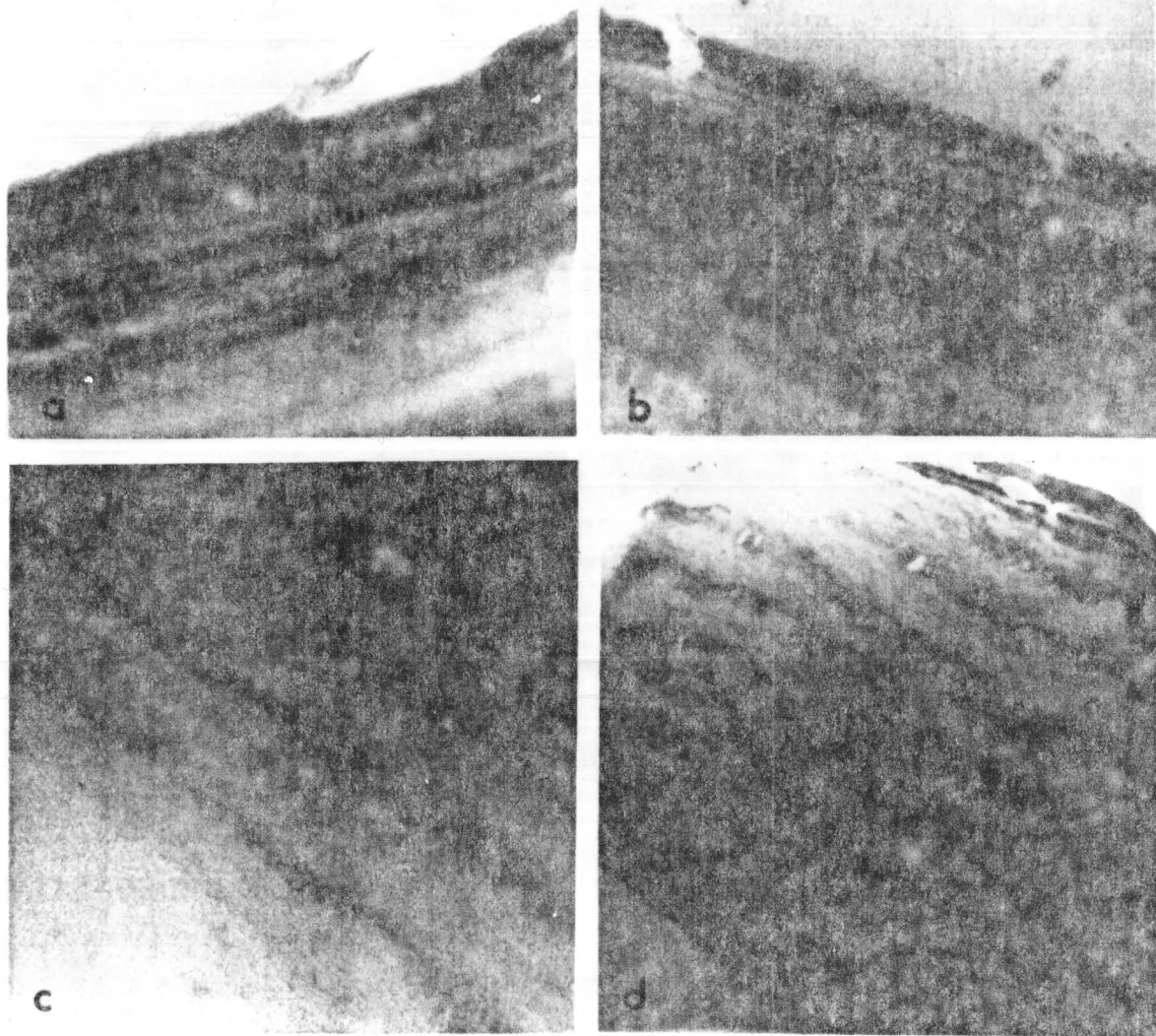


Figure 12: Photomicrographs of those specimens where there are age disagreements.

- a) Specimen 5 (male): age estimate is 5 years 11 months (100X).
- b) Specimen 21 (female): age estimate is 2 years and 3 months (100X)
- c) Specimen 59 (female): age estimate is 4 years and 1 month (100X).
- d) Specimen 73 (female): age estimate is 11 years and 5 months (40X)

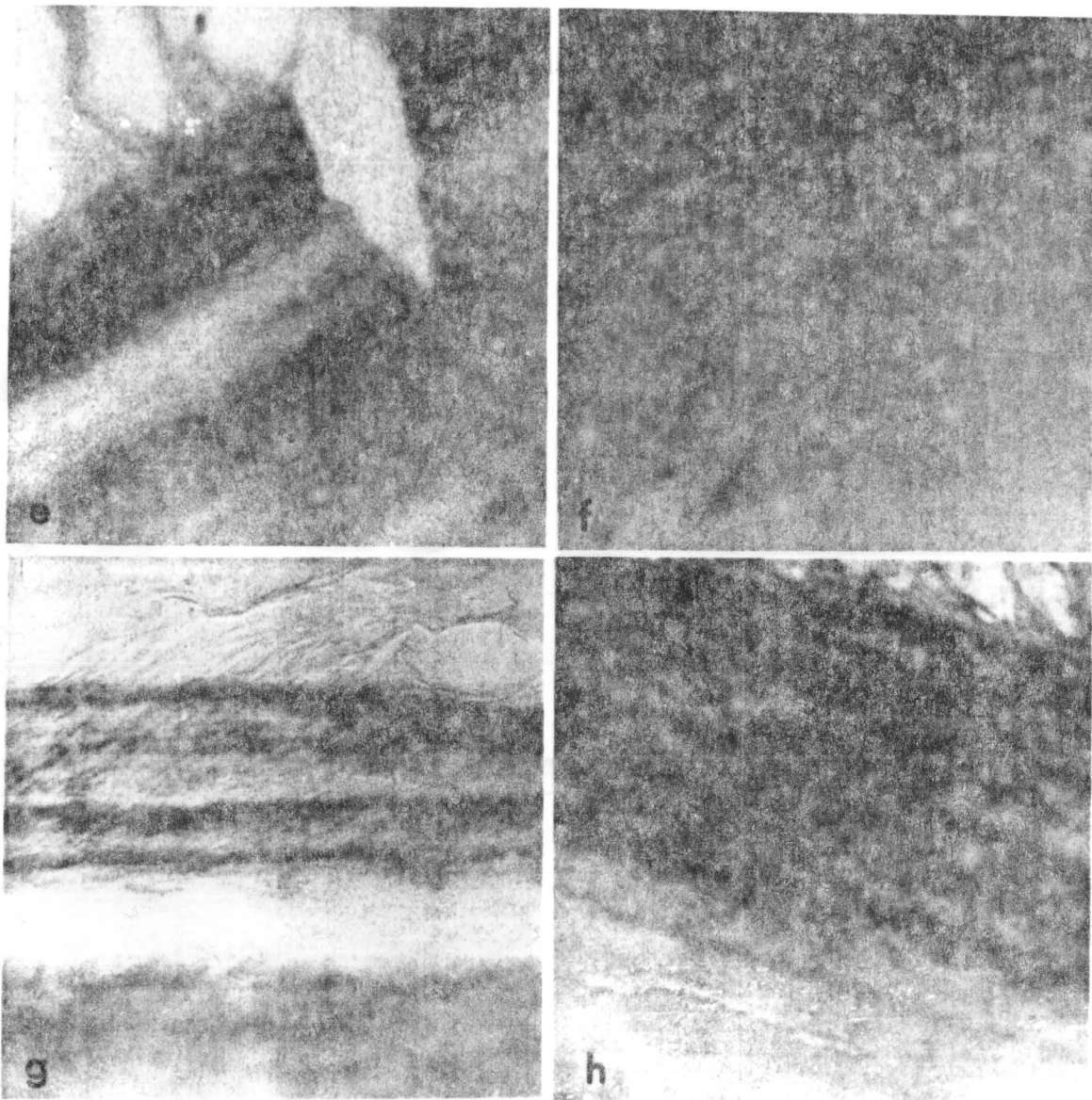


Figure 12: (cont'd)

- e) Specimen 78 (male): age estimate is 4 years and 6 months. (100X).
- f) Specimen 80 (male): age estimate is 5 years and 7 months. (100X).
- g) Specimen 95 (female): age estimate is 3 years and 10 months (100X).
- h) Specimen 98 (female): age estimate is 8 years and 11 months (100X).

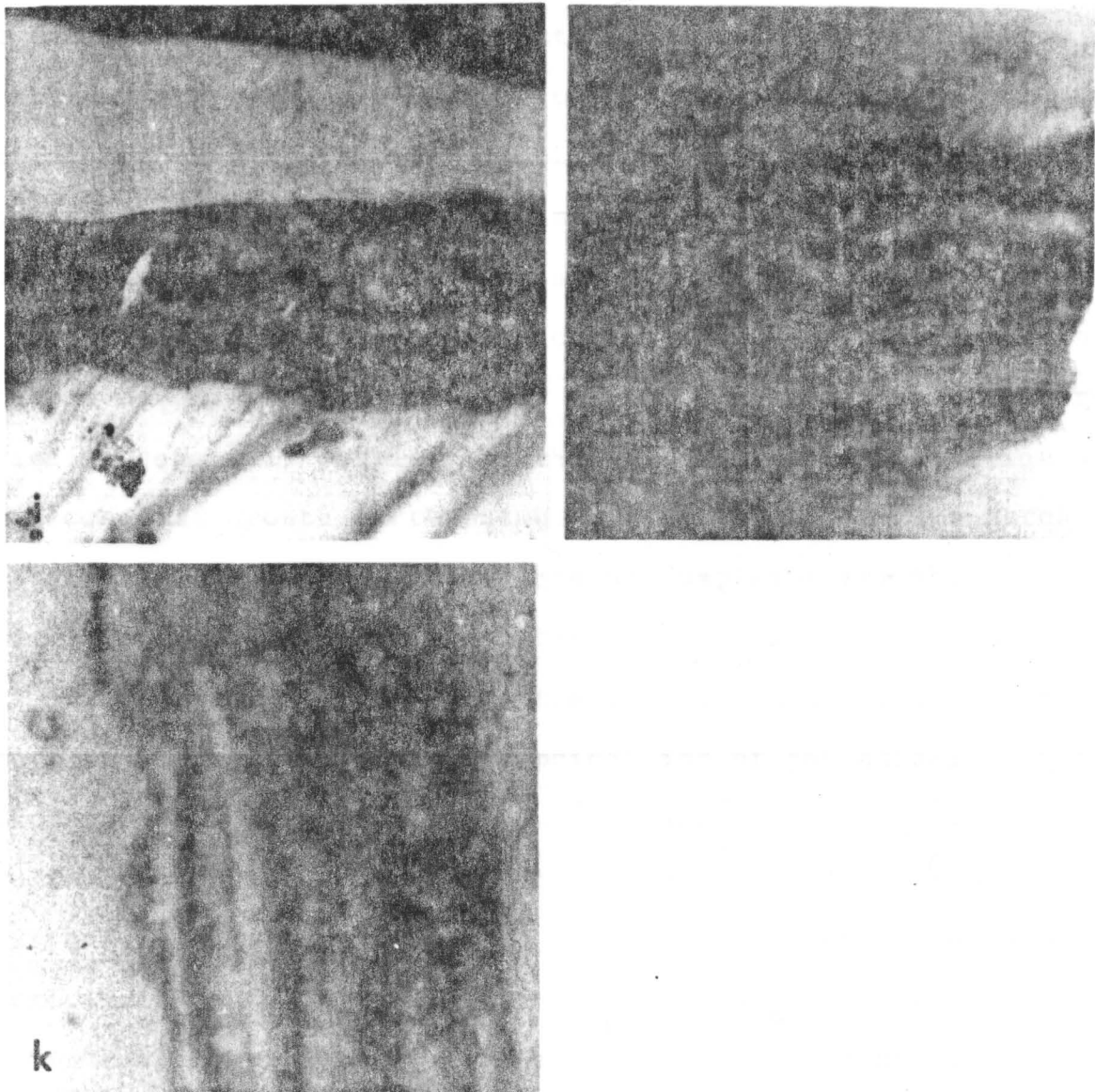


Figure 12: (cont'd)

- i) Specimen 159 (female): age estimate is 5 years and 2 months (100X).
- j) Specimen 171 (male): age estimate is 7 years and 5 months (100X).
- k) Specimen 186 (female): age estimate is 6 years and 9 months (100X).

estimates. As noted above, there is a greater chance of error in the examination of transverse sections. Erickson's (1967) use of 95 micron transverse sections further compounds the problem. In sections of this thickness, closely spaced annuli tend to blend together. For deer such as specimen 73, this leads to an age estimate which is one year less than the actual count.

Misinterpretations are also common when examining the thin sections of animals shot in April or May. In deer, annulus formation is generally complete by the end of March. Deposition of the succeeding growth increment generally begins in late March-early April. As a result, the annulus completes its formation several months before the birth date of the animal. For animals shot during this interval then, the annuli count for any tooth is always one more than the chronological age of the animal. In the photomicrograph of specimen 5, for instance, there are 4 distinct annuli although this animal is only 3 years and 11 months old. A revision of the slides for these 11 animals, however, revealed no discrepancies.

In sum, despite their limitations, cementum annuli, as seen in decalcified and stained thin sections, are at present the best criteria available for determining the age of mule deer with a full permanent dentition. The method is not infallible although the error range is substantially less than in any of the other aging techniques presently employed in faunal studies.

Summary:

In brief, this chapter outlines the importance of age determination in zooarchaeology and reviews the methods presently employed in aging prehistoric fauna from the osteological remains. It then recommends annuli counts, as seen in decalcified and stained thin sections, for age estimation in mature mule deer. This technique is relatively accurate as indicated by studies with known age animals. Further, in this study, there is an 88% agreement between independent counts of annuli in the central incisor and the first molar. Here, disagreements never exceed plus or minus one year. Cementum annuli counts thus provide reliable absolute age estimates for prehistoric fauna. Further, if complemented by an analysis of tooth eruption and replacement schedules, this technique enables accurate aging of all mule deer represented by mandibles or portions thereof.

7. Seasonality Assessment

The analysis of seasonal growth rings in fish scales or deer teeth, ... would do much to answer our questions about seasonality in the Driftless Area during prehistory but such work has yet to be carried out extensively here (Emerson 1979:290).

Introduction:

One of the main objectives of any faunal analysis is to determine the seasonality of animal exploitation and, by inference, the season of site occupation. In general, estimates of the date of death are derived from certain osteological indicators. From these data, archaeologists then infer the seasonality of human activities and the season of site occupation. For stock-rearing societies, seasonality estimates provide an archaeological basis for evaluating the prehistoric patterns of herd management. Such assessments, for instance, validate or refute the reported autumn slaughter of young livestock to overcome the shortage of winter fodder (see Higgs and White 1963, and Saxon and Higham 1969). In the study of prehistoric hunting and gathering societies, assessing seasons of death helps establish seasonal patterns of animal exploitation. The zooarchaeologist thus determines the annual cycle of resource exploitation and attempts to relate the peak periods of exploitation with the behavior patterns of the prey or the economic requirements of the group (see Cleland 1966; Emerson 1979, 1980; Flannery 1967, 1968, and Smith 1975a, 1978).

To infer seasonality from the osteological indicators of a

species one must assume a temporal uniformity in the behavior and growth patterns of the animal. For most ungulates, diurnal and seasonal changes in the climate and floral environment regulate basic behavior patterns. Palynological data suggest a relative uniformity in the climate and flora during the Holocene. It is therefore not unreasonable to assume a basic similarity in the behavior patterns of modern and prehistoric ungulate populations. Similarly, paleontological evidence indicates a relatively uniform growth pattern for ungulates during the last 10,000 years. To assume comparable growth patterns in modern and prehistoric ungulates is thus not unreasonable. Consequently, inferences on the season of death as derived from established osteological indicators are assumed to be reliable.

Faunal indicators of seasonality are, by their very nature, indicative of only certain seasons. Few, if any, osteological indicators are reliable for all seasons. In northern latitudes, for instance, the presence of migratory or hibernating species in an assemblage implies an exploitation which coincides with the presence of such animals in the site area (Bokonyi 1970). The absence of such remains, on the other hand, suggests very little in terms of seasonality. Specific osteological indicators are equally restrictive and vary from species to species. Only the presence of such skeletal elements provides any evidence for seasonal assessments. Their absence reflects either periods of non-exploitation or sampling bias. As a result, only a small proportion of any faunal assemblage yields information on the season of death.

The results of any faunal analysis lead only to inferences concerning the season of death of an animal. In practice, such inferences are restricted to those few animals whose skeletal elements were examined. To suggest a seasonal exploitation of these animals assumes only that human predation was the immediate cause of death. Inferring a comparable fate for all members of a species however assumes that the analyzed sample is indeed representative of the entire faunal assemblage. Such assumptions are often unjustifiable and lead to erroneous models of seasonal exploitation.

To infer periodic occupation and abandonment of a particular site area from the osteological indicators of seasonality assumes the temporal equivalence of at least two events, the death of the animal and the occupation of the site. Implicit in this argument is the approximate simultaneity of procurement, utilization and discard of the animal and its remains at the site (Artz 1980). Rarely are such assumptions explicitly stated in any report (see Smith 1978). Instead, most faunal analysts and archaeologists tend to equate, without reservations, the seasonal exploitation of a species with the seasonal occupancy of a site (see Emerson 1979 for a discussion). Concurrently, they associate the absence of seasonal indicators with periods of non-exploitation and, by extension, periodic abandonment of the site. All too often such researchers ignore deviations from normality in their search for behavior patterns inherent in their models of seasonal movements. In fact, the presence or absence of seasonality indicators in any faunal assemblage, may reflect sample bias or a seasonal pursuit

of various resources rather than a periodic occupation and abandonment of the site. Thus, as noted by Artz (1980:52), inferring a season of site occupation "...requires the pursuit of numerous independent and complementary lines of inquiry, all of which are potentially capable of contributing to the overall understanding of site seasonality".

The present discussion recognizes but does not consider the problems inherent in the assessment of site seasonality. Here, inferences on seasonality are restricted to the exploitation of a faunal resource. The present chapter therefore focuses on the derivation of seasonality from the osteological indicators in a faunal assemblage. As such, it reviews and evaluates zooarchaeological methods for deriving seasonality from the osteological elements of ungulates. It then examines the potential of growth increments in such determinations and presents a quantitative approach for estimating the approximate date of death of mature mule deer from annuli in the cementum of the first mandibular molar.

Seasonality Indicators in Zooarchaeology:

In ungulate populations, the postcranial skeleton provides little evidence for the determination of seasonality. The best postcranial indicators of seasonality are fetal remains. To most faunal analysts, the presence of fetal bones in their assemblage indicates an exploitation of females during the latter months of gestation (Ham and Broderick 1981; Pitts 1979, and Quigg 1974).

Assuming relative uniformity in the rutting and calving seasons,
the presence of fetal remains thus suggests a winter-spring kill.
To obtain more accurate estimates of the date of death, some zoo-archaeologists attempt to determine the approximate age of the fetus. Wilson (1974), for instance, uses a comparative sample of known-age fetuses to evaluate the size and relative development of his archaeological material. He discusses the occurrence of stratification in the diaphyses of fetal long bones but fails to confirm its relationship with age. Other analysts measure fetal long bones and translate such measurements into an age in utero for the fetus (Bouchud 1975 and Spiess 1979). Spiess' (1979:187) calculations, for example, yield a date of death which, in his opinion, is always within one month of the actual date of death.

Typically, fetuses are present in most reproductive females during certain months of the year. Abnormal pregnancies do occur but are rare in most populations. The abundance of fetal remains in any faunal assemblage is thus limited. Fetal bones are also characteristically porous and fragile. Hence, they are extremely susceptible to any cultural, mechanical and chemical degradation. The probability of encountering, recognizing and recovering such remains is thus understandably low. Consequently, the absence of fetal remains may indicate poor preservation, sampling error or cultural bias, not seasonality. Further, any age estimate based on measurements alone becomes suspect.

In young calves, bone growth and fusion of the epiphyses provide relatively accurate age estimates. Assuming a restricted calving season, such age estimates translate into an approximate

date of death (see Bouchud 1966; Pitts 1979, and Stewart 1973). In general however, age estimates based on bone growth and the rate of epiphyseal fusion are subject to the vagaries discussed in the previous chapter. The estimated ages at death, therefore, incorporate great time intervals with concomitant ranges for the inferred season of death (see Williams 1978).

Healed lesions in the postcranial skeleton are also interpreted as evidence for seasonality (Noe-Nygaard 1975 and Pitts 1979). Here, inferences on the date of death are based on the biology and behaviour of elk (Alces alces) and red deer (Cervus elaphus). According to Noe-Nygaard (1975:15), "...wintertime is the period when the chances of hitting the same animal for the second time are greatest...". In her estimation therefore, partially healed lesions in the osteological sample indicate an exploitation during the winter months. Implicit or explicit in this argument, however, is an assumed fall hunting season.

In zooarchaeology, most seasonality estimates for ungulates derive from specific cranial features. In cervids, for instance, antlers frequently serve as seasonal indicators (Chaplin 1971; Gilbert 1973, and Olsen 1971). Here, of course, shed antlers are excluded. Prehistorically, antlers were an important source of raw material for the production of tools (Baker 1930; Dart 1957a, 1957b, and Spiess 1979). The collection of antlers thus was opportunistic and, in all probability, reflected the quality of the osteological material. Shed antlers preserve for several years in most environments. Their retrieval therefore may occur at any time of year. As a result they mean very little in terms of sea-

sonality. Only frontal pedicles with or without antlers suggest a seasonal exploitation of cervids. Here also, crania supporting antlers may be gathered at any time of year (see Hill 1975b), but the probability of such occurrence is much lower.

For most North American cervids, there exists a definite annual periodicity to the growth, development and shedding of antlers. In general, antler growth begins in spring and ceases in fall. The subsequent shedding of the fully hardened antlers usually occurs in winter or early spring. In zooarchaeological assemblages therefore, all frontal bones with pedicles devoid of antlers imply a season of death from late winter to early spring while skull fragments supporting antlers suggest a summer-fall date of death (see Emerson 1979; Guilday 1962; Parmalee, et al. 1972, and Smith 1975a). It is also possible, in faunal samples, to differentiate antlers in velvet from those which are fully hardened. Typically, growing antlers acquire a rough and porous surface after the decay of the velvet. Fully hardened antlers, on the other hand, maintain a relatively smooth and hard cortex, even after years of burial (see Pitts 1979 and Spiess 1979). The general texture of the archaeological specimen thus indicates the growth stage of the antler at the time of death. An alternative basis for this distinction is the appearance of the blood vessel openings in the burr or coronet at the base of the antler (Smith 1978). The passages for the blood vessels are open during the velvet or growth stage and grow shut during the rutting season. Hence, all antler-burr sections with closed passages indicate the presence of fully hardened antlers and an attendant fall-winter

season of death. Here, the state of vascularization may be determined from radiographs (Bouchud 1975) or from histological preparations (Smith 1978). Antlers also show external signs of the upcoming shedding. Typically, a resorption line on the antler cortex below the burr indicates incipient antler shedding (Bouchud 1975 and Spiess 1979).

With few exceptions (see Ryel 1963), only male cervids support antlers. Accordingly, only a sex specific proportion of any assemblage provides evidence for seasonality. In caribou, where both sexes support antlers, there is considerable diversity in the growth, development and shedding of antlers. This variation relates to the age, sex and physiological condition of the animal (Spiess 1979). In mature males, for example, antler growth normally begins in March or April. These animals usually drop their antlers from October to December though, for some, antler shedding occurs as late as March. For pregnant does, on the other hand, antler growth and shedding coincides with parturition which occurs in June (see Skoog 1968). As a result, Spiess (1979:100) suggests that we ignore antler-based seasonality estimates in caribou, "...except for the clearly unambiguous case of large adult male antlers".

Cervid crania are also extremely fragile and susceptible to cultural and mechanical degradation. Hence, poor preservation biases their recovery. Further, skulls, particularly the neurocrania, are frequently left at the kill site. The probability of recovering cervid frontal bones with or without antlers is thus understandably low.

For bovids, horn cores are occasionally used as seasonal indicators. Arnold (1978), for example, measures the horn cores of muskoxen to determine the ages of his animals and, by extension, to infer an approximate date of death. As noted in the previous chapter, horn core dimensions relate to the age, sex and physical condition of the animal. As such, their association with age requires further testing using a sample of animals of known-age. Until such work is done, age determinations and seasonal assessments from bovid horn cores remain speculative.

In zooarchaeology, most estimates of the season of capture among ungulates are inferred from estimates of the age at death. As a result, reliable indicators of age also serve as seasonal indicators. For ungulates, the dentition provides the most reliable age estimates. Not surprisingly therefore, most seasonality estimates derive from the age structure of young animals whose permanent teeth are erupting at the time of death (see Emerson 1979; Gilbert 1973; Latady 1978; Parmalee, et al. 1972, and Smith 1975a). For such animals, the margin of error in aging is assumed to be less than one month in either direction (Emerson 1979). According to Spiess (1979) however, only mandibles with erupting first molars allow such precision and, therefore, are useful for dating the season of death.

Seasonal estimates, as derived from the teeth of immature animals, usually indicate a fall season of capture (Emerson 1979; Frison 1974; Frison and Reher 1970; Latady 1978, and Smith 1975a, 1975b). Here, the age determinations compare well with those of wildlife management personnel. This is not to imply that the age

estimates are incorrect but rather to point out that our present comparative samples are biased. They consist primarily of deer shot during the present fall hunting season. Such samples fail to indicate the true variation in the eruption dates of most permanent teeth. Until our comparative samples include animals shot throughout the year, perhaps only those mandibles with erupting or newly erupted first molars are reliable for inferences on the season of death. Such assessments, however, pertain only to the seasonal exploitation of immature animals which, in themselves, constitute only a small proportion of the total faunal sample (Higgs and White 1963).

For older ungulates, inferences on the season of capture occasionally derive from age determinations based on tooth wear (see Bouchud 1966; Frison and Reher 1970; Klein, et al. 1981, and Reher 1974). The accurate aging of old animals to within one or three months (Carter 1975) using tooth wear seems impracticable. As noted in the previous chapter, age estimates based on a study of tooth wear are inaccurate to the year, let alone the month. In my opinion therefore, such age estimates cannot establish an approximate date of capture.

Seasonality estimates for mature ungulates also derive from an examination of annuli in the cementum of individual teeth (see Bourque, et al. 1978; Kay 1971; Saxon and Higham 1968, 1969, and Spiess 1976). Basically, the method involves the thin sectioning of archaeological specimens and the microscopic examination of the cementum deposit to evaluate the status of the outer layer. Here, a stained thin section with a dark band outermost suggests

a date of capture from late December to early April. For an animal with the light staining band outermost, the date-of-death estimate depends on a subjective evaluation of outer band width. If the light band is narrow, then the animal was killed in the few months succeeding the apposition of the dark staining band. Death thus probably occurred somewhere between late April and early August. If, on the other hand, the light staining band is of approximately the same width as previous light bands, then death occurred within a few months prior to the formation of the next dark band. Here, a death between late August and early December is implied.

In zooarchaeology today, most seasonality estimates, based on growth increments, derive from the examination of polished sections or undecalcified thin sections (see Benn 1974; Bourque, et al. 1978; Kay 1971; Saxon and Higham 1969, and Spiess 1976, 1978, 1979). This apparently reflects the poor success rate in the decalcification and staining of imperfectly preserved teeth (see Spiess 1979). According to Grue and Jensen (1979), however, only decalcified and stained preparations provide satisfactory thin sections for establishing the approximate time of annulus formation. In their opinion, the newly formed growth increments usually do not show up clearly in ground half-tooth sections or in undecalcified thin sections until they are sealed off from the edge of the cementum layer. In such sections, therefore, the new increments are recognizable only at a later state.

For zooarchaeologists to utilize the results of wildlife researchers in their interpretations and inferences thus seems

somewhat inappropriate. Most wildlife biologists today employ the superior decalcified and stained preparations in their study of age structure. Consequently, zooarchaeologists must develop histological procedures for the analysis of imperfectly preserved osteological material (see Andersen and Jorgensen 1960; Ascenzi 1955, and Stout 1978). Failing this, they must rely on studies where comparable histological preparations were employed (Aitken 1975; Gasaway, et al. 1978; Mitchell 1963, 1967; Ransom 1966, and Wolfe 1969 for example).

Evaluating the stage of annulus formation in decalcified and stained preparations is also problematical. Here, for instance, the stain often tends to concentrate near the edge of the section suggesting the initial deposition of the dark staining band (see Jensen and Nielsen 1968). For experienced researchers however, this is a minor problem (see Grue and Jensen 1979). The presence of false annuli or accessory lines also causes an apparent stain concentration near the periodontal membrane which, in my opinion, is often difficult to distinguish from the initial apposition of the narrow band. Here, as in other stained preparations, it may be advisable to use a staining procedure which differentiates old and new cementum (Sauer 1973). In longitudinal thin sections, there is also some variation in the stage of annulus formation throughout the cementum deposit. This, of course, presents some problems in the interpretation of transverse sections where there is minimal exposure of the cementum layer. The approach outlined below circumvents most of these problems as, here, the analysis is based on a quantitative estimate of outer increment width

rather than a qualitative judgement of its appearance.

In sum, inferences concerning the season of death among prehistoric ungulates derive from a number of osteological indicators. In most faunal assemblages however, seasonal indicators are scarce and represent only a small age- or sex-specific proportion of the total sample. Osteological indicators are also, by their very nature, season-specific. Few, if any, suggest an exploitation throughout the year. Furthermore, most seasonality estimates incorporate a range of several months. Such assessments often fail to establish conclusively the distinctive patterns of seasonal exploitation inherent in our predictive models. The accurate reconstruction of seasonal exploitation patterns for prehistoric populations thus requires more precise estimates of the date of death for all exploited faunal resources. As noted below, the incremental growth zones in the cementum of molars are capable of providing such date-of-death estimates.

Theoretical Basis:

The rhythmic apposition of dental cementum resulting in the formation of incremental lines appears to occur in every species of terrestrial mammal possessing teeth with closed roots (Grue and Jensen 1979 and Morris 1972). In white-tailed deer, cementum growth apparently reflects seasonal variations in the physiology of the animal (Sauer 1973). Here, the growth increments in teeth seem "...to result from adaptive seasonal changes in endocrine functions with concomitant changes in food intake and in various

serum parameters " (Sauer 1973:65). For every year therefore, cementum apposition is rhythmic with a period of rapid cementum growth followed by one of reduced or arrested growth. In decalcified and stained thin sections, this results in the formation of annual increments. Assuming a knowledge of the synchronicity between the apposition of each band and the time of year, it then becomes practicable to predict a deer's date of death from the appearance of the outer increment.

For ungulates, cementum apposition is a continuous process (Bolden 1962; Gottlieb 1943 and Kronfeld 1938). Here, the width of the outer increment increases throughout most of the year. It is thus possible to determine the month of death from an estimate of outer increment width. According to Spiess (1979:69) however, such "...mathematical precision in the estimation of band width is unwarranted and would lend false precision to the results". In his opinion, there exists too much variation in the width of light bands to permit a precise estimate of band width. This is compounded by a tendency for the bands to decrease in width with advancing age. As discussed in the previous chapter, there is considerable variability in the appearance of growth increments throughout the cementum layer. Yet, for each molar, there also exists, in longitudinal sections at least, an area with distinct, evenly spaced annuli. Only such deposits are, in my opinion, amenable to measurement for an estimation of band width.

Methodology:

All first mandibular molars of the mule deer in this sample were decalcified, sectioned, stained and examined microscopically as specified in chapter three of this thesis. For an accurate estimate of outer increment width, the entire periodontal border of each longitudinal section was examined to assess the overall appearance of the outermost increment. This was necessary to recognize the variation within the deposit and to ascertain the status of the last increment. Only areas with distinct, evenly spaced annuli and an accurate representation of the outer layer then were selected for mensuration and quantification.

The objective of the present quantitative analysis was to relate the date of death to a measure of cementum growth. As a result, the calendar year was translated into weeks of cementum growth. In mature Rocky Mountain mule deer, the apposition of new cementum begins in March. Here, quantifiable amounts of new cementum are usually visible in the longitudinal thin sections of deer killed between the 12th and 18th of March. For purposes of the present study then, this interval represents the first week of cementum growth. Subsequent weeks of cementum apposition and their respective calendrical dates are listed in Appendix X of this thesis.

Any estimate of increment width assumes an understanding of the growth rate within the selected areas of the cementum layer. To establish such growth rates, it is necessary to record the placement of each growth layer relative to the dentino-cementum

interface. This establishes the thickness of the cementum layer after each year of cementum apposition. In the present analysis, an ocular micrometer was used to record the cumulative distances between the dentino-cementum interface and the outer edge of the first and all subsequent annuli as shown in Figures 13 and 14. Here, all measurements were taken under oil immersion, that is a magnification of 1000X. In the case of specimen 102, for instance, the thickness of the cementum layer after one year of growth was 21 units; after two years, 42 units; after three years, 61 units; after four years, 82 units, and after five years, 97 units.

Under oil immersion, even the narrow, dark staining band appears relatively wide. Delineating the outer edge of an annulus under such magnification thus becomes somewhat subjective. This subjectivity introduces an inherent source of measurement error. For each specimen, therefore, several disparate areas of the cementum deposit were measured.

Not all specimens have distinct, uniformly spaced annuli throughout the cementum deposit. The deposits of some molars, such as specimen 38, were unsuitable for either age estimates or seasonality assessments. For others, such as specimens 3, 8, 9, 29, 33, 34, 35, 57, 60, 64, 65, 78, 79 and 83, the growth increments were distinct enough for an age estimate but their uneven spacing prohibited the derivation of a growth rate. The deposits of still other deer, such as specimen 75, were unsatisfactory for age determination but adequate for seasonality estimates. Here, as in many of the older specimens, distinct, evenly spaced annuli

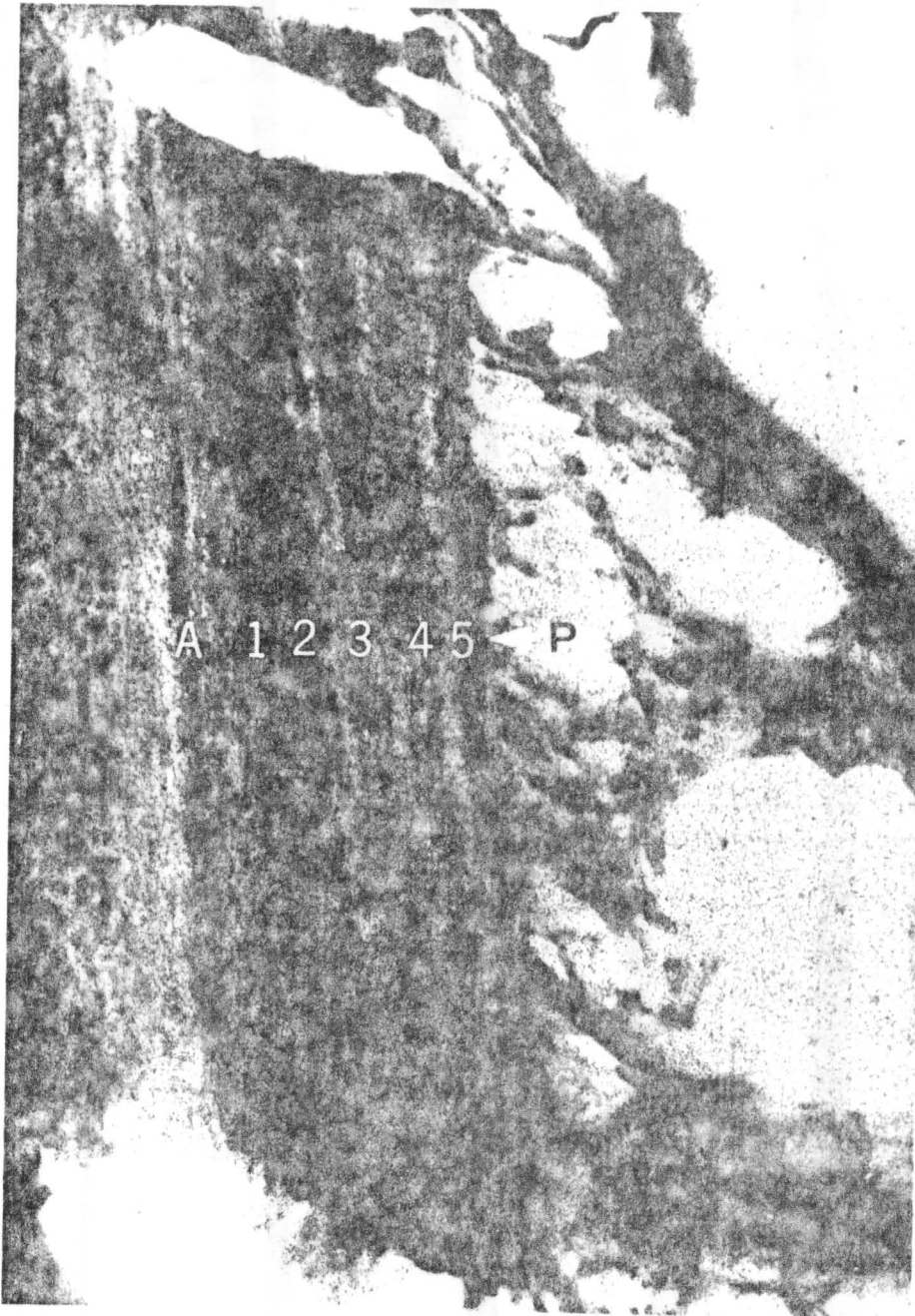


Figure 13: Photomicrograph of specimen 102 showing the dentino-cementum interface (A), the cementum annuli (1-5) and the periodontal border (P).

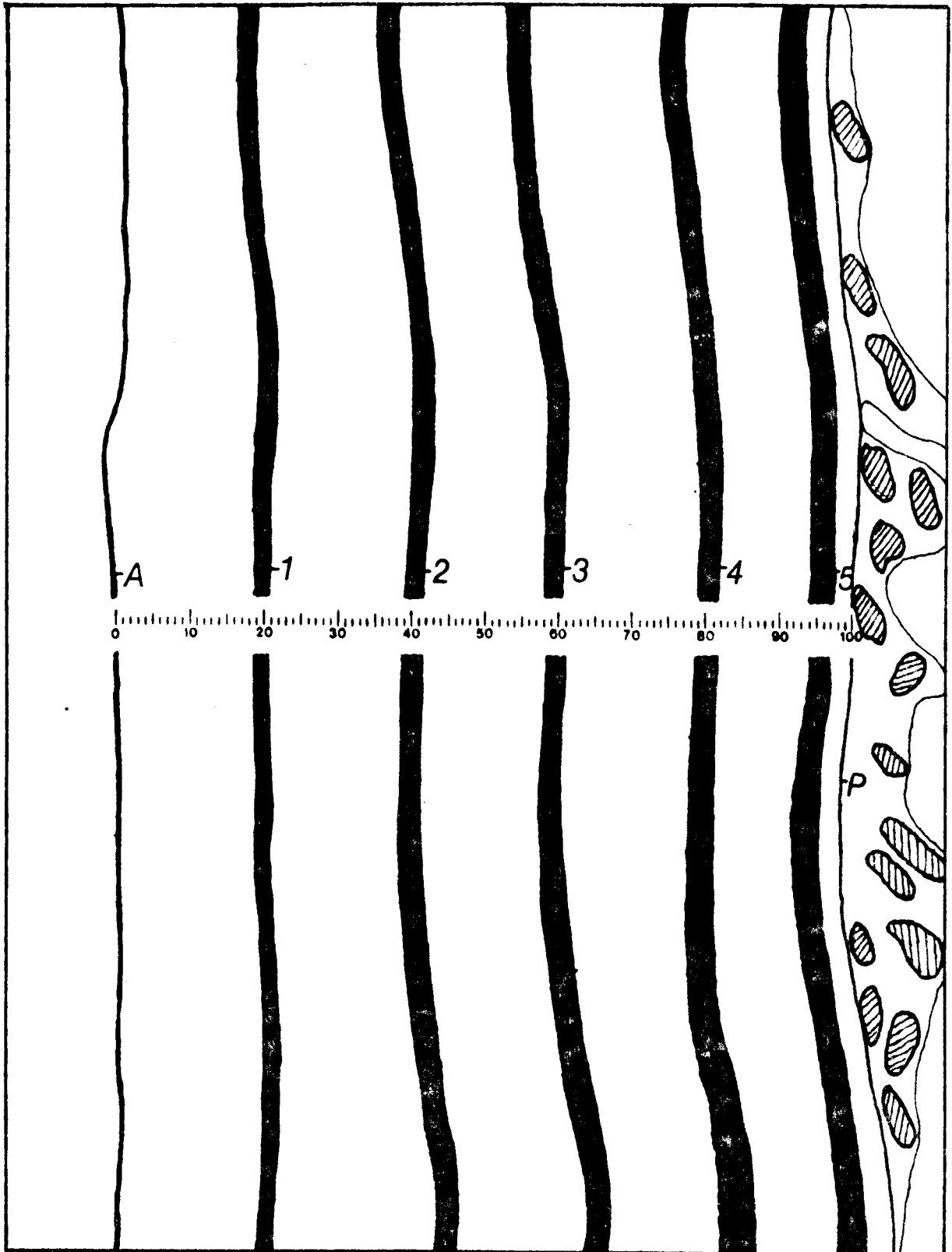


Figure 14: Diagram of the cementum deposit for specimen 102 showing the procedure for measuring the cumulative thickness of the deposit after each year of cementum growth.

were present in only the outer part of the cementum layer. Such deposits were unfit for aging but still quite useful for seasonal dating, provided the last 3 or 4 annuli and the outer increment were unaffected. For such molars, only the evenly spaced annuli were measured. In the case of specimen 46, for example, a ninety four month old deer, only the last five annuli were suitable for mensuration. These measurements however, provide sufficient data for the derivation of a growth curve and a respective seasonality determination. In all, seventy-one deer had cementum deposits deemed acceptable for the quantitative analysis. The respective measurements for each of these specimens are listed in Appendix XI of the thesis.

To determine the growth rate of the cementum it is necessary to derive a metrical or mathematical relationship between the increased thickness of the cementum layer and the age of the animal (see Ray 1976). According to Coutts and Higham (1971) and Coutts and Jones (1974), the derivation of such relationships for shellfish is possible by means of simple regression analysis. In this study therefore, the data for each measured deposit were plotted on a system of Cartesian coordinates with the cumulative thickness of the cementum as the dependent variable (Y) and age, in months, as the independent variable (X). For specimen 102, the distribution of the data points produces the curvilinear plot illustrated in Figure 15. Here, the tendency for growth increments to decrease in thickness with advancing age is evident.

The addition of 10 to X, an inversion of this value and a logarithmic transformation of $(X + 10)$ and Y yields the linear

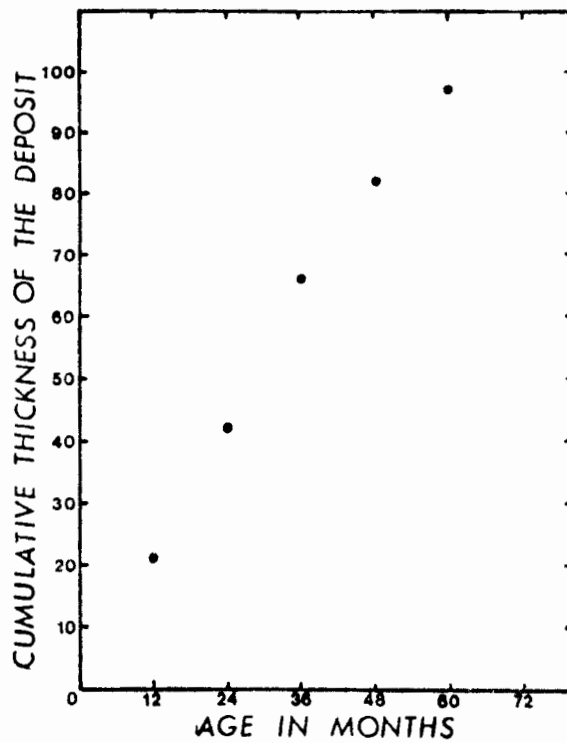


Figure 15: Relationship between age in months and the cumulative thickness of the cementum deposit.

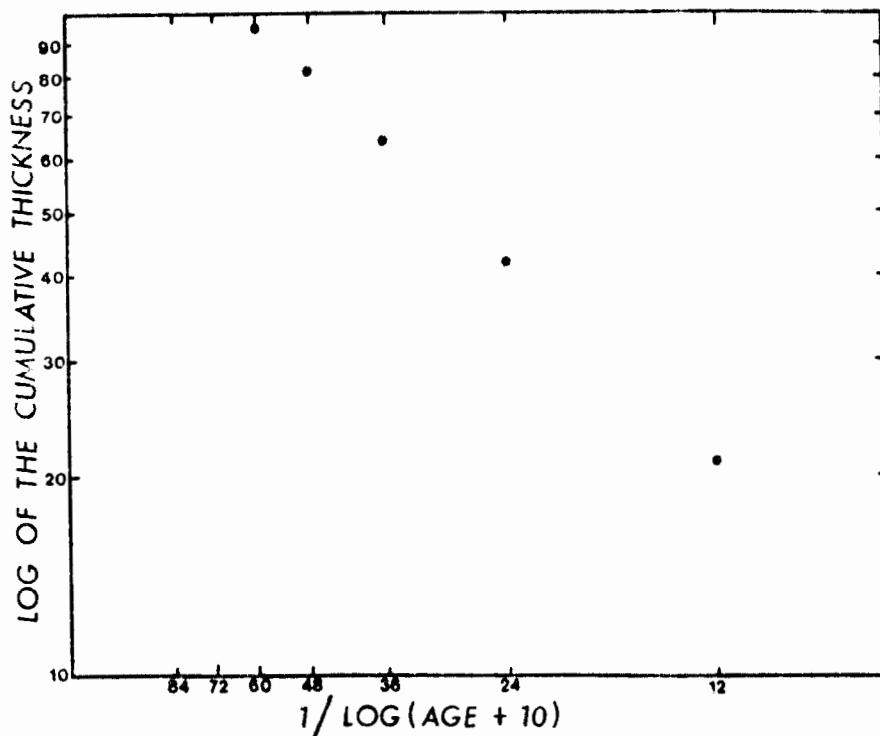


Figure 16: Relationship between $1/\log(\text{age}+10)$ and log of the cumulative thickness of the cementum deposit.

plot illustrated in Figure 16. Here, the correlation coefficient is $r=-1.00$ and the best-fit regression equation for this relationship is:

$$\log \hat{Y} = 3.78 - 3.31 \frac{1}{\log(X + 10)} \quad (10)$$

where Y is the cumulative thickness of the cementum deposit and X is the age, in months, of the deer. This equation expresses, in mathematical terms, the rate of cementum growth for specimen 102 in the measured part of the deposit.

The above equation now enables us to predict the cumulative thickness of the cementum deposit for specimen 102 after the sixth year of cementum growth. Inserting a value for X , in this case 72 months, and solving for Y , we obtain a value of 111.91. This predicted value represents the expected total thickness of the cementum deposit after the sixth year of cementum growth assuming, of course, no substantial alterations in the growth pattern during the sixth year.

The plots of the data points varied for each set of ocular measurements. Consequently, each set of data was plotted separately on metric or logarithmic graph paper. Not all plots were curvilinear. In fact, the measurements for many of the younger animals produced only linear plots. This is consistent with the observations of Sergeant and Pimlott (1959). These authors note a linear increase in the thickness of the cementum deposit for most younger animals.

Initially, correlation coefficients were calculated for each set of data. In most cases however, these were equal to 1.00 or

-1.00 depending on the slope of the regression equation. As a result, in subsequent computations, correlation coefficients were derived only for those sets of measurements where there was an apparent deviation from linearity. Even here, the coefficients were never less than $r=0.99$ or $r=-0.99$.

For each set of data, least squares regression equations were calculated. These provided estimates for the expected total thickness of each measured deposit. The respective regression equations and predicted values for each specimen are listed in Appendix XI.

From the measurements and computations, it now becomes possible to calculate a ratio of outer increment width over expected increment width. Here, outer increment width is the total thickness of the cementum layer at the time the animal died minus the measured thickness of the deposit at the time the last annulus formed. For specimen 102, the thickness of the cementum layer at the time of death was 100 units. Here then, the outer increment width is $100-97$ or 3 units. The expected increment width is the predicted width of the cementum layer minus the measured thickness of the deposit at the time the last annulus formed. In the case of specimen 102, this value is $111.91 - 97$ or 14.91 units. For this animal then, the ratio is $3/14.91$ or 0.201. This value represents the proportion of the annulus which was present at the time the deer died. Specimen 102 was shot on June 12 during the 14th week of cementum growth. For mature mule deer killed during this interval in the Cache la Poudre drainage, we would expect 0.201 or approximately 20 percent of the outer increment to be

present in a longitudinal thin section of the first mandibular molar.

The derivation of the ratio, as presented, incorporates an inherent source of error. The calculation of any predicted value by means of a regression formula necessarily includes an implicit error range. In the present study, the latter were not computed since the correlation coefficients were so high. Instead, for each specimen, ratios were calculated for various sets of ocular measurements from different parts of the deposit. The mean of these ratios then was considered a more accurate representation of the proportionate cementum growth in each animal. In the case of specimen 102, for instance, the ratios for the four series of measurements range from 0.190 to 0.228 with a mean of 0.203. Of course, not all means derive from four sets of measurements. In a few cases, only one or two areas within the cementum layer were measurable. For other teeth, as many as ten disparate areas were measured. In most cases however, five sets of measurements were recorded and provided the data for the calculation of means. The respective ratio means for each specimen measured are listed in Appendix XII of this thesis.

The ratios and ratio means provide a quantitative measure of the proportionate cementum growth in the outer increment of each deer molar. As the deer were collected at periodic intervals throughout the year, it now becomes possible to relate the proportionate growth of an annulus and the week of cementum growth. The data thus were plotted on a system of Cartesian coordinates with the week of cementum growth as the independent variable (X)

and the ratio means as the dependent variable (Y).

The resultant plot, as illustrated in Figure 17, depicts the behaviour of the ratio means relative to specified intervals of cementum growth. As such, it presents the proportional increase in outer increment width relative to time and, thus, illustrates the annual pattern of cementum growth in mature mule deer from the Cache la Poudre area.

In these animals, cementum apposition apparently begins in the latter weeks of March. For deer shot at this time of year, there is, in longitudinal thin sections, a quantifiable increase in outer increment width relative to the last complete annulus. Cementum growth then continues for approximately forty-two weeks or until the latter part of December. Thereafter, there is no detectable increase in the thickness of the cementum deposit until the latter part of March.

It is also possible to characterize, in mathematical terms, the growth episodes of the cementum deposit. For the ten week interval of minimal or arrested growth, the ratio means approximate unity. For the 42 weeks of growth, on the other hand, there is an apparent linear increase in the ratio relative to time. Here, there exists a strong positive correlation ($r=0.98$) between the two variables. It is thus, possible, by means of regression analysis, to describe the rate of increase in the ratio means relative to time for this part of the distribution. Here, the best-fit regression equation for the 42 week interval is:

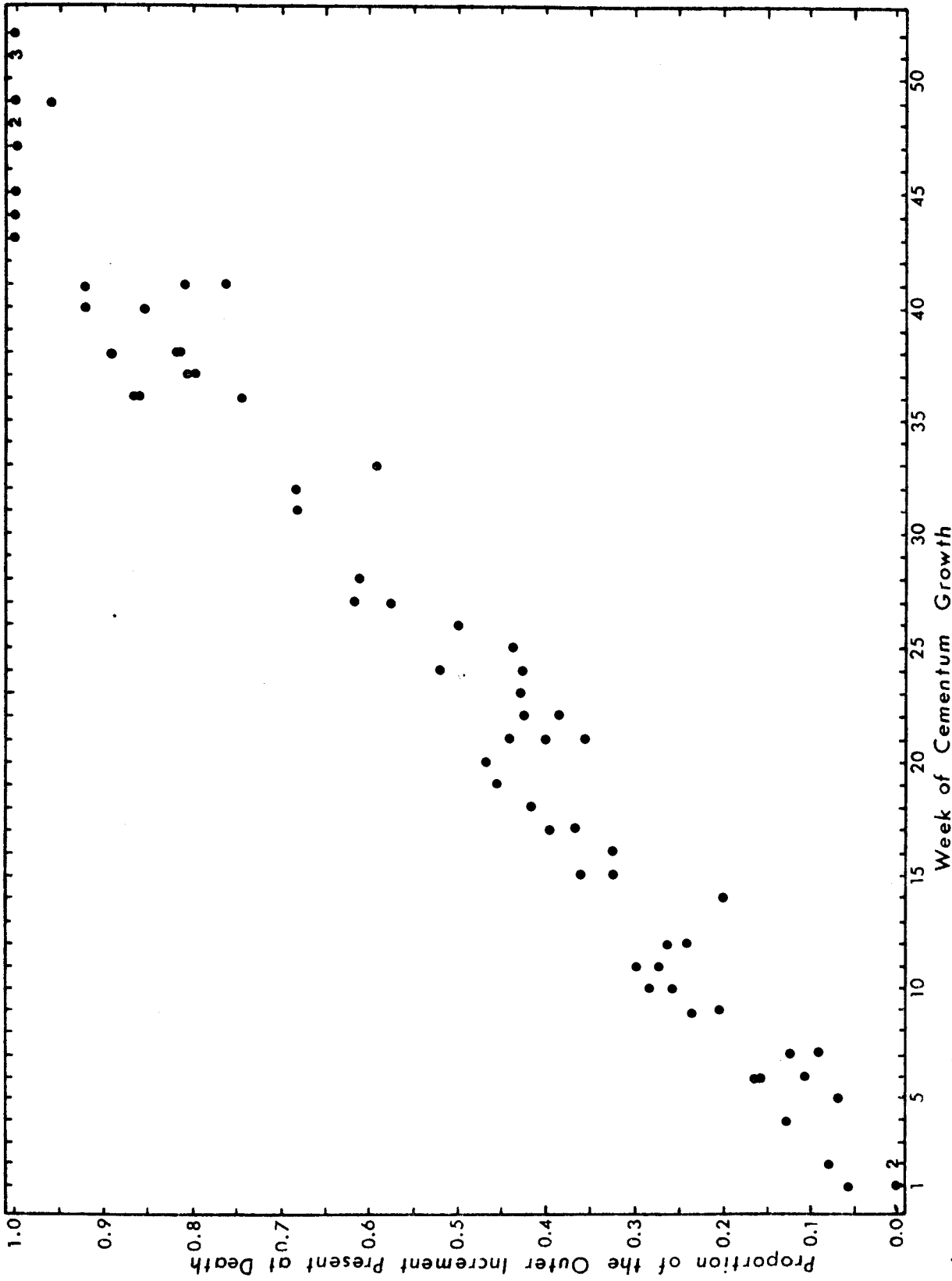


Figure 17: Relationship between the week of cementum growth and the proportion of outer increment present at the time of death.

$$\hat{y} = 0.0212 (X) + 0.00279 \quad (11)$$

where X is the week of cementum growth and y is the proportionate increase in the width of the outer annulus. Here, the regression equation is used strictly as a descriptive statistic and applies only for values of X from 1 to 42.

The growth pattern of the cementum deposit, as described, is consistent with the annual physiological growth of mature mule deer. According to Anderson, et al. (1974), the mature animals in the Cache la Poudre reserve increase in weight throughout the summer months and attain their peak weights in October-November. During the subsequent winter months, there is an apparent weight loss until the end of March or the beginning of April. From this time on, the animal again gradually increases in weight. The annual cycle of weight gain and weight loss in mature mule deer thus corresponds, quite closely, to the annual growth pattern of the cementum deposit.

For zooarchaeological purposes, the calculation of ratios and ratio means, as presented, provides a quantitative measure of outer increment width. The resultant value, as shown above, relates to the week of cementum growth and, by extension, to the deer's date of death. For archaeological specimens, it is thus possible to establish dates of death from the incremental layers in the cementum of the first mandibular molar. If, for example, the ratio approximates unity, a winter death from late December to early March is implied. Here, increased precision in the seasonality estimate is not possible given present analytical

procedures. If, on the other hand, the ratio mean is a value between 0 and 1, a more accurate estimate of the date of death is possible. Here, reference to the plot in Figure 17 and Appendix X is necessary. From these, it is possible, in my opinion, to infer conservatively a month of death for the animal. Greater precision in the seasonality estimate for this 42 week interval of cementum growth is not possible until further research is conducted.

Recommendations for Further Research:

As noted by Pye (1964:26), "'Research' is very often a euphemism for trying the wrong ways first, as we all must do". For the present study, "the least efficient ways" is probably a more appropriate expression.

The principle objective of this phase of the research was to quantify outer increment width and, as such, to derive an annual growth pattern for the cementum deposit of mature mule deer. As a result, several disparate locales within the deposits of each tooth were examined and measured in order to discover potential variation within the cementum layer. For mule deer molars, there is a quantifiable increase in outer increment width throughout most of the year. Furthermore, there seems to be no significant variation in outer increment width for the measured areas within the deposit.

This approach, although necessary, is not the most efficient nor the most accurate. For future researchers, it is therefore

preferable to designate specific locales within the deposit for examination and mensuration and to restrict the analyses to those parts of the deposit. For the first mandibular molars of mature mule deer, the areas best suited for such a quantitative analysis are located near the cemento-enamel interface of the proximal and distal roots.

Within these deposits, as noted in the previous chapter, the incremental growth lines are evenly, but closely, spaced. Such close spacing of the annuli usually affects the accuracy of the ocular measurements. Here, insufficient magnification increases the magnitude of the potential error. A difference of one, for example, in an ocular reading of ten is greater, by a factor of one, than a similar error for an ocular reading of 100. Higher magnifications thus decrease the magnitude of the measurement error. As a result, it is preferable to use the higher powered microscopes. Here, the transmission electron microscope is particularly appropriate as, on this instrument, it is possible to photograph each specimen at a constant magnification. Recording the relative position of each growth increment from the photograph is then possible using a digitizer.

The least squares regression equations, as derived above, are based on a small sample (less than ten) of observations. A more appropriate approach is to record several measurements for each of the designated deposits and to derive one growth curve per tooth based on these measurements. In this case, the larger sample sizes increase the reliability of the estimates for the regression parameters. Furthermore, the calculation of a single

regression equation is much more expedient.

The regression equations, as computed above, are also based on cumulative measurements. There is thus a lack of independence for the Y variables. They are said to be autocorrelated (Ostrom 1978). For small samples, there is no significant effect on the parameter estimates but there are problems with the estimated variances. For larger samples however, the least squares parameter estimates are said to be inefficient (Ostrom 1978). To overcome this problem, it is necessary to determine the width of each increment and to correlate these with the age of the animal. This is possible, using the cumulative ocular measurements, by subtracting $Y_{j+1} - Y_j$ for each annulus. The regression equation which derives from these data then provides estimates of the expected outer increment width. This approach thus eliminates many of the calculations noted above.

Here, the ratio is derived, as before, using the above estimate for the expected outer increment width. In this instance however, only one ratio is derived for each animal. Furthermore, it is possible to derive an empirical estimate of the variance for these ratios. The annual growth pattern of the cementum deposit then is determined from one ratio per animal rather than a ratio mean. Such data are obviously more conducive to statistical manipulation.

Ratios are not normally distributed (Sokal and Rohlf 1969). To obtain an acceptable degree of symmetry, it is thus necessary to transform the data. Here, the arcsine transformation is appropriate (Sokal and Rohlf 1969) and should be applied prior to

the derivation of the annual growth pattern for the cementum deposit.

For zooarchaeological purposes, the growth pattern of the cementum layer is of interest only inasmuch as it relates to an animal's date of death. The transformed data thus should be plotted as the independent variable and the week of cementum growth should become the dependent variable. Such data permit the calculation of a more appropriate regression equation. This equation, if derived as stated, provides estimates of the date of death from the proportionate growth in the outer increment. Using these data, it also becomes possible to calculate an error range for the seasonality estimates.

Summary:

In brief, this chapter reviews seasonality assessments in zooarchaeology and discusses the potential of cementum growth increments for such determinations. The results of this study indicate that there is an observable linear increase in outer increment width for the first forty-two weeks of cementum growth or from mid-March until late-December. Thereafter, there is no detectable increase in the cementum deposit as determined from a ratio of outer increment width over expected increment width. This growth pattern enables more accurate predictions of the season of death. In fact, month-of-death estimates are now possible from mid-March until the end of December. For the

winter months, on the other hand, only the season-of-death is estimable. Greater precision in these seasonality estimates, however, is not possible until further research is conducted.

8. Conclusions and Recommendations for Future Research

Man's mind clumsily and tediously and laboriously patches little trivialities together and gets a result - such as it is (Twain 1962:211).

This thesis presents the results of an osteometric and histological analysis of the mandible in mature Rocky Mountain mule deer from the Cache la Poudre drainage. Its principle objective was to discover more accurate approaches to the estimation of a deer's absolute age, sex, weight and season of death from a single anatomical element. As such, this research was successful.

In mature Rocky Mountain mule deer, the mandible is a good predictor of the deer's live and dressed carcass weight. By means of simple regression analysis, significant correlations were found to exist between various dimensions of the mandible and the bled carcass weight, eviscerated carcass weight and skinned and eviscerated carcass weight of mature animals. The strength of these associations increases substantially if the sample is subdivided into two groups based on seasonal weight gains and losses. Here, correlation coefficients exceed 0.80 for one group and 0.90 for the other. Several regression equations are also presented for estimating the weight of individual deer from the osteometric attributes of its mandible.

Given these results, it is not unreasonable to assume that similar associations exist for other North American ungulates. In fact, most skeletal elements probably relate to the weight of

such animals. It is thus recommended that future researchers attempt to discover the nature and strength of such associations. Here, the collection, weighing and measurement of a modern sample is necessary to derive the appropriate regression constants. The resultant regression equations then become powerful statistical tools for the prediction of animal weight directly from the elements present in the faunal assemblages.

In zooarchaeology, the desired weight estimates are variable and reflect the specific research objectives of the analyst. As a result, it is desirable, when preparing comparative specimens, to record separate weights for all edible organs and tissues. If future researchers compile such data, it will become practicable to estimate any desirable weight directly from the osteometric attributes of prehistoric bones. Further, if the animals are dissected properly it may be possible to predict the weight of selected portions directly from the dimensions of the appropriate bones.

In mature Rocky Mountain mule deer, the mandible also indicates the sex of the animal. In the present research, selected mandibular measurements were subjected to discriminant function analysis to obtain weighted values for the segregation of males and females. The technique is shown to be from 88 to 94 percent accurate in the separation of male and female mule deer from the Cache la Poudre population. Variations in the accuracy of the technique reflect the number and type of measurements used.

Three specimens from the sample were also withheld to test the reliability of one discriminant function. Here, all three

specimens were classified correctly on the basis of the function. Discriminant function analysis thus appears to be a reliable statistical technique for identifying and classifying the sex of mature mule deer from selected mandibular measurements. Further testing of the function using mandibles of known sex from Cache la Poudre mule deer is, however, desirable.

Technically, the discriminant functions presented in this thesis apply only to mature mule deer from the Cache la Poudre area. Here therefore, further testing is necessary to establish the applicability of these functions in sexing other mule deer from differing geographical proveniences. Discriminant function analysis may also apply to the mandibles of younger mule deer or to the same elements of other North American ungulates. In fact, the technique may prove useful in sexing animals using other skeletal elements. Here again, modern samples are essential to derive and test the appropriate functions.

In the analysis of prehistoric mule deer, further testing of these functions is also necessary. Here, secular trends and geographical variations in the growth of mule deer may influence the relevance of these equations. It is thus recommended that future zooarchaeologists verify the reliability of the above functions using the mandibles of known-sex deer from different temporal proveniences. Here, methods for the identification and recovery of sexable mandibles from prehistoric contexts are presented.

In mature Rocky Mountain mule deer, it is also possible to determine the absolute age of the animal from annuli counts in the cementum of the first mandibular molar. For such age deter-

minations, decalcified and stained longitudinal thin sections are shown to be the most reliable histological preparations. Here, the accuracy of the technique has been confirmed by studies with known-age animals. In the present study, ninety-one deer were aged independently from cementum annuli counts of the central incisor and the first molar. Here, age estimates in 80 of these animals are in perfect agreement. For the remaining 11 deer, the disagreements in the age estimates do not exceed plus or minus one year. Possible explanations for the observed differences are discussed.

Of immediate concern to zooarchaeological research is the development of an appropriate histological procedure for the analysis of prehistoric materials. In my opinion, the production of decalcified and stained thin sections from imperfectly preserved archaeological teeth may be difficult but nevertheless possible. It is also necessary to confirm the accuracy of the technique in aging other species of archaeological importance. Given these data, it then becomes possible to compare the rates of tooth wear in modern and prehistoric animals, to study more accurately the dynamics of prehistoric faunal populations and to compare the longevity in modern and prehistoric populations.

From decalcified and stained thin sections of the first mandibular molar, it is also possible to infer, with accuracy, the season of death for mature Rocky Mountain mule deer. Chapter seven of this study presents a methodology for the quantification of outer increment width. The result is a ratio of the observed outer increment width over the expected outer increment width. A

plot of the ratio means for each specimen relative to the known date of death then reveals an annual pattern of cementum growth. Here, the earliest detectable increase in the cementum deposit relative to the last annulus occurs in the thin sections of deer shot in late March. From this date until the end of December, there is a gradual increase in the width of the outer increment. From the end of December until the end of March, on the other hand, there is no detectable increase in the thickness of the deposit given the present analytical procedures. This is assumed to represent an episode of minimal or arrested growth.

It is possible, as noted in the study, to describe, in mathematical terms, the relationship of ratio means and time of year. For archaeological specimens therefore, it is possible to calculate a ratio mean and to relate this value to an approximate date of death. If, for example, the ratio mean equals one, then a winter death from late December to early March is indicated. If, on the other hand, the ratio mean is a value between 0 and 1, it is then possible to infer a month of death for mature deer. Greater precision in the seasonality estimates is not possible until further research is conducted.

As shown in this study, there is a quantifiable increase in outer increment width throughout most of the year. For future researchers, it is thus essential to quantify more accurately the extent of cementum growth in the outer increment and to derive a predictive equation which is more appropriate for the analysis of prehistoric fauna. The growth pattern of the cementum, as described, also applies only to mature mule deer from the Cache la

Poudre reserve. It is thus necessary to discover a comparable relationship for all North American ungulates which are important to archaeologists. This, again, requires the collection of an appropriate research collection.

In brief, this thesis outlines the potential interpretive value of the mule deer mandible. As shown by the present study, this skeletal element is capable of providing accurate estimates of a mature deer's absolute age, sex, weight and season of death. Further, the results of this research suggest interesting avenues for future zooarchaeological research in North America.

Appendix I: This table lists the identification number, sex, date of death, Erickson's (1967) age estimate and my age estimate for each of the 102 mandibles used in this research.

No.	Sex	Date of death	Erickson's age estimate		my age estimate	
			years	months	years	months
2	F	20 April 1961	7	10	7	10
3	F	27 April 1961	7	10	7	10
4	F	8 May 1961	3	11	3	11
5	M	16 May 1961	6	11	5	11
6	F	23 May 1961	3	11	3	11
7	F	30 May 1961	2	11	2	11
8	M	6 June 1961	8	0	8	0
9	M	13 June 1961	7	0	7	0
10	F	20 June 1961	3	0	3	0
12	F	6 July 1961	3	1	3	1
13	F	13 July 1961	7	1 *	6	1
14	F	20 July 1961	2	1	2	1
16	M	2 Aug. 1961	4	2	4	2
17	F	14 Aug. 1961	3	2	3	2
18	F	22 Aug. 1961	2	2	2	2
19	F	31 Aug. 1961	5	2	5	2
21	F	12 Sept. 1961	3	3	2	3
26	F	14 Nov. 1961	2	5	2	5
27	M	29 Nov. 1961	3	5	3	5
29	F	13 Dec. 1961	13	6	13	6
30	F	20 Dec. 1961	9	6	9	6
33	F	19 Jan. 1962	3	7	3	7
34	F	23 Jan. 1962	5	7	5	7
35	F	30 Jan. 1962	2	7	2	7
37	F	13 Feb. 1962	4	8	4	8
38	F	20 Feb. 1962	5	8	-	-
39	M	27 Feb. 1962	2	8	2	8
41	F	20 March 1962	5	9	5	9
42	F	22 March 1962	3	9	3	9
45	F	12 April 1962	10	10	10	10
46	F	20 April 1962	7	10	7	10
47	F	26 April 1962	2	10	2	10
57	F	9 July 1962	2	1 *	3	1
59	F	23 July 1962	3	1	4	1
60	M	30 July 1962	6	1	6	1
64	F	27 Aug. 1962	2	2	2	2
65	M	5 Sept. 1962	7	3 *	9	3
66	F	11 Sept. 1962	3	3	3	3
72	F	23 Oct. 1962	3	4	3	4
73	F	15 Nov. 1962	10	5	11	5
74	M	21 Nov. 1962	2	5	2	5
75	F	28 Nov. 1962	9	5	--	--
77	F	12 Dec. 1962	4	6	4	6

Appendix I: (cont'd)

78	M	19 Dec.	1962	3	6	4	6
79	F	26 Dec.	1962	8	6	8	6
80	M	2 Jan.	1963	4	7	5	7
81	M	9 Jan.	1963	4	7	4	7
82	F	16 Jan.	1963	6	7	6	7
83	F	23 Jan.	1963	9	7 *	11	7
84	F	30 Jan.	1963	4	7 *	3	7
85	M	6 Feb.	1963	2	8	2	8
88	F	27 Feb.	1963	4	8	4	8
89	M	6 March	1963	5	9	5	9
90	F	13 March	1963	8	9	8	9
91	F	20 March	1963	8	9 *	10	9
93	F	8 April	1963	8	10	8	10
95	F	22 April	1963	4	10	3	10
98	F	13 May	1963	7	11	8	11
99	M	20 May	1963	2	11	2	11
100	M	27 May	1963	4	11	4	11
101	F	5 June	1963	4	0	4	0
102	M	12 June	1963	5	0	5	0
105	M	2 July	1963	10	1	10	1
109	F	30 July	1963	2	1	2	1
110	F	6 Aug.	1963	6	2	6	2
112	F	20 Aug.	1963	5	2	5	2
115	F	18 Sept.	1963	3	3	3	3
120	F	22 Oct.	1963	10	4	--	--
122	M	20 Nov.	1963	4	5	4	5
125	F	10 Dec.	1963	3	6	3	6
126	F	17 Dec.	1963	8	6	8	6
130	F	21 Jan.	1964	9	7	9	7
133	M	11 Feb.	1964	4	8	4	8
134	F	18 Feb.	1964	7	8	7	8
136	F	3 March	1964	2	9	2	9
138	M	17 March	1964	5	9	5	9
142	M	8 April	1964	5	10	5	10
144	M	28 April	1964	6	10	6	10
146	F	12 May	1964	3	11	3	11
149	M	2 June	1964	3	0	3	0
153	F	30 June	1964	6	0	6	0
155	F	13 July	1964	3	1	3	1
159	F	11 Aug.	1964	4	2	5	2
167	M	12 Oct.	1964	3	4	3	4
168	M	20 Oct.	1964	4	4	4	4
169	F	4 Nov.	1964	3	5	3	5
170	M	10 Nov.	1964	2	5	2	5
171	M	17 Nov.	1964	6	5	7	5
173	F	8 Dec.	1964	8	6	8	6
175	M	23 Dec.	1964	2	6	2	6
178	M	19 Jan.	1965	8	7 *	--	--
181	F	10 Feb.	1965	5	8	5	8
183	F	24 Feb.	1965	10	8	10	8
185	M	11 March	1965	4	9	4	9

Appendix I: (cont'd)

186	F	17 March 1965	5	9	6	9
187	M	24 March 1965	4	9	4	9
190	F	13 April 1965	2	10	2	10
05	M	29 Nov. 1961	3	5	3	5
09	F	23 June 1962	2	0 *	2	0
018	F	28 April 1963	4	10	4	10
028	F	16 April 1964	4	10	4	10
033	F	25 March 1965	7	9	7	9

* These age estimates derive from an assessment of tooth wear.

Appendix II: Description of the 11 mandibular measurements with instructions for each mensuration using a left mandible. This list also provides the corresponding measurements of von den Driesch (1976:56-57) and Rees (1969:102). Dental terminology follows that of Riney (1951).

Measurement 1: Aboral length of the angular process. To quantify this length one measures the distance from the caudal border of the ascending ramus to an imaginary line extending from the aboral border of the mandibular condyle to the gonion caudale (von den Driesch 1976). To measure this distance, place the mandible, buccal side down, in the left corner of the board. Measurement 1 is then the maximum distance, measured to the nearest mm, from the "left wall" to the caudal border of the ascending ramus.

Measurement 2: Mandible length to the alveolus of the canine. (Rees' measurement 7). This measurement is the maximum distance from the gonion caudale to the aboral border of the canine socket. To obtain measurement 2, place the mandible, buccal side down, in the left corner of the board and read this mandibular length to nearest millimeter.

Measurement 3: Mandible length to the alveolus of P_2 (von den Driesch's measurement 5). Measurement 3 is the distance from the gonion caudale to the mesial border of the P_2 socket. Again, place the mandible, buccal side down, on the board and read this length to the nearest millimeter.

Measurement 4: Total length of the mandible (von den Driesch's measurement 1). This length measure represents the maximum distance from the gonion caudale to the infradentale (see von den Driesch 1976). In this case, place the mandible, lingual side down, in the right corner of the mandible board and read, to the nearest mm, the total length of the mandible excluding incisors.

Measurement 5: Mandible length to the alveolus of M_3 (von den Driesch's measurement 3). This is the distance from the gonion caudale to the aboral margin of the M_3 socket. As for measurement 4, place the mandible, lingual side down, on the board and read this distance to the nearest millimeter.

Measurement 6: Diastema length (Rees' measurement 1 and von den Driesch's measurement 11). This length, measured to the nearest 0.1 mm with dial calipers, is the distance from the aboral margin of the canine socket to the mesial border of the alveolus of P_2 .

Appendix II: (cont'd)

Measurement 7: Height of the corpus in the area of the diastema (Rees' measurement 2). Dimension 7 is the minimum distance, measured to the nearest 0.1 mm with dial calipers, between the dorsal and ventral borders of the diastema posterior to the mandibular symphysis.

Measurement 8: Width of the corpus in the diastema region (Rees' measurement 3). This is the minimum distance, measured as above, between the buccal and lingual borders of the diastema posterior to the symphysis.

Measurement 9: Corpus width (Rees' measurement 4). This distance, measured as above, is the width of the mandibular corpus at the mesial cusps of M_1 . As such, measurement 9 is the minimum distance between the lingual and buccal surfaces of the mandibular corpus in this region.

Measurement 10: Corpus height (Rees' measurement 5 and von den Driesch's measurement 15b). This measurement is the minimum distance between the dorsal border of the mandibular body medial to the anterior cusps of M_1 and the ventral border of the corpus. To obtain this height, measure, to the nearest 0.1 mm using dial calipers, the lingual side of the corpus in the specified region.

Measurement 11: Middle height of the ascending ramus (Rees' measurement 6 and von den Driesch's measurement 13). This height is the distance, measured to the nearest 0.1 mm, from the deepest point of the mandibular notch to the deepest point of the notch on the ventral border of the angular process.

Appendix III: This table lists the identification number, sex, and age in months of each specimen as well as the respective mandibular measurements* and weights** for each deer in the sample.

I.D.		M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	W1	W2	W3	W4	
No.	Sex	Age															
2	F	94	9	216	145	225	57	70.5	14.7	7.0	13.9	25.0	75.0	57.0	00.0	53.2	00.0
3	F	94	8	216	148	226	62	66.8	13.3	6.4	13.4	22.7	72.5	65.0	44.2	49.7	00.0
4	F	47	11	212	148	222	55	63.5	12.8	6.9	13.8	20.5	69.1	56.1	38.9	51.9	00.0
5	M	83	11	229	152	238	66	76.5	15.7	9.1	13.9	27.4	80.3	70.1	50.4	62.1	00.0
6	F	47	9	205	143	214	59	61.0	12.4	6.6	13.9	21.5	67.8	61.6	39.1	56.6	00.0
7	F	35	11	208	144	218	53	63.4	14.7	7.0	14.8	23.5	71.6	66.8	43.0	00.0	00.0
8	M	96	9	226	151	235	68	75.0	16.4	9.1	14.2	29.2	78.6	80.2	55.4	70.7	00.0
9	M	84	11	216	146	226	59	69.9	15.7	6.9	12.9	24.9	78.9	87.0	66.4	78.9	00.0
10	F	36	10	203	140	213	54	61.3	12.7	5.7	12.9	21.4	68.5	53.6	38.7	47.9	00.0
12	F	37	11	214	144	224	55	67.3	13.4	6.2	13.4	22.6	69.4	53.1	40.0	48.5	00.0
13	F	85	8	205	142	214	53	61.9	11.7	7.1	13.8	22.7	71.1	58.0	42.7	00.0	00.0
14	F	25	9	202	141	212	51	58.6	13.0	7.0	12.8	23.4	69.4	51.7	36.9	45.0	00.0
16	M	50	12	217	148	226	59	68.5	12.9	7.1	13.1	24.9	77.0	80.5	57.3	72.0	00.0
17	F	38	8	214	147	225	55	65.6	13.6	6.8	15.2	21.4	69.6	59.1	39.4	49.6	00.0
18	F	26	11	209	145	216	53	62.0	15.1	6.2	14.7	24.0	71.8	58.1	40.6	50.7	00.0
19	F	62	10	217	149	227	63	67.3	12.9	7.1	12.8	21.1	71.4	71.6	47.6	00.0	00.0
21	F	39	10	000	000	000	50	00.0	00.0	0.0	14.7	23.0	74.5	67.4	49.4	59.4	00.0
26	F	29	10	000	146	000	51	00.0	00.0	0.0	14.1	22.9	72.1	58.8	44.3	53.8	00.0
27	M	41	11	233	156	245	63	75.9	16.0	8.9	15.2	28.0	73.7	96.7	76.1	91.9	00.0
29	F	162	7	212	141	220	58	69.1	11.8	7.1	12.7	21.7	70.4	62.2	46.8	55.9	00.0
30	F	114	8	215	145	222	57	68.1	13.3	6.6	13.3	23.6	68.2	65.3	47.0	58.4	00.0
33	F	93	11	220	151	229	63	67.5	14.0	6.5	14.6	24.1	77.3	68.5	48.3	60.3	43.7
34	F	67	8	210	142	219	58	69.0	13.0	6.4	11.6	23.3	69.8	63.3	46.5	57.6	41.4
35	F	31	10	210	144	220	51	64.0	11.4	6.0	12.3	20.4	71.8	55.7	41.4	00.0	37.1
37	F	56	7	204	141	216	56	61.7	14.4	6.7	14.3	22.0	71.3	58.1	41.1	00.0	37.0
38	F	68	10	216	145	225	53	70.0	15.0	6.9	13.9	25.7	80.9	69.2	49.2	00.0	45.3
39	M	32	12	224	150	235	59	72.9	15.0	7.1	15.8	22.4	70.6	64.6	46.4	57.7	42.2
41	F	69	8	199	137	208	48	61.2	11.9	6.8	13.8	22.3	66.1	52.4	36.9	47.8	33.2
42	F	45	9	202	140	209	56	60.3	11.6	5.9	12.1	20.0	69.6	49.9	36.1	00.0	32.4
45	F	130	8	212	140	220	54	69.7	15.0	7.7	13.6	25.3	73.2	59.8	41.2	00.0	39.0

Appendix III: (cont'd)

I.D.	No.	Sex	Age	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	W1	W2	W3	W4
46	F	94	9	198	132	208	208	46	65.3	11.9	6.0	12.1	25.1	64.5	48.2	32.9	00.0	29.9
47	F	34	9	217	147	226	226	59	70.6	14.3	6.3	14.1	22.0	70.2	66.5	47.2	61.0	42.6
57	F	25	9	201	138	000	000	52	00.0	12.9	6.4	12.7	20.6	71.2	60.8	44.1	52.9	40.0
59	F	37	9	219	146	230	230	53	71.8	14.0	6.9	13.6	23.4	77.3	69.1	46.3	58.7	42.8
60	M	73	11	227	155	238	238	62	72.8	16.8	7.5	14.2	24.3	79.6	112.3	83.0	100.5	70.6
64	F	26	10	208	144	217	217	50	64.2	13.7	6.0	14.9	21.5	70.8	55.7	37.0	46.7	33.8
65	M	87	11	240	160	249	249	69	80.4	16.0	8.1	15.1	29.2	77.0	106.0	79.2	94.6	68.2
66	F	38	8	221	150	227	227	59	71.5	13.8	7.0	13.8	23.9	73.8	71.4	49.5	61.6	44.2
72	F	40	10	208	146	218	218	55	63.2	13.6	7.2	13.7	21.7	68.5	60.8	43.8	52.8	39.4
73	F	125	9	215	145	224	224	57	68.9	14.4	7.1	12.4	26.6	73.5	67.4	47.1	58.3	42.2
74	M	29	13	000	000	000	000	50	66.1	13.4	7.4	14.5	22.8	68.3	61.2	48.5	57.2	42.6
75	F	113	10	216	148	226	226	62	68.8	14.8	7.2	14.4	25.9	72.4	67.6	48.6	60.1	43.6
77	F	54	8	000	139	000	000	51	00.0	14.2	5.8	13.5	23.3	69.2	56.6	41.6	49.8	37.6
78	M	42	11	212	142	221	221	56	69.3	13.4	6.8	12.7	20.9	72.7	72.0	56.6	00.0	50.0
79	F	102	8	209	139	218	218	54	67.5	13.1	6.8	12.9	24.1	72.6	52.5	39.5	00.0	35.0
80	M	55	11	220	152	232	232	61	68.5	15.8	7.5	14.1	24.2	75.0	80.7	58.8	00.0	50.9
81	M	55	9	222	145	233	233	57	75.8	15.2	7.0	13.8	25.8	72.3	83.8	60.7	73.4	53.2
82	F	79	8	213	144	222	222	55	70.3	13.2	7.0	14.0	23.8	70.9	64.2	46.1	00.0	41.7
83	F	115	8	214	144	223	223	59	69.5	14.4	7.2	15.3	26.2	72.7	67.0	47.5	00.0	43.0
84	F	55	8	200	138	211	211	51	60.9	13.0	6.6	13.1	22.7	68.5	56.7	40.8	50.3	37.0
85	M	32	10	000	147	000	000	53	00.0	00.0	0.0	00.0	00.0	72.1	70.4	49.1	61.2	44.0
88	F	56	10	212	147	222	222	55	63.8	13.6	6.6	14.8	24.7	72.1	57.9	39.3	51.2	35.7
89	M	69	12	236	155	244	244	71	77.0	15.4	8.2	13.1	28.7	81.3	76.3	55.2	66.9	49.9
90	F	105	8	212	142	222	222	61	68.9	12.2	6.1	11.8	26.3	71.8	60.2	44.4	00.0	39.6
91	F	105	9	217	147	227	227	59	69.2	14.3	7.2	13.9	24.7	78.1	68.7	46.3	62.4	42.2
93	F	106	10	219	148	229	229	66	71.3	13.5	7.4	13.1	26.7	78.9	65.5	44.3	58.9	40.0
95	F	58	8	202	137	211	211	52	63.8	12.2	7.2	13.6	24.2	68.6	49.5	35.2	45.1	32.1
98	F	95	9	218	145	227	227	57	71.7	14.2	8.1	15.5	24.5	74.1	63.6	47.3	58.2	43.3
99	M	35	12	220	153	233	233	58	66.4	15.8	7.9	15.3	25.9	75.0	66.5	49.9	59.1	45.0
100	M	59	11	219	148	226	226	53	69.8	16.6	7.6	13.9	23.3	76.4	78.3	60.4	70.2	53.9
101	F	48	8	214	149	225	225	54	63.8	13.4	6.7	13.9	21.7	70.0	70.8	43.1	00.0	39.8

Appendix III: (cont'd)

I.D.		No.	Sex	Age	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	W1	W2	W3	W4
102	M	60	12	218	147	227	58	70.4	15.2	8.0	13.2	25.9	76.1	71.8	52.2	63.9	46.6		
105	M	121	11	227	148	236	64	77.9	16.4	7.7	12.6	25.7	77.0	100.8	69.6	86.6	62.8		
109	F	25	9	199	138	208	47	60.5	12.4	6.6	12.9	20.5	70.5	53.5	38.2	46.9	35.3		
110	F	74	7	212	146	221	51	65.6	12.9	7.1	14.8	22.5	71.7	65.7	44.5	57.0	40.4		
112	F	62	10	202	135	210	52	64.8	12.9	5.8	12.3	20.6	65.1	62.2	45.9	56.8	41.3		
115	F	39	9	211	142	222	55	67.8	13.9	6.4	14.2	22.5	77.3	66.8	50.0	60.2	44.6		
120	F	124	9	214	146	218	57	68.5	12.7	6.6	13.4	22.3	73.7	70.2	49.3	60.0	44.0		
122	M	53	12	230	153	241	63	76.9	15.7	7.2	14.3	26.7	79.1	103.5	86.0	99.3	76.3		
125	F	42	7	200	137	210	49	62.4	11.9	6.6	13.0	21.4	65.9	57.8	42.1	51.2	37.9		
126	F	102	9	205	139	214	58	63.9	13.0	7.0	13.6	22.8	72.0	60.7	45.9	55.7	41.7		
130	F	115	9	220	149	231	63	69.1	15.4	7.5	13.1	26.9	73.0	68.1	48.3	62.3	44.0		
133	M	56	11	235	159	245	69	74.7	14.0	8.2	14.1	23.2	80.0	81.0	60.7	72.4	53.5		
134	F	92	8	206	138	215	55	69.2	13.6	7.6	13.4	23.8	72.5	57.2	40.3	52.1	36.3		
136	F	33	8	208	140	218	49	66.2	12.8	6.5	13.5	21.6	66.0	51.0	34.3	45.8	31.0		
138	M	69	9	230	157	237	63	72.3	15.0	8.3	13.3	25.7	83.4	77.9	58.0	00.0	52.2		
142	M	70	10	227	150	235	64	75.9	14.4	8.0	13.8	25.7	76.0	74.3	53.6	65.5	49.2		
144	M	82	11	232	149	239	65	82.8	16.4	7.6	13.2	30.0	79.3	78.9	59.1	70.1	53.8		
146	F	47	9	203	140	213	53	61.5	12.4	6.6	14.0	22.9	71.8	60.6	39.6	55.0	36.6		
149	M	36	11	223	152	231	61	70.2	13.0	7.4	15.2	23.5	68.8	61.1	44.0	53.5	40.6		
153	F	72	8	218	148	229	63	69.7	13.9	6.5	12.4	24.1	73.7	65.3	49.9	59.7	46.0		
155	F	37	9	209	143	219	53	64.9	13.0	7.4	13.5	24.0	71.9	54.6	36.8	46.5	34.4		
159	F	50	7	198	137	200	49	59.2	13.5	6.4	13.9	22.5	68.7	58.1	37.8	47.8	34.0		
167	M	40	11	219	149	231	59	70.8	13.0	7.1	13.2	22.1	73.4	90.4	66.8	81.8	59.8		
168	M	52	12	219	149	230	57	69.4	15.1	7.7	14.6	24.0	77.7	100.1	75.4	91.0	66.8		
169	F	41	9	213	144	222	56	68.4	13.7	6.3	12.2	22.6	73.5	61.8	47.0	56.2	41.6		
170	M	29	13	210	147	218	55	64.0	13.6	7.2	15.3	21.3	74.5	74.8	56.8	68.2	49.2		
171	M	77	13	224	146	233	62	78.7	14.9	6.8	12.0	29.0	82.3	91.2	73.8	85.7	65.5		
173	F	102	8	206	142	213	54	61.8	12.6	6.4	13.4	22.9	70.7	64.2	44.7	54.7	39.9		
175	M	30	10	214	147	222	56	65.7	14.7	7.0	13.7	22.9	69.4	74.9	54.6	67.1	48.2		
178	M	103	11	000	155	000	68	00.0	16.8	7.4	14.5	25.6	79.0	86.5	62.6	76.2	55.8		
181	F	68	8	211	142	220	60	68.3	12.5	6.8	13.2	24.0	72.9	57.3	38.9	50.9	35.4		

Appendix III: (cont'd)

I.D.	No.	Sex	Age	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	W1	W2	W3	W4
183	F	128	9	07	143	057	74	00.0	00.0	14.9	7.7	14.3	24.1	72.3	67.2	47.6	61.2	42.7
185	M	57	16	08	164	055	73	00.0	00.0	13.4	8.0	14.3	27.3	95.2	84.6	41.2	74.3	55.4
186	F	64	9	10	142	NR	55	00.0	00.0	12.0	6.7	14.1	23.8	65.1	51.5	34.3	45.3	31.0
187	M	57	13	30	151	056	58	00.0	00.0	15.3	7.9	15.1	25.3	72.4	63.7	47.4	56.9	42.4
190	F	34	11	06	141	065	54	00.0	00.0	13.5	6.2	14.4	23.7	73.7	57.9	33.8	46.3	30.6
195	M	41	11	21	149	228	58	70.3	15.1	15.1	8.1	14.7	24.0	74.4	0.0	00.0	00.0	00.0
198	F	56	9	27	135	21	40	66.0	13.3	13.3	5.8	12.8	22.4	64.1	20.0	11.3	00.0	00.0
33	F	93	9	5	167	043	32	00.0	00.0	16.0	6.9	13.7	26.3	73.2	73.8	46.8	57.7	00.0

*Measurements were recorded in millimeters

**Weights were recorded in kilograms

Appendix IV: This chart describes the basic procedure and appropriate settings for x-raying and film development.

In this research, a portable x-ray unit and Kodak Occlusal Ultra Speed D Safety film were used to record the progress of the decalcification process. Every 2 hours, the molars were removed from the acid, placed on film with their position recorded and x-rayed to evaluate the extent of demineralization. During this x-raying, the exposure data were as follows:

Voltage	70 kV
Amperage	20 mA
Exposure time	0.15 seconds
Focus-film distance	35 cm

Development of the film occurred approximately 15 minutes after the exposure. The chemical baths for film development were maintained at a constant temperature of 68° F. The basic procedure for film development was as follows:

Developer	- 5 minutes with agitation every minute.
Rinse	- 20 seconds
Fixer	- 10 minutes with agitation every minute.
Rinse	- 20 minutes

After the final rinse the film was dipped in Kodak Photoflo to eliminate drying spots for subsequent photography. Within 30 minutes final results of the radiographic analysis were available for inspection.

Appendix V: This table lists the identification numbers, thicknesses, weights and decalcification times of the lingual sections of the deer molars.

Identification Number	Thickness (mm)	Weight (gm)	Decalcification time in hours
81	3.25	2.2	20
110	2.85	1.8	15
100	2.55	1.5	11
170	2.80	2.4	15
60	3.15	1.4	21
5	2.95	1.7	16
171	3.35	2.1	23
05	3.35	2.3	24
93	2.75	1.6	14
168	3.25	1.7	21
133	3.00	1.8	16
27	2.45	1.2	12
167	2.30	1.6	11
9	2.95	1.5	15
14	3.05	1.9	18
138	2.50	1.6	13
149	2.35	1.1	11
78	2.85	2.1	15
159	3.30	1.9	18
4	2.85	1.8	14
105	3.40	1.9	22
16	2.65	1.8	12
91	3.70	2.0	25
35	3.45	2.6	23
13	3.60	1.7	22
88	3.70	2.3	27
146	3.85	2.0	29
90	3.25	1.6	20
8	3.40	1.3	21
80	3.40	1.9	22
82	3.25	1.6	22
3	2.90	1.5	17
134	2.80	1.3	16
153	2.90	1.4	14
125	3.30	1.8	20
84	3.35	1.6	21
30	3.60	1.9	22
10	2.95	1.7	15
12	2.85	1.7	13
130	2.80	1.5	15
79	2.70	1.2	15
38	3.40	2.3	21
173	3.25	1.9	20
181	2.80	1.1	15
018	3.30	2.2	20

Appendix V: (cont'd)

73	2.90	1.2	15
19	2.65	1.2	11
6	2.80	1.1	13
169	3.25	1.9	20
47	2.90	1.3	13
112	3.20	1.8	16
83	2.65	1.6	13
59	3.15	2.0	17
126	2.55	1.0	15
190	3.00	2.1	18
29	2.50	1.3	10
45	2.85	1.2	14
46	2.00	0.9	8
41	3.10	2.3	16
42	3.05	1.2	18
33	3.35	1.9	21
185	2.90	1.8	16
187	3.25	2.1	20
85	3.30	2.0	18
183	3.20	1.8	21
65	2.60	0.7	10
64	3.15	2.0	18
17	2.90	1.4	15
21	3.35	2.2	19
169	3.25	1.8	18
98	3.45	1.6	22
09	2.85	1.4	14
7	2.80	1.3	14
77	3.20	1.8	18
178	3.15	1.6	17
186	2.80	1.2	15
120	2.55	0.9	14
144	2.70	1.3	14
033	3.05	1.7	18
57	2.15	1.6	8
26	3.05	1.4	14
101	3.20	1.8	18
66	2.65	1.7	12
18	2.85	2.3	14
109	2.65	2.2	14
028	3.10	1.7	18
142	3.55	1.4	20
34	2.10	1.1	10
72	2.65	1.5	13
95	2.80	1.8	16

Appendix VI: A detailed outline of the laboratory procedure used in the present research with minor revisions and recommendations for the analysis of archaeological specimens.

1. After cleaning and identifying the mandible, assign an identification number to the specimen. Catalogue the mandible using a permanent marker or India ink and nail polish. Record this information in a permanent file.
2. Measure the specimen. Try to obtain as many measurements as possible before removing any tooth for age determination or seasonality assessment.
3. Photograph the specimen as subsequent analysis destroys the corpus of the mandible. Include a scale in your photograph.
4. X-ray the mandible to determine the best location for the cut. If an x-ray unit is lacking, remove the entire alveolar region or cut out, at least, three molars to ensure the removal of a usable tooth.
5. Use a good coping saw to cut out the tooth of your choice. Do not damage the roots of adjacent teeth and remove as much of the tooth's alveolus as possible. Try to keep the tooth in its socket throughout the analysis.
6. Use a permanent marker to inscribe the specimen identification number on the buccal surface of the corpus.
7. Submerge the specimen in 10% formol saline for at least 24 hours. Use approximately 150 ml of fixative for this preliminary fixation. For archaeological specimens, it is advisable to fix the entire mandible before removing the tooth.
8. Rinse briefly in cold tap water.
9. Use a glass plate, grit and water as a lubricant, to grind down manually the lingual surface of the alveolus to within a millimeter of the molar root. The relative fragility of the archaeological specimen will dictate the coarseness of the grit. At the same time frost a number of petrographic slides using a medium grit.
10. Mount the specimen, lingual side down, on a petrographic slide using Flo-Texx or some other inexpensive commercial mounting medium.
11. Allow sufficient time for mounting medium to dry.
12. When the medium is dry, mount the slide on the vacuum chuck of the Isomet or similar low speed diamond saw.

Appendix VI: (cont'd)

13. Section the molar approximately 3 mm from its lingual edge. Adjust the blade speed and the weight of the support arm to accommodate the nature of the archaeological specimen.
14. Prepare two identification tags, each containing the specimen number. Use a durable substance, such as dymo tape, which will not deteriorate in either formol saline or nitric acid. Perforate plastic vials of a suitable size using either a hot needle or an electric drill.
15. When cut, place the buccal section of the specimen in formol saline for another 12 hours. Rinse in cold tap water and store this section of the tooth in a vial until further analysis. Be sure to include one of the identification tags with this part of the specimen.
16. Place the lingual section with the attached slide in xylene or toluene for about 20 minutes to dissolve the mounting medium.
17. Clear the xylene/toluene in an alcohol bath and hydrate the specimen in tap water.
18. Air dry the specimen for approximately 10 minutes.
19. Record the identification number, thickness and weight of this section.
20. Place the lingual section of the specimen with its identification tag in a perforated plastic vial.
21. Immerse this vial in 10% formol saline at a rate of 100 ml of solution per gram of tissue. Allow at least 48 hours for this primary fixation.
22. Rinse overnight in cold tap water to remove excess fixative.
23. Submerge the perforated plastic vial containing the specimen in 1N nitric acid solution at a rate of 100 ml per gram of tissue. For a fragile archaeological specimen use 4N formic acid or a comparable weak acid solution. Use the same volume of formic acid but remember to replace the solution every 24 hours. If the temperature of the laboratory is relatively high, place the acid solutions in a bath of water to maintain a constant temperature.
24. If x-ray unit is available, x-ray the specimen at regular intervals after the sixth hour of decalcification to determine precisely the end point of decalcification. Remove the specimen as soon as decalcification is complete.

Appendix VI: (cont'd)

25. If x-ray unit is not available, insert specimen thickness into equation I and solve. Allow ± 2 standard deviations to this value to insure complete decalcification.
N.B. This equation applies only when the researcher uses 100 ml of 1N nitric acid per gram of tissue. The equation does not apply for other acids nor for different volumes or different concentrations of nitric acid. Avoid the use of mechanical techniques to determine the end point of decalcification.
26. After decalcification, rinse the specimen in cold tap water for at least 12 hours to remove excess acid.
27. For fragile archaeological material, immerse the specimen in a secondary fixative, preferably buffered formol saline, for another 12 hours.
28. Rinse in cold tap water for several hours.
29. Store the specimen with its identification tag in distilled or tap water until further processing.
30. At least one day before sectioning, prepare a number of gelatin-coated slides.
31. Subdivide the decalcified lingual section into four segments before sectioning.
32. For archaeological specimens, carefully remove any grit or dirt trapped in the pulp cavity, alveolus or periodontal bone before mounting the segments for sectioning. Such impurities will ruin the microtome knife.
33. Mount each segment on a separate microtome stub using cryoform. Orient the specimen so that the smooth, flat surface is exposed to the cutting edge of the microtome knife.
34. Place the stubs with mounted tooth segments and identification tags in the microtome chamber. Allow specimens sufficient time to freeze. Orient all stubs inside the chamber so that tooth segments are parallel to each other. When cryoform freezes, the mounted specimens are not visible within the medium.
35. When adequately frozen (usually after 15 minutes), trim the cryoform blocks to within millimeters of the specimen.
36. Mount a stub into the specimen holder of the microtome. Orient the stub so that the long axis of the specimen is parallel to the edge of the microtome knife. Make sure that the cementum layer is outer most. Secure the block in the specimen holder.

Appendix VI: (cont'd)

37. Advance the block manually to within microns of the knife, then begin sectioning. Observe the sectioning procedures and recommendations outlined in chapter 3.
38. Use a Q-tip to discard the initial incomplete sections from the knife edge. Within forty cuts one should obtain complete sections. At this time, cut twelve serial sections. These generally lie flat on the microtome knife.
39. Open microtome chamber and lift the anti-roll plate. Gently lower a clean, gelatin-coated slide over the cut sections. The cold sections will adhere to the warm slide.
40. Withdraw slide with adherent sections and place on a dark, preferably black, surface. The dark background enhances section visibility.
41. Using a pipette, gently add a few drops of distilled water to the slide. Sections should flatten considerably. Using a dissecting needle, carefully orient all sections parallel to each other in the center of the slide.
42. When all sections are centered properly, remove excess water with pipette. To drain remaining water, place a Kleenex or some other absorbent paper near the edge of the slide and tilt gently. Excess water will gravitate toward the absorbent tissue.
43. After adequate drainage, transfer slide to a hot plate set at 40°C. Allow slides approximately one hour to dry.
44. Prepare two slides, each containing 10-12 sections, for each tooth segment.
45. While slides are drying, prepare the staining baths. Arrange the baths in the sequence as follows:
 - 1 bath distilled water (optional)
 - 1 bath 0.05% Toluidine blue O
 - 1 bath distilled water
 - 1 bath distilled water
 - 1 bath 50% alcohol
 - 1 bath 70% alcohol
 - 1 bath 95% alcohol
 - 1 bath 100% alcohol
 - 1 bath 100% alcohol
 - 1 bath xylene
 - 1 bath xylenePrepare cover glasses and Permount also.
46. Transfer slides to appropriate slide holders.

Appendix VI: (cont'd)

47. Immerse slides into distilled water for two minutes. This step is optional.
48. Immerse slides into stain (toluidine blue O) for 15 seconds. For archaeological specimens, it is preferable to use a lower dye concentration (0.01%) and a longer staining interval.
49. Transfer slides to the first bath of distilled water for 5 minutes.
50. Then transfer slides into second bath of distilled water. While the slides are in this bath, verify the quality of staining for each slide. Restain if necessary.
51. If staining is satisfactory, dehydrate slides in graded baths of alcohol. Leave slides in each bath for approximately 2 minutes.
52. Transfer slides to first bath of xylene for 2 minutes and prepare coverslips.
53. Move slides to the second bath of xylene. Remove slides, one at a time, to apply the coverslips.
54. Place several drops of Permunt on the coverslip. Tilt slide toward the coverslip and gently lower.
55. When the coverslip is in place, transfer slide to a slide warmer set at 35°C. Air bubbles will gravitate toward the edge of the coverslip.
56. Let slides dry overnight.
57. Use a razor to remove excess Permunt. In the case of untidy slides, use a Q-tip soaked in xylene.
58. If the slide is still untidy, use a commercial glass cleaner for final cleansing.
59. Store slides in a dust free container to await examination.

Appendix VII: This chart lists the basic formulae for the chemical solutions used in the present study.

10% formol-saline

Formalin concentrate (40% formaldehyde)	100 ml
Sodium chloride	9 gm
Distilled water	900 ml

To neutralize or buffer any formalin solution add sufficient calcium carbonate to attain the desired pH.

1N nitric acid

Commercial (70%) nitric acid	63 ml
Dilute to 1000 ml in distilled water	

4N formic acid

Formic acid (88%)	150 ml
Dilute to 1000 ml in distilled water	

Gelatin solution for coating slides

Gelatin	0.5 gm
Potassium chrome alum. $\text{Cr}_2(\text{SO}_4)_2 \cdot \text{K}_2\text{SO}_4$	0.1 gm
Distilled water	100 ml

Add gelatin to the water. Heat this solution gently to dissolve the gelatin. After dissolution of the gelatin add the potassium chrome aluminum. The latter inhibits the formation of mold.

To coat slides, wash the slides in absolute alcohol. Rinse the slides in 3 separate baths of distilled water and drain. Dip individual slides in the gelatin solution, drain and allow time to dry. When dry, place the gelatin-coated slides in a clean, dust-free slide box. Use as required.

0.05% Toluidine Blue O

Toluidine Blue O	1 gm
Distilled water	200 ml

Appendix VIII: List of regression equations and their respective correlation coefficients for measurements 3, 4, 5, 6 and 11.

1) Using bled carcass weight or weight 1 as the dependent variable, the regression equations are:

For the total sample:

	Weight 1	
Measurement 3	$\log \hat{Y} = 3.07 (\log X) - 4.81$	$r = 0.66$
Measurement 4	$\log \hat{Y} = 3.18 (\log X) - 5.64$	$r = 0.76$
Measurement 5	$\log \hat{Y} = 1.67 (\log X) - 1.23$	$r = 0.69$
Measurement 11	$\log \hat{Y} = 2.10 (\log X) - 2.10$	$r = 0.68$

For deer shot from June to January:

	Weight 1	
Measurement 3	$\log \hat{Y} = 3.72 (\log X) - 6.20$	$r = 0.68$
Measurement 4	$\log \hat{Y} = 3.67 (\log X) - 6.79$	$r = 0.80$
Measurement 5	$\log \hat{Y} = 2.03 (\log X) - 1.87$	$r = 0.76$
Measurement 11	$\log \hat{Y} = 2.66 (\log X) - 3.11$	$r = 0.71$

For deer shot from February to May:

	Weight 1	
Measurement 3	$\log \hat{Y} = 2.65 (\log X) - 3.95$	$r = 0.82$
Measurement 4	$\log \hat{Y} = 2.64 (\log X) - 4.40$	$r = 0.87$
Measurement 5	$\log \hat{Y} = 1.28 (\log X) - 0.55$	$r = 0.73$
Measurement 11	$\log \hat{Y} = 1.72 (\log X) - 1.41$	$r = 0.82$

2) Using eviscerated carcass weight or weight 2 as the dependent variable, the regression equations are:

For deer shot from June to January:

	Weight 2	
Measurement 3	$\log \hat{Y} = 3.71 (\log X) - 6.32$	$r = 0.61$
Measurement 4	$\log \hat{Y} = 3.93 (\log X) - 7.53$	$r = 0.77$
Measurement 5	$\log \hat{Y} = 2.28 (\log X) - 2.47$	$r = 0.77$
Measurement 11	$\log \hat{Y} = 2.93 (\log X) - 3.75$	$r = 0.71$

Appendix VIII: (cont'd)

For deer shot from February to May:

	Weight 2	
Measurement 3	$\log \hat{Y} = 3.10 (\log X) - 5.07$	$r = 0.83$
Measurement 4	$\log \hat{Y} = 3.17 (\log X) - 5.81$	$r = 0.91$
Measurement 5	$\log \hat{Y} = 1.61 (\log X) - 1.31$	$r = 0.80$
Measurement 11	$\log \hat{Y} = 2.01 (\log X) - 2.10$	$r = 0.83$

3) Using the edible meat weight or weight 4 as the dependent variable, the regression equations are:

For deer shot from June to January:

	Weight 4	
Measurement 3	$\log \hat{Y} = 3.38 (\log X) - 5.65$	$r = 0.62$
Measurement 4	$\log \hat{Y} = 3.68 (\log X) - 6.99$	$r = 0.78$
Measurement 5	$\log \hat{Y} = 2.13 (\log X) - 2.23$	$r = 0.76$
Measurement 11	$\log \hat{Y} = 2.72 (\log X) - 3.40$	$r = 0.71$

For deer shot from February to May:

	Weight 4	
Measurement 3	$\log \hat{Y} = 1.76 (\log X) - 1.63$	$r = 0.81$
Measurement 4	$\log \hat{Y} = 3.23 (\log X) - 5.99$	$r = 0.92$
Measurement 5	$\log \hat{Y} = 3.07 (\log X) - 5.04$	$r = 0.83$
Measurement 11	$\log \hat{Y} = 2.06 (\log X) - 2.23$	$r = 0.82$

Appendix IX: List of linear discriminant functions to use in the analysis of mandible fragments. For each function, the critical value, Mahalanobis D and probability of misclassification is included.

Equation 1:

For a mandible fragment where measurements 1, 2, 5, 6, 7, 8, 9, 10, 11 are quantifiable, the appropriate discriminant function is:

$$a=0.708(M1)+0.032(M2)-0.030(M5)+0.106(M6)+0.322(M7)+1.212(M8)-0.300(M9)-0.218(M10)-0.048(M11)$$

Here, the Mahalanobis D is 3.504, the critical value is 19.96 and the probability of misclassification is 0.04.

Equation 2:

If measurements 1, 3, 5, 9, 10 and 11 are quantifiable, the appropriate discriminant function is:

$$a=0.672(M1)+0.091(M3)+0.015(M5)-0.009(M9)+0.119(M10)+0.019(M11).$$

In this case, the Mahalanobis D is 2.687, the critical value is 25.08 and the probability of misclassification is 0.09.

Equation 3:

For a fragment where measurements 1, 5, 9, 10 and 11 are quantifiable, the linear discriminant function becomes:

$$a=0.720(M1)+0.076(M5)+0.157(M9)+0.091(M10)+0.044(M11)$$

Here, the Mahalanobis D is 2.619, the critical value is 19.21 and the probability of misclassification is 0.10.

Equation 4:

If measurements 5, 6, 7, 8, 9, 10 and 11 are quantifiable, the appropriate discriminant function is:

$$a=0.032(M5)+0.134(M6)+0.588(M7)+0.985(M8)-0.111(M9)-0.353(M10)+0.042(M11).$$

In this case, the Mahalanobis D is 2.49, the critical value is 19.65 and the probability of misclassification is 0.11.

Appendix IX: (cont'd)

Equation 5:

Using measurements 6, 7, 8, 9 and 10, the appropriate discriminant function is:

$$a = 0.160(M6) + 0.626(M7) + 1.079(M8) - 0.149(M9) - 0.331(M10).$$

Here, the Mahalanobis D is 2.456, the critical value is 17.71 and the probability of misclassification is 0.11.

Equation 6:

For a fragment where measurements 1, 2, 6, 7, 8, 9, 10 and 11 are quantifiable, the linear discriminant function is:

$$a = 0.708(M1) + 0.014(M2) + 0.115(M6) + 0.337(M7) + 1.19(M8) - 0.267(M9) - 0.232(M10) - 0.048(M11).$$

In this case, the Mahalanobis D is 3.4948, the critical value is 18.59 and the probability of misclassification is 0.04.

Equation 7:

Using measurements 3, 5, 6, 7, 8, 9, 10 and 11, the appropriate discriminant function is:

$$a = 0.107(M3) - 0.038(M5) + 0.25(M6) + 0.536(M7) + 0.926(M8) - 0.288(M9) - 0.286(M10) + 0.013(M11).$$

Here, the Mahalanobis D is 2.58, the critical value is 26.53 and the probability of misclassification is 0.10.

Appendix X: This table lists the weeks of cementum growth and their corresponding calendrical dates.

Week of Cementum Growth	Calendrical Dates
Week 1	March 12 - March 18
Week 2	March 19 - March 25
Week 3	March 26 - April 1
Week 4	April 2 - April 8
Week 5	April 9 - April 15
Week 6	April 16 - April 22
Week 7	April 23 - April 29
Week 8	April 30 - May 6
Week 9	May 7 - May 13
Week 10	May 14 - May 20
Week 11	May 21 - May 27
Week 12	May 28 - June 3
Week 13	June 4 - June 10
Week 14	June 11 - June 17
Week 15	June 18 - June 24
Week 16	June 25 - July 1
Week 17	July 2 - July 8
Week 18	July 9 - July 15
Week 19	July 16 - July 22
Week 20	July 23 - July 29
Week 21	July 30 - August 5
Week 22	August 6 - August 12
Week 23	August 13 - August 19
Week 24	August 20 - August 26
Week 25	August 27 - September 2
Week 26	September 3 - September 9
Week 27	September 10 - September 16
Week 28	September 17 - September 23
Week 29	September 24 - September 30
Week 30	October 1 - October 7
Week 31	October 8 - October 14
Week 32	October 15 - October 21
Week 33	October 22 - October 28
Week 34	October 29 - November 4
Week 35	November 5 - November 11
Week 36	November 12 - November 18
Week 37	November 19 - November 25
Week 38	November 26 - December 2
Week 39	December 3 - December 9
Week 40	December 10 - December 16
Week 41	December 17 - December 23
Week 42	December 24 - December 31
Week 43	January 1 - January 7
Week 44	January 8 - January 14

Appendix X: (cont'd)

Week 45	January 15 - January 21
Week 46	January 22 - January 28
Week 47	January 29 - February 4
Week 48	February 5 - February 11
Week 49	February 12 - February 18
Week 50	February 19 - February 25
Week 51	February 26 - March 4
Week 52	March 5 - March 11

Appendix XI: Ocular measurements and the respective regression equations for each of the measured cementum deposits. This table also lists the estimated thickness of the cementum deposit at the end of the current year of cementum growth and the proportion of the final increment evident in the thin section.

I.D.	No.	Cocular measurements	Estimated width of deposit	Equation	Proportion of outer increment	%
2	12	32 39 47 54 65 66+	72.87	$\hat{Y}=4.71+0.71(X)$	1.5/7.87	0.190
	--	35 47 61 72 83 85	96.06	$\hat{Y}=1.01(X)-0.9$	2/13.06	0.153
4	28	47 60 70 72	77.62	$\log \hat{Y}=2.09-14.06(1/X+10)$	2/7.44	0.262
	24	37 52 67 73	81.00	$\hat{Y}=1.20(X)+9.0$	3/14.00	0.214
	25	39 54 68 71	82.50	$\hat{Y}=1.20(X)+10.50$	3/14.50	0.207
	26	43 57 72 76	87.70	$\hat{Y}=1.27(X)+11.50$	4/15.70	0.255
	24	40 55 70 74	85.80	$\hat{Y}=1.28(X)+9.00$	4/15.80	0.253
	26	42 54 71 74	85.30	$\hat{Y}=1.23(X)+11.50$	3/14.30	0.210
	26	40 55 69 73	83.50	$\hat{Y}=1.20(X)+11.50$	4/14.50	0.276
5	--	17 39 63 88 94	111.30	$\hat{Y}=1.98(X)-7.50$	6/23.3	0.258
	--	32 51 70 89 107 113	126.48	$\hat{Y}=1.57(X)-5.40$	6/19.48	0.308
	18	33 49 64 78 94 98+	108.84	$\hat{Y}=1.26(X)+3$	4.5/14.84	0.303
	67	107 152 189 244 289 301	330.51	$\hat{Y}=3.71(X)+18.87$	12/41.51	0.289
	--	53 69 85 103 108	118.72	$\hat{Y}=1.38(X)+2.8$	5/15.72	0.318
	--	-- 17 39 62 68	84.75	$\hat{Y}=1.88(X)-73.17$	6/22.75	0.264
	--	-- 13 32 49 54	67.33	$\hat{Y}=1.50(X)-4.67$	5/18.33	0.272
6	28	51 73 92 96	107.12	$\log \hat{Y}=3.58-2.86(1/\log X+10)$	4/15.12	0.265
	25	45 65 81 85+	94.29	$\log \hat{Y}=3.53-2.87(1/\log X+10)$	4.5/13.29	0.339
	26	42 54 65 67+	73.44	$\log \hat{Y}=3.08-2.24(1/\log X+10)$	2.5/8.44	0.296
	27	40 55 69 73+	83.30	$\hat{Y}=12.5+1.18(X)$	4.5/14.3	0.315
	17	27 37 46 49	56.10	$\hat{Y}=7.5+0.81(X)$	3/10.1	0.297
	7	18 41 66 71	89.67	$\hat{Y}=2(X)-6.33$	5/18.67	0.268

Appendix XI: (cont'd)

I.D.	No.	Ocular measurements	Estimated width of deposit	Equation	Proportion of outer increment	%
7	18	41 66 71	89.67	$\hat{Y}=2(X)-6.33$	5/18.67	0.268
	18	36 66 71	88.00	$\hat{Y}=2(X)-8.0$	5/17.00	0.294
	14	29 44 48	59.00	$\hat{Y}=1.25(X)-1.0$	4/15.00	0.267
	16	35 54 59	72.84	$\hat{Y}=1.58(X)-3.0$	5/18.84	0.265
	18	38 62 67	83.17	$\hat{Y}=1.83(X)-4.67$	5/21.17	0.236
10	21	38 56 62	73.41	$\hat{Y}=1.46(X)+3.33$	6/17.41	0.345
	17	33 49 55	64.84	$\hat{Y}=1.33(X)+1.0$	6/15.84	0.379
	19	37 50 54	61.06	$\log \hat{Y}=2.09-17.69(1/X+10)$	4/11.06	0.362
	30	60 95 107	126.75	$\hat{Y}=2.71(X)-3.33$	12/31.75	0.378
	22	39 51 54	59.61	$\log \hat{Y}=2.04-15.39(1/X+10)$	3/8.61	0.348
	21	39 52 56	62.35	$\log \hat{Y}=2.08-16.58(1/X+10)$	4/10.35	0.386
	--	16 37 43	54.59	$\hat{Y}=1.54(X)-19.33$	6/17.59	0.341
12	14	26 40 44+	52.51	$\hat{Y}=1.08(X)+0.67$	4.5/12.51	0.360
	--	18 34 40	49.84	$\hat{Y}=1.33(X)-14.00$	6/15.84	0.379
	--	40 61 69	82.00	$\hat{Y}=1.75(X)-2.00$	8/21	0.381
13	17	30 42 54 59	66.80	$\hat{Y}=1.03(X)+5$	5/12.80	0.391
	15	27 37 47 59 68 73	79.35	$\hat{Y}=0.89(X)+4.59$	5/11.35	0.441
	18	35 55 79 108 129 138	150.47	$\hat{Y}=1.90(X)-9.13$	9/21.47	0.419
14	22	42 51	62.12	$\hat{Y}=1.67(X)+2.0$	9/20.12	0.447
	26	45 54	63.88	$\hat{Y}=1.58(X)+7.0$	9/18.88	0.477
	23	43 52	63.12	$\hat{Y}=1.67(X)+3.0$	9/20.12	0.447
16	34	64 95 123 137	153.3	$\hat{Y}=2.48(X)+4.50$	14/30.3	0.462
	30	55 75 97 106	119.4	$\hat{Y}=1.84(X)+9.0$	9/22.4	0.402
	26	54 78 103 114	129.3	$\hat{Y}=2.13(X)+1.50$	11/26.3	0.418
	25	51 70 84 95	106.3	$\hat{Y}=1.63(X)+8.50$	11/22.3	0.493

Appendix XI: (cont'd)

I.D. No.	Ocular measurements	Estimated width of deposit	Equation	Proportion of outer increment	%
17	10 23 36 41+	48.84	$\hat{Y}=1.08(X)-3.00$	5.3/12.84	0.413
	12 24 37 42	49.25	$\hat{Y}=1.04(X)-0.67$	5/12.25	0.408
	17 28 38 43	48.91	$\hat{Y}=0.88(X)+6.67$	5/10.91	0.458
	26 36 44 46	48.38	$\log \hat{Y}=1.85-9.61(1/X+10)$	2/4.38	0.457
	32 44 56 61	68.00	$\hat{Y}=1(X)+20.00$	5/12.00	0.417
	34 55 70 75	81.26	$\log \hat{Y}=2.14-13.38(1/X+10)$	5/11.26	0.444
	39 53 67 73	81.16	$\hat{Y}=1.17(X)+25.00$	6/14.16	0.424
18	9 19 23	28.88	$\hat{Y}=0.83(X)-1.00$	4/9.88	0.405
	30 47 54	64.12	$\hat{Y}=1.42(X)+13$	7/17.12	0.409
	16 31 37+	46.00	$\hat{Y}=1.25(X)+1.0$	6.5/15.00	0.433
	10 23 29	35.88	$\hat{Y}=1.08(X)-3.0$	6/12.88	0.466
19	23 42 58 66 76 80+	86.28	$\log \hat{Y}=3.28-2.57(1/\log X+10)$	4.5/10.28	0.438
	24 43 59 71 80 85	92.35	$\log \hat{Y}=3.32-2.59(1/\log X+10)$	5/12.35	0.405
	24 44 62 75 83 86+	90.34	$\log \hat{Y}=2.17-17.55(1/X+10)$	3.5/7.34	0.477
	25 41 58 67 77 81	85.88	$\log \hat{Y}=3.21-2.44(1/\log X+10)$	4/8.88	0.450
	44 55 69 82 100 110	123.82	$\log \hat{Y}=1.56+0.0074(X)$	10/23.82	0.420
	31 39 45 51 58 61	64.60	$\hat{Y}=25+0.55(X)$	3/6.6	0.455
	28 43 59 78 92 99	109.20	$\hat{Y}=11.10+1.36(X)$	7/17.02	0.411
21	27 43 51	58.88	$\hat{Y}=11.00+1.33(X)$	8/15.88	0.504
	24 40 49	55.88	$\hat{Y}=1.33(X)+8$	9/15.88	0.567
	22 36 44	50.12	$\hat{Y}=1.17(X)+8$	8/14.12	0.567
	17 29 36	41.00	$\hat{Y}=X+5$	7/12.00	0.583
	19 30 37	41.12	$\hat{Y}=8+0.92(X)$	7/11.12	0.630
	17 32 41	47.00	$\hat{Y}=1.25(X)+2.0$	9/15.00	0.600
	15 27 34	39.00	$\hat{Y}=X+3$	7/12.00	0.583
26	17 35 51	53.00	$\hat{Y}=1.5(X)-1$	16/18	0.889

I.D. No.	Ocular measurements	Estimated width of deposit	Equation	Proportion of outer increment	%
26	18 44 62	70.12	$\hat{Y}=2.17(X)-8$	18/26.12	0.689
	18 38 53	58.12	$\hat{Y}=1.67(X)-2$	15/20.12	0.746
	31 57 82	83.12	$\hat{Y}=2.17(X)+5$	25/26.12	0.957
	31 58 85	85.00	$\hat{Y}=2.25(X)+4$	27/27	1.000
27	39 81 106 134	142.00	$\log \hat{Y}=3.91-3.10(1/\log X+10)$	28/36	0.778
	110 147 188 221	226.33	$\hat{Y}=3.25(X)+70.33$	33/38.33	0.861
	50 80 110 134	140.00	$\hat{Y}=2.5(X)+20.00$	24/30.00	0.800
30	14 32 45 57 70 81	82.61	$\log \hat{Y}=3.69-3.39(1/\log X+10)$	11/12.61	0.872
	17 31 45 60 72	73.90	$\hat{Y}=1.19(X)+2.5$	12/13.9	0.863
	15 27 41 56 67	68.90	$\hat{Y}=1.14(X)+0.50$	11/12.9	0.853
	23 47 69 86 99 112 128	129.79	$\log \hat{Y}=3.69-3.11(1/\log X+10)$	15/17.79	0.899
37	23 39 57 74 91	91.30	$\hat{Y}=1.43(X)+5.5$	17/17.3	0.983
	23 39 53 76 93	93.30	$\hat{Y}=1.48(X)+4.5$	17/17.3	0.983
	17 34 58 81 99+	101.50	$\hat{Y}=1.80(X)-6.5$	13.5/20.5	0.902
	24 45 62 75 92	90.57	$\log \hat{Y}=3.48-2.81(1/\log X+10)$	17/15.57	1.092
	110 127 145 162 179	179.50	$\hat{Y}=1.45(X)+92.5$	17/17.5	0.971
	45 65 83 96 107	106.28	$\log \hat{Y}=3.04-1.87(1/\log X+10)$	11/10.28	1.070
39	18 35 58	56.88	$\hat{Y}=1.83(X)-9$	23/21.88	1.051
	21 43 64	64.88	$\hat{Y}=1.83(X)-1.0$	21/21.88	0.960
	21 43 64	64.88	$\hat{Y}=1.83(X)-1.0$	21/21.88	0.960
	22 42 63	62.12	$\hat{Y}=1.67(X)+2.0$	21/20.12	1.044
	18 39 60	60.00	$\hat{Y}=1.75(X)-3.0$	21/21	1.000
	19 32 45	44.88	$\hat{Y}=1.08(X)+6.0$	13/12.88	1.009
41	13 29 42 62 74 87	87.90	$\log \hat{Y}=3.90-3.74(1/\log X+10)$	13/13.9	0.935
	13 26 34 43 55 65	64.38	$\hat{Y}=0.84(X)+3.90$	10/9.38	1.066

Appendix XI: (cont'd)

I.D. No.	Ocular measurements				Estimated width of deposit				Equation	Proportion of outer increment	%
41	11	23	32	43	52	59+	60.10		$\log \hat{Y} = 3.51 - 3.31(1/\log X + 10)$	7.5/8.1	0.926
	--	43	52	58	66	75	73.86		$\hat{Y} = 0.63(X) + 28.5$	9/7.86	1.145
	--	50	70	86	104	121	121.76		$\hat{Y} = 1.48(X) + 15.2$	17/17.76	0.957
42	68	79	89	100			99.91		$\hat{Y} = 0.88(X) + 57.67$	11/10.91	1.008
	37	60	83	106			106.16		$\hat{Y} = 1.92(X) + 14.0$	21/21.16	0.992
	--	17	37	56+			57.16		$\hat{Y} = 1.67(X) - 23.0$	19.5/20.16	0.967
	30	62	96	129			128.67		$\hat{Y} = 2.75(X) - 3.33$	33/32.67	1.010
	45	76	104	129			128.37		$\log \hat{Y} = 3.56 - 2.56(1/\log X + 10)$	25/24.37	1.026
	16	29	38	48			48.06		$\log \hat{Y} = 3.19 - 2.66(1/\log X + 10)$	10/10.06	0.994
45	--	7	21	35	50	62	75	88	101		
	114	116					128.06		$\hat{Y} = 1.11(X) - 5.14$	1/14.06	0.071
46	--	37	49	63	74	89	102	115	116		
	--	--	--	15	24	38	47	58	59		
	--	--	--	49	58	67	79	91	93		
	--	--	--	--	--	71	91	113	116		
47	37	57	72	73			86.03		$\log \hat{Y} = 3.08 - 2.02(1/\log X + 10)$	1/14.03	0.071
	22	39	54	56			70.17		$\hat{Y} = 1.33(X) + 6.33$	2/16.17	0.124
	25	44	61	62			75.70		$\log \hat{Y} = 3.41 - 2.70(1/\log X + 10)$	1/14.70	0.068
	25	44	66	68			86.08		$\hat{Y} = 1.71(X) + 4.00$	2/20.08	0.100
	23	38	54	55+			69.25		$\hat{Y} = 1.29(X) + 7.33$	1.5/15.25	0.098
	31	53	74	76			95.59		$\hat{Y} = 1.79(X) + 9.67$	2/21.59	0.093
59	57	79	95	112	121		131.10		$\hat{Y} = 1.51(X) + 40.5$	9/19.1	0.471
	--	27	56	83	97		111.13		$\hat{Y} = 2.33(X) - 28.67$	14/28.13	0.498
	--	20	48	78	91		106.87		$\hat{Y} = 2.42(X) - 38.33$	13/28.87	0.450
	--	23	50	81	94		109.53		$\hat{Y} = 2.42(X) - 35.67$	13/28.53	0.456
	--	37	72	109	126		144.67		$\hat{Y} = 3.0(X) - 35.33$	17/35.67	0.477

I.D. No.	Ocular measurements							Estimated width of deposit	Equation	Proportion of outer increment	%
50	--	17	34	50	58		66.97	$\hat{Y}=1.38(X)-15.88$	8/16.97	0.471	
60	--	33	46	58	69	81	92.96	$\hat{Y}=0.99(X)+9.8$	5/11.96	0.418	
	17	31	45	56	65	73	83.17	$\log \hat{Y}=3.37-2.86(1/\log X+10)$	4/10.17	0.393	
	24	34	45	56	65	77	87.19	$\hat{Y}=0.88(X)+13.27$	4/10.19	0.393	
	--	--	20	30	43	54	65.64	$\hat{Y}=0.96(X)-15$	5/11.64	0.430	
	--	31	47	60	72	84	94.82	$\log \hat{Y}=3.65-3.3(1/\log X+10)$	4/10.82	0.366	
65	9	17	24	32	40	54	89.98	$\hat{Y}=0.71(X)+4.0$	5/9.98	0.501	
85											
	12	21	28	36	46	53	82.97	$\hat{Y}=0.65(X)+4.97$	4/7.97	0.502	
79											
	--	--	18	28	36	46	82.90	$\hat{Y}=0.77(X)-9.5$	5/9.9	0.505	
78											
	18	31	43	51			55.59	$\hat{Y}=1.04(X)+5.67$	8/12.59	0.635	
66	15	27	38	47			52.67	$\hat{Y}=1.00(X)+4.67$	9/14.67	0.613	
	15	25	37	44			47.83	$\hat{Y}=0.92(X)+3.67$	7/10.83	0.646	
	17	29	43	51			55.51	$\hat{Y}=1.08(X)+3.67$	8/12.51	0.639	
	16	26	40	47			51.33	$\hat{Y}=1.0(X)+3.33$	7/11.33	0.613	
	27	41	56	64			70.41	$\hat{Y}=1.21(X)+12.33$	8/14.41	0.555	
72	--	47	61	69			75.16	$\hat{Y}=1.17(X)+19.0$	8/14.16	0.565	
	--	41	56	66			71.00	$\hat{Y}=1.25(X)+11.0$	10/15.00	0.667	
	--	44	61	71			78.16	$\hat{Y}=1.42(X)+10.0$	10/17.16	0.583	
	--	44	59	68			74.00	$\hat{Y}=1.25(X)+14.0$	9/15.00	0.600	
	20	38	55	65			72.75	$\hat{Y}=1.46(X)+2.67$	10/17.75	0.563	
	29	48	71	83			91.33	$\hat{Y}=1.75(X)+7.33$	12/20.33	0.590	
	29	45	64	74			81.08	$\hat{Y}=1.46(X)+11.00$	10/17.08	0.585	

Appendix XI: (cont'd)

I.D. No.	Ocular measurements										Estimated width of deposit	Equation	Proportion of outer increment	\bar{t}
73	21	43	64	80	104	120	132	144	146.33	$\log \hat{Y} = 3.84 - 3.39(1/\log X + 10)$	12/14.33	0.837		
	--	--	--	--	78	85	90	97	98.52	$\hat{Y} = 0.58(X) + 15.0$	7/8.52	0.823		
	--	--	--	--	122	132	140	148	149.33	$\hat{Y} = 0.75(X) + 41.33$	8/9.33	0.857		
	25	42	63	77	95				96.30	$\hat{Y} = 1.48(X) + 7.5$	18/19.3	0.932		
74	42	59	72						76.12	$\hat{Y} = 1.42(X) + 25.0$	13/17.12	0.759		
	61	81	98						101.12	$\hat{Y} = 1.67(X) + 41.0$	17/20.12	0.845		
	25	45	61						65.12	$\hat{Y} = 1.67(X) + 5.0$	16/20.12	0.795		
	80	102	120						123.88	$\hat{Y} = 1.83(X) + 58.0$	18/21.88	0.823		
	30	51	68						72.00	$\hat{Y} = 1.75(X) + 9$	17/21.00	0.810		
75	19	40	61	79					82.00	$\hat{Y} = 1.75(X) - 2$	18/21	0.857		
	--	47	64	80					81.16	$\hat{Y} = 1.42(X) + 13$	16/17.16	0.932		
	--	43	55	66					67.00	$\hat{Y} = X + 19$	11/12	0.917		
	17	31	44	56					57.91	$\hat{Y} = 1.13(X) + 3.67$	12/13.91	0.863		
77	--	42	53	63	73				73.97	$\hat{Y} = 0.88(X) + 21.17$	10/10.97	0.912		
	23	40	52	62	72				72.94	$\log \hat{Y} = 3.18 - 2.43(1/\log X + 10)$	10/10.94	0.914		
	--	42	50	57	64+				64.97	$\hat{Y} = 0.63(X) + 27.17$	7.5/7.97	0.941		
	--	35	45	54	62				63.10	$\hat{Y} = 0.76(X) - 17.5$	8/9.1	0.879		
	21	34	46	55	63				63.22	$\log \hat{Y} = 3.08 - 2.36(1/\log X + 10)$	8/8.22	0.973		
80	21	34	45	56	73	83			83.60	$\hat{Y} = 1.05(X) + 8.0$	10/10.6	0.943		
	18	30	41	51	66	77			76.18	$\hat{Y} = 0.94(X) + 8.5$	11/10.18	1.081		
	--	13	24	39	48	61			61.00	$\hat{Y} = 1.00(X) - 11.0$	13/13	1.000		
	18	33	43	60	73	87			86.38	$\hat{Y} = 1.14(X) + 4.30$	14/13.38	1.046		
	22	36	47	58	74	84+			85.20	$\hat{Y} = 1.05(X) + 9.60$	10.5/11.2	0.937		
81	--	26	37	49	61				60.43	$\hat{Y} = 0.96(X) + 2.83$	12/11.43	1.050		
	19	29	41	50	61				61.30	$\hat{Y} = 0.88(X) + 8.5$	11/11.30	0.973		

Appendix XI: (cont'd)

I.D.	No.	Ocular measurements	Estimated width of deposit	Equation	Proportion of outer increment	%
81	15	25 37 47 58	58.00	$\hat{Y}=0.50(X)+4.0$	11/11	1.000
	25	36 47 57 67	67.90	$\hat{Y}=0.89(X)+14.5$	10/10.9	0.963
	22	31 41 51 61	60.60	$\hat{Y}=0.81(X)+12.0$	10/9.6	1.041
82	9	19 30 41 51 61	61.56	$\hat{Y}=0.88(X)-1.80$	10/10.56	0.945
	--	95 119 140 163 187	185.92	$\hat{Y}=1.83(X)+26.0$	24/22.92	1.047
	24	35 48 66 78	78.10	$\hat{Y}=1.16(X)+8.5$	12/12.1	0.992
	15	24 37 43 50 58 67+	67.57	$\hat{Y}=0.71(X)+7.93$	9.5/9.57	0.993
84	16	31 43 58	57.24	$\hat{Y}=1.13(X)+3.0$	15/14.24	1.053
	13	24 34 44+	44.91	$\hat{Y}=0.88(X)+2.67$	10.5/10.91	0.962
	11	22 30 39+	39.92	$\hat{Y}=0.79(X)+2.0$	9.5/9.92	0.958
	21	32 45 57	56.67	$\hat{Y}=X+8.67$	12/11.67	1.028
	31	47 57 70	70.25	$\hat{Y}=1.04(X)+20.33$	13/13.25	0.981
85	21	32 43	43.12	$\hat{Y}=0.92(X)+10.0$	11/11.12	0.989
	18	31 44	43.88	$\hat{Y}=1.08(X)+5.0$	13/12.88	1.009
	20	31 42	42.12	$\hat{Y}=0.92(X)+9.0$	11/11.12	0.989
	26	37 48	48.12	$\hat{Y}=0.92(X)+15.0$	11/11.12	0.989
	18	28 38	37.88	$\hat{Y}=0.83(X)+8.0$	10/9.88	1.012
	14	25 36	36.12	$\hat{Y}=0.92(X)+3.0$	11/11.12	0.989
88	--	34 48 62 76	76.20	$\hat{Y}=1.17(X)+6.0$	14/14.2	0.986
	22	38 50 62 77	77.00	$\hat{Y}=1.15(X)+8.0$	15/15	1.000
	18	36 48 62 77	77.00	$\hat{Y}=1.2(X)+5.0$	15/15	1.000
	--	23 45 63 84	83.87	$\hat{Y}=1.57(X)-16.33$	21/20.87	1.006
	25	39 53 64 78	77.90	$\hat{Y}=1.09(X)+12.50$	14/13.9	1.007
89	18	34 49 60 70 80+	80.38	$\log \hat{Y}=3.38-2.82(1/\log X+10)$	10.5/10.38	1.012
	18	29 40 53 65 76	76.16	$\hat{Y}=0.98(X)+5.60$	11/11.16	0.986

Appendix XI: (cont'd)

I.D. No.	Ocular measurements										Estimated width of deposit	Equation	Proportion of outer increment	%
89	17	33	47	59	67	79					78.83	$\log \hat{Y} = 3.45 - 2.97(1/\log X + 10)$	12/11.83	1.014
	27	45	61	76	87	97					97.01	$\log \hat{Y} = 3.31 - 2.53(1/\log X + 10)$	10/10.01	0.999
90	--	--	--	--	43	86	131	176	209		243.02	$\log \hat{Y} = 4.19 - 3.45(1/\log X + 10)$	2/34.02	0.059
	211													
91	14	28	49	75	132	174	201	238	274		367.57	$\hat{Y} = 2.82(X) - 38.51$	3/37.57	0.080
	297	330	333											
95	15	34	51	64	66						74.61	$\log \hat{Y} = 2.19 - 22.18(1/X + 10)$	2/10.61	0.188
	12	25	36	47	48						59.20	$\hat{Y} = 0.97(X) + 1.0$	2/12.20	0.164
	10	23	35	47	49						59.80	$\hat{Y} = 1.03(X) - 2.0$	2/12.80	0.156
	32	56	75	92	94+						107.05	$\log \hat{Y} = 3.39 - 2.51(1/\log X + 10)$	2.5/15.05	0.166
	16	34	54	68	71						87.20	$\hat{Y} = 1.47(X) - 1.0$	3/19.20	0.156
99	54	78	100	106							123.49	$\hat{Y} = 1.92(X) + 31.33$	6/23.49	0.255
	24	49	75	82							100.57	$\hat{Y} = 2.13(X) - 1.67$	7/25.57	0.274
	79	102	129	135							153.17	$\hat{Y} = 2.08(X) + 53.33$	6/24.17	0.248
	49	90	128	137							167.92	$\hat{Y} = 3.29(X) + 10.00$	9/39.92	0.225
	48	77	111	120							141.91	$\hat{Y} = 2.63(X) + 15.67$	9/30.91	0.291
100	7	22	39	57	70	77					92.26	$\log \hat{Y} = 4.58 - 5.0(1/\log X + 10)$	7/22.26	0.314
	10	28	48	64	75	78					86.58	$\log \hat{Y} = 2.28 - 28.08(1/X + 10)$	3/11.58	0.259
	24	44	68	91	111	116					133.78	$\hat{Y} = 1.84(X) + 1.30$	6/22.78	0.263
	19	38	63	82	99	104					116.86	$\log \hat{Y} = 3.94 - 3.58(1/\log X + 10)$	5/17.86	0.280
	18	35	52	65	75	78+					88.95	$\log \hat{Y} = 3.56 - 3.08(1/\log X + 10)$	3.5/13.95	0.251
	17	32	44	59	73	77					86.82	$\hat{Y} = 1.16(X) + 3.30$	4/13.82	0.289
	12	22	33	45	53	55					59.76	$\log \hat{Y} = 3.45 - 3.20(1/\log X + 10)$	2/6.76	0.296
	18	33	50	61	75	78+					89.76	$\hat{Y} = 1.18(X) + 4.80$	3.5/14.76	0.237

Appendix XI: (cont'd)

I.D. No.	Ocular measurements										Estimated width of deposit	Equation	Proportion of outer increment	%
102	21	42	61	82	97	100	111.91	$\log \hat{Y} = 3.78 - 3.31(1/\log X + 10)$	3/14.91	0.201				
	16	35	55	73	89	92	104.63	$\log \hat{Y} = 3.96 - 3.71(1/\log X + 10)$	3/15.63	0.192				
	12	28	47	65	81	84	96.76	$\log \hat{Y} = 4.13 - 4.10(1/\log X + 10)$	3/15.76	0.190				
	8	17	25	36	46	48	54.78	$\hat{Y} = 0.79(X) - 2.1$	2/6.78	0.228				
105	15	35	57	82	100	120	202.65	$\log \hat{Y} = 4.19 - 4.05(1/\log X + 10)$	7/17.65	0.397				
	185	192												
109	25	40	46				55.00	$\hat{Y} = 1.25(X) + 10$	6/15.00	0.400				
	51	66	71				81.00	$\hat{Y} = 1.25(X) + 36$	5/15.00	0.333				
	35	46	50				57.12	$\hat{Y} = 0.92(X) + 24$	4/11.12	0.360				
	50	89	102				128.00	$\hat{Y} = 3.25(X) + 11$	13/39	0.333				
110	13	27	36	42	51	61	70.37	$\hat{Y} = 0.76(X) + 6.53$	4/9.37	0.427				
	12	23	33	42	49	58	67.47	$\hat{Y} = 0.75(X) + 4.47$	4/9.47	0.422				
112	22	39	56	68	79	84	89.39	$\log \hat{Y} = 3.40 - 2.77(1/\log X + 10)$	5/10.39	0.481				
	19	35	53	67	78	85	91.12	$\log \hat{Y} = 3.56 - 3.06(1/\log X + 10)$	7/13.12	0.534				
	18	33	50	62	75	81	86.07	$\log \hat{Y} = 3.53 - 3.05(1/\log X + 10)$	6/11.07	0.542				
	20	35	49	52	72	77	81.52	$\log \hat{Y} = 3.36 - 2.77(1/\log X + 10)$	5/9.52	0.525				
	--	17	34	51	66	75	83.24	$\hat{Y} = 1.37(X) - 15.40$	9/17.24	0.522				
115	18	32	42	50			54.67	$\hat{Y} = X + 6.67$	8/12.67	0.631				
	18	30	40	45			48.07	$\log \hat{Y} = 3.02 - 2.36(1/\log X + 10)$	5/8.07	0.620				
	12	27	41	51			55.95	$\log \hat{Y} = 3.84 - 3.69(1/\log X + 10)$	10/14.95	0.668				
	50	64	81	89			95.92	$\hat{Y} = 1.29(X) + 34.0$	8/14.92	0.536				
122	18	36	49	65	73		75.32	$\log \hat{Y} = 3.53 - 3.05(1/\log X + 10)$	8/10.32	0.775				
	20	38	57	69	82		84.18	$\log \hat{Y} = 3.60 - 3.09(1/\log X + 10)$	13/15.13	0.856				
	20	40	58	71	83		85.98	$\log \hat{Y} = 3.62 - 3.11(1/\log X + 10)$	12/14.98	0.801				
	--	16	36	56	71+		76.20	$\hat{Y} = 1.67(X) - 24.0$	15.5/20.20	0.767				

Appendix XI: (cont'd)

I.D. No.	Ocular measurements	Estimated width of deposit	Equation	Proportion of outer increment %
122	-- -- 19 36 49+	53.20	$\hat{Y}=1.42(X)-32.0$	13.5/17.2 0.785
125	14 28 38 45	46.54	$\log \hat{Y}=1.98-18.15(1/X+10)$	7/8.54 0.820
	15 29 40 46	47.55	$\log \hat{Y}=1.98-17.61(1/X+10)$	6/7.55 0.795
	-- 14 24 33	33.84	$\hat{Y}=0.83(X)-6.0$	9/9.84 0.915
	-- 15 33 49	51.00	$\hat{Y}=1.5(X)-21.0$	16/18 0.889
	16 28 39 48	49.57	$\hat{Y}=0.88(X)+7.33$	10/10.57 0.851
126	-- 15 33 54 66 78 93 102 112+	114.76	$\log \hat{Y}=3.69-3.30(1/\log X+10)$	9.5/12.76 0.745
	-- -- 48 63 80 98 113 126+	130.44	$\hat{Y}=1.38(X)-18.6$	13.5/17.44 0.774
133	19 37 49 59 67	66.55	$\log \hat{Y}=2.07-17.26(1/X+10)$	8/7.55 1.060
	18 35 50 60 68	67.77	$\log \hat{Y}=2.10-18.81(1/X+10)$	8/7.77 1.030
	22 36 50 63 77	76.90	$\hat{Y}=1.14(X)+8.50$	14/13.9 1.007
	10 18 27 36 44	44.80	$\hat{Y}=0.73(X)+1$	8.5/8.8 0.966
134	14 25 36 57 66 74 82 90	90.34	$\hat{Y}=0.69(X)+24.1$	8/8.34 0.959
	18 30 40 55 64 72 82 90	90.34	$\hat{Y}=0.74(X)+19.3$	8/8.34 0.959
136	50 63 76	75.88	$\hat{Y}=1.08(X)+37$	13/12.88 1.009
	-- 20 40	40.12	$\hat{Y}=1.67(X)-20$	20/20.12 0.994
	-- 16 32	31.88	$\hat{Y}=1.33(X)-16$	16/15.88 1.008
	-- 26 52	52.12	$\hat{Y}=2.17(X)-26$	26/26.12 0.995
	20 29 38	38.00	$\hat{Y}=0.75(X)+11$	9/9 1.000
	-- 42 83	84.00	$\hat{Y}=3.5(X)-42$	41/42 0.976
138	18 36 48 60 72 84	84.00	$\hat{Y}=1(X)+12$	12/12 1.000
142	-- 26 50 73 94 118	117.38	$\hat{Y}=1.89(X)-18.7$	24/23.38 1.027
	-- 27 56 77 105 133	130.36	$\hat{Y}=2.13(X)-23.0$	28/25.36 1.104

Appendix XI: (cont'd)

I.D. No.	Ocular measurements										Estimated width of deposit	Equation	Proportion of outer increment	%
142	--	24	42	61	77	100					95.26	$\hat{Y}=1.48(X)-11.3$	23/18.26	1.260
144	--	--	17	27	38	52	62	63+			73.86	$\hat{Y}=0.96(X)-18.3$	1.5/11.86	0.126
	--	9	19	28	36	42	48	49			54.69	$\log\hat{Y}=2.10-38.5(1/X+10)$	1/6.69	0.149
	--	9	19	28	40	49	60	61+			69.87	$\hat{Y}=0.85(X)-11.73$	1.5/9.87	0.152
	--	9	19	29	39	50	60	61			69.90	$\hat{Y}=0.85(X)-11.7$	1/9.9	0.101
	--	10	20	31	44	54	68	69			77.92	$\hat{Y}=0.96(X)-14.24$	1/9.92	0.101
146	19	36	58	77	81						96.30	$\hat{Y}=1.63(X)-1.5$	4/19.3	0.207
	14	34	54	75	78+						94.90	$\hat{Y}=1.69(X)-6.5$	3.5/19.9	0.176
	34	69	107	146	155						182.70	$\hat{Y}=3.12(X)-4.5$	9/36.7	0.245
	--	22	52	85	91						116.30	$\hat{Y}=2.63(X)-41.5$	6/31.3	0.192
	12	30	54	74	78						95.00	$\hat{Y}=1.75(X)-10.0$	4.5/21	0.214
149	13	26	39	42							51.84	$\hat{Y}=1.08(X)$	3/12.84	0.234
	23	42	69	74							90.83	$\hat{Y}=1.92(X)-1.33$	5/21.83	0.229
	29	52	81	86							102.16	$\hat{Y}=2.17(X)-2.0$	5/21.16	0.236
	27	47	76	82							98.92	$\hat{Y}=2.04(X)+1.0$	6/22.92	0.262
	15	41	73	80							101.16	$\hat{Y}=2.42(X)-15.0$	7/28.16	0.249
	14	27	40	43							52.84	$\hat{Y}=1.08(X)+1.0$	3/12.84	0.234
153	11	22	33	43	55	61	64				70.20	$\log\hat{Y}=3.56-3.38(1/\log X+10)$	3/9.20	0.326
159	--	39	62	82	101	108					117.52	$\log\hat{Y}=4-3.69(1/\log X+10)$	7/16.52	0.424
	--	37	57	76	94	99+					108.94	$\log\hat{Y}=3.92-3.60(1/\log X+10)$	5.5/14.94	0.368
	15	29	49	65	81	87+					98.20	$\hat{Y}=1.4(X)-2.6$	6.5/17.2	0.378
	--	48	75	95	114	121+					133.84	$\log\hat{Y}=3.91-3.41(\log X+10)$	7.5/19.84	0.378
167	--	22	49	66+							76.00	$\hat{Y}=2.25(X)-32$	17.5/27	0.648
	23	50	82	102							110.75	$\hat{Y}=2.46(X)-7.33$	20/28.75	0.696

Appendix XI: (cont'd)

I.D. No.	Ocular measurements	Estimated width of deposit	Equation	Proportion of outer increment	δ
167	19 48 82 104 22 51 81 101	112.91 110.41	$\hat{Y}=2.63(X)-13.33$ $\hat{Y}=2.46(X)-7.67$	23/30.91 20/29.41	0.711 0.680
168	11 23 34 45 53 18 28 38 48 54+ 12 17 23 28 32 15 35 48 64 74+	56.40 57.80 33.50 80.30	$\hat{Y}=0.94(X)$ $\hat{Y}=0.83(X)+8$ $\hat{Y}=0.45(X)+6.5$ $\hat{Y}=1.33(X)+0.5$	8/11.4 6.5/9.8 4/5.5 10.5/16.3	0.702 0.663 0.727 0.644
171	-- 18 31 47 59 71 83 94 -- 19 31 45 56 65 74 82	97.38 85.02	$\hat{Y}=1.09(X)-7.26$ $\log \hat{Y}=3.95-4.09(1/\log X+10)$	11/14.38 8/11.02	0.765 0.725
175	13 23 32 32 18 34 49 42+ 12 23 34 60 29 47 62 60+	32.88 49.88 34.12 65.12	$\hat{Y}=0.83(X)+3$ $\hat{Y}=1.33(X)+2$ $\hat{Y}=0.92(X)+1$ $\hat{Y}=1.5(X)+11$	9/9.88 15/15.88 11/11.12 15/18.00	0.911 0.945 0.989 0.833
05	12 29 42 53+ 12 23 34 42+ 13 31 46 60 17 33 47 60+ 15 28 43 54+	57.69 45.16 63.30 62.33 56.83	$\log \hat{Y}=3.91-3.79(1/\log X+10)$ $\hat{Y}=0.95(X)+1$ $\log \hat{Y}=3.99-3.86(1/\log X+10)$ $\hat{Y}=1.25(X)+2.33$ $\hat{Y}=1.17(X)+0.67$	11.5/15.69 8.5/11.16 15/17.3 13.5/15.33 11.5/13.83	0.733 0.762 0.867 0.881 0.832
09	27 47 53+ 21 42 53 19 32 37 18 30 34	68.79 63.00 44.88 42.00	$\hat{Y}=1.67(X)+7.0$ $\hat{Y}=1.75(X)$ $\hat{Y}=1.08(X)+6.00$ $\hat{Y}=X+6.0$	6.5/21.79 6/21 5/12.88 4/12	
78	13 30 45 59 72 16 32 48 62 71+ -- 35 47 60 69+	75.30 74.23 71.90	$\hat{Y}=1.28(X)-1.5$ $\log \hat{Y}=3.67-3.32(1/\log X+10)$ $\hat{Y}=1.04(X)+9.5$	13/16.3 9.5/12.23 9.5/11.9	0.798 0.777 0.798

Appendix XI: (cont'd)

I.D. No.	Ocular measurements				Estimated width of deposit	Equation	Proportion of outer increment	%
78	20	35	52	65	74	$\log \hat{y} = 3.45 - 2.9(1/\log X + 10)$	9/10.54	0.854
--	35	35	47	58	65+	$\log \hat{y} = 3.21 - 2.55(1/\log X + 10)$	7.5/9.28	0.808

Appendix XII: This table lists the specimens used in the establishment of the annual growth pattern for the cementum deposits. Included are the week of cementum growth as derived from the animal's date of death and the respective means for the ratios of observed outer increment width over expected increment width.

Specimen Number	Week of Cementum Growth	Ratio Means
2	Week 6	0.171
4	Week 9	0.240
5	Week 10	0.287
6	Week 11	0.302
7	Week 12	0.266
10	Week 15	0.363
12	Week 17	0.368
13	Week 18	0.417
14	Week 19	0.457
16	Week 21	0.444
17	Week 23	0.432
18	Week 24	0.428
19	Week 25	0.438
21	Week 27	0.576
26	Week 36	0.856
27	Week 38	0.813
30	Week 41	0.872
37	Week 49	1.000
39	Week 51	1.004
41	Week 2	0.006
42	Week 2	0.000
45	Week 5	0.071
46	Week 6	0.106
47	Week 7	0.092
59	Week 20	0.471
60	Week 21	0.400
65	Week 26	0.503
66	Week 27	0.618
72	Week 33	0.593
73	Week 36	0.862
74	Week 37	0.806
75	Week 38	0.892
77	Week 40	0.924
78	Week 41	0.808
80	Week 43	1.001
81	Week 44	1.005
82	Week 45	0.994
84	Week 47	0.996

Appendix XII: (cont'd)

85	Week 48	0.996
88	Week 51	1.000
89	Week 52	1.003
90	Week 1	0.059
91	Week 2	0.080
95	Week 6	0.166
99	Week 10	0.256
100	Week 11	0.274
102	Week 14	0.203
105	Week 17	0.397
109	Week 21	0.357
110	Week 22	0.425
112	Week 24	0.521
115	Week 28	0.614
122	Week 37	0.797
125	Week 40	0.854
126	Week 41	0.760
133	Week 48	1.016
134	Week 49	0.959
136	Week 51	0.997
138	Week 1	0.000
142	Week 4	0.130
144	Week 7	0.126
146	Week 9	0.207
149	Week 12	0.241
153	Week 16	0.326
159	Week 22	0.387
167	Week 31	0.684
168	Week 32	0.684
171	Week 36	0.745
175	Week 41	0.920
05	Week 38	0.815
09	Week 15	0.326

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