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Recent Advances in Ageing
and Sexing Animal Bones

For Vasili and Marilena

*Proceedings of the 9th Conference of the International Council
of Archaeozoology, Durham, August 2002*

Series Editors: Umberto Albarella, Keith Dobney and Peter Rowley-Conwy

Recent Advances in Ageing and Sexing Animal Bones

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*Cover image: Ursus americanus baculum, mandible and innominate,
photo taken by Haskel Greenfield*

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Preface

Umberto Albarella, Keith Dobney and Peter Rowley-Conwy

This book is one of several volumes which form the published proceedings of the 9th meeting of the International Council of Archaeozoology (ICAZ), which was held in Durham (UK) 23rd–28th August 2002. ICAZ was founded in the early '70s and has ever since acted as the main international organisation for the study of animal remains from archaeological sites. The main international conferences are held every four years, and the Durham meeting – the largest ever – follows those in Hungary, the Netherlands, Poland, England (London), France, USA, Germany and Canada. The next meeting will be held in Mexico in 2006. The Durham conference – which was attended by about 500 delegates from 46 countries – was organised in 23 thematic sessions, which attracted, in addition to zooarchaeologists, scholars from related disciplines such as palaeoanthropology, archaeobotany, bone chemistry, genetics, mainstream archaeology etc.

The publication structure reflects that of the conference, each volume dealing with a different topic, be it methodological, ecological, palaeoeconomic, sociological, historical or anthropological (or a combination of these). This organisation by theme rather than by chronology or region, was chosen for two main reasons. The first is that we wanted to take the opportunity presented by such a large gathering of researchers from across the world to encourage international communication, and we thought that this could more easily be achieved through themes with world-wide relevance. The second is that we thought that, by tackling broad questions, zooarchaeologists would be more inclined to take a holistic approach and integrate their information with other sources of evidence. This also had the potential of attracting other specialists who shared an interest in that particular topic. We believe that our choice turned out to be correct for the conference, and helped substantially towards its success. For the publication there is the added benefit of having a series of volumes that will be of interest far beyond the restricted circle of specialists on faunal remains. Readers from many different backgrounds, ranging from history to zoology,

will certainly be interested in many of the 14 volumes that will be published.

Due to the large number of sessions it would have been impractical to publish each as a separate volume, so some that had a common theme have been combined. Far from losing their main thematic focus, these volumes have the potential to attract a particularly wide and diverse readership. Because of these combinations (and because two other sessions will be published outside this series) it was therefore possible to reduce the original 24 sessions to 14 volumes. Publication of such a series is a remarkable undertaking, and we are very grateful to David Brown and Oxbow Books for agreeing to produce the volumes.

We would also like to take this opportunity to thank the University of Durham and the ICAZ Executive Committee for their support during the preparation of the conference, and all session organisers – now book editors – for all their hard work. Some of the conference administrative costs were covered by a generous grant provided by the British Academy. Further financial help came from the following sources: English Heritage, Rijksdienst voor het Oudheidkundig Bodemonderzoek (ROB), County Durham Development Office, University College Durham, Palaeoecology Research Services, Northern Archaeological Associates, Archaeological Services University of Durham (ASUD), and NYS Corporate Travel. Finally we are extremely grateful for the continued support of the Wellcome Trust and Arts and Humanities Research Board (AHRB) who, through their provision of Research Fellowships for Keith Dobney and Umberto Albarella, enabled us to undertake such a challenge.

The present volume publishes the proceedings of the session 'Ageing and Sexing', which was among the first to be proposed for ICAZ 2002 and ended up being one of the strongest and best attended. This was in large part due to Deborah Ruscillo's excellent organisational skills, but also to the inherent interest and appropriateness of this subject for an ICAZ conference. Whether we study material from Argentina or Japan, from the Palaeolithic or the medieval

period, we still need to deal with the issue of ageing and sexing animal bones. A methodological session may be of little interest outside the field of zooarchaeology, but this is compensated for by the fact that *all* animal bone specialists will be interested in it. Initially Deborah wanted simply to find the best venue to present her interesting new method of sexing mammal bones through shape analysis. However, here was an opportunity to be more ambitious and organise a whole session dedicated to sexing and ageing studies. Things went ahead as planned and this book represents the culmination of almost three years of work, begun with a cosy conversation in the warm environment of the Ruscillo/Cosmopoulos home in Winnipeg (as the external temperature approached *minus* 30°C!).

The publication in 1982 of the volume “Ageing and sexing animal bones from archaeological sites”, edited by Bob Wilson, Caroline Grigson and Sebastian Payne, represented a milestone in the development of zooarchaeological studies, and the book is, unsurprisingly, one of the most cited publications in zooarchaeology. Since then, as Terry O’Connor highlights in his introduction to the present

volume, much more work has been done in refining ageing and sexing methods and in improving our understanding of body development and sexual variation in the vertebrate skeleton. However, so far zooarchaeologists are still by and large adopting ageing and sexing methods that are pre- rather than post- 1982. The challenge of this book is therefore not just to add more information, but also to persuade zooarchaeologists that the time is ripe for experimenting with new methods and for analysing data by taking into account the substantial new advances that this discipline has produced in more recent years. Only time will tell if this volume will have achieved this ambitious goal, but whatever the case, we have little doubt that it will represent an indispensable tool for zooarchaeologists worldwide.

Final special thanks must go to Vasili and Marilena Cosmopoulos (Deborah’s son and daughter), who had the good grace to be born during the final stages of the editing of this volume. We could not have expected a better omen for the success of the book.

Acknowledgments

These proceedings are a direct result of the teamwork and collegiality of the authors involved. Always polite and accommodating, the participants of the Ageing and Sexing Session were a pleasure to work with, and I thank them for their cooperation and their contributions to methodology in zooarchaeology. The participants of the session also acted as referees of the published proceedings; each participant reviewed two papers submitted for publication to ensure the quality and accuracy of the information presented herein. For the sake of keeping costs low, raw data for the various studies presented in this volume could not be published. The authors are happy to provide raw data from their research upon request (addresses provided at the end of each chapter).

The session would not have been such a success were it not for the tireless support and direction of the conference organizers. This publication was made possible by these same individuals who also bravely took on the series

editing and organization after the conference ended. On behalf of all the participants of the Ageing and Sexing Session, I wish to express our appreciation for the commitment of Umberto Albarella, Keith Dobney, Peter Rowley-Conwy and Deborah Jaques for the conference preparations and publication series organization. I would also like to thank Simon Davis and Caroline Grigson for chairing the morning and afternoon sections of the ageing and sexing colloquium, and also for acting as referees for some papers submitted here.

Travel and accommodation grants for the participants were supplied thanks to generous funding from the Institute for Aegean Prehistory (INSTAP). We are grateful for their support and their broad vision of archaeological research. INSTAP is one of the few organizations that realize the potential of zooarchaeological studies in the quest of studying ancient peoples.

7. Accuracy of Age Determinations from Tooth Crown Heights: a Test Using an Expanded Sample of Known Age Red Deer (*Cervus elaphus*)

T. E. Steele

The utility of the Quadratic Crown Height Method (QCHM) for estimating animal age-at-death from hypsodont ungulate teeth was tested using a sample of known-age Rocky Mountain elk (Cervus elaphus) from western Montana. There is no difference in wear rate between males and females, so the sample can be analyzed in its entirety. Regression of age on lower first molar crown height (n = 163) shows that there is a good relationship between crown height and age, and regression equations can satisfactorily estimate age from crown height in specimens from the population that provided the known-age individuals. However, fixed regression equations can only adequately estimate age in samples whose teeth are the same size as the known-age sample, and C. elaphus body and tooth size varies in time and space. Therefore, flexible equations such as those from the QCHM are desirable, but the QCHM did not adequately estimate age in the known-age sample. I adjusted the formula by changing the age of potential ecological longevity to the age of the tooth's longevity, and I confirmed that the quadratic curve best fits the data for lower first molars. I also compared the relationship between crown height and age in C. elaphus to the relationship found in known-age samples of Odocoileus virginianus and Rangifer tarandus.

Introduction

Faunal analysts have long recognized that the age distribution of a species in a sample provides data about the species' life history patterns and the specimens' depositional history, but assigning specimens into age classes is not always easy. Numerous methods exist for assessing age-at-death of archaeological specimens (papers in this volume, Amorosi 1989; Morris 1972; Pike-Tay 2000; Wilson, Grigson, and Payne 1982), but epiphyseal fusion, tooth cementum annuli, and tooth development, eruption, and wear remain the most frequently applied methods (for summaries see Klein and Cruz-Uribe 1984; O'Connor 2000; Reitz and Wing 1999). Methods based on tooth eruption and wear are most frequently used, because they monitor age throughout an animal's life, not just during growth (e.g. epiphyseal fusion) and because they are non-destructive and do not require specialized technical skill and equipment (e.g. counting cementum annuli). Wear often is documented by coding stages, but many researchers have utilized

metric measurements of tooth crown height. Measurements are preferable to coded stages because they are replicable, easy to apply to isolated teeth, and more amenable to quantitative analyses. While raw measurements can be directly compared, often measurements are used with equations that can estimate age-at-death in months. This study assesses the utility of the Quadratic Crown Height Method (QCHM), which is a set of flexible formulae that can be used to estimate age-at-death from tooth crown heights.

The Known-Age Sample

In order to investigate the relationship between crown height and age, I used a sample of Rocky Mountain elk (*Cervus elaphus*, Linnaeus 1758) mandibles from western Montana just north of Yellowstone National Park, Wyoming in the United States. These specimens originate from individuals that were marked as calves and were

subsequently retrieved at hunter checkpoints, and therefore have known age-at-death (in months) and, in most cases, known sex. This sample was created from two sources. One source was the mandibles collected by Quimby and Gaab (1957) for their wear-stage study (housed by the Fish and Wildlife Management Program, Montana State University-Bozeman). C. Wolf measured tooth crown heights on 170 specimens from this sample, and these measurements were used by Klein and colleagues (Klein, Allwarden, and Wolf 1983; Klein and Cruz-Uribe 1983; Klein *et al.* 1981) in their studies of the relationship between tooth crown height and age. These measurements are also used here. The second source of known-age specimens was collected by Hamlin *et al.* (2000) to compare estimates of age using wear stages to those based on incisor cementum annuli (housed by the Montana Department of Fish, Wildlife, and Parks-Bozeman). I measured tooth crown heights on 56 of these mandibles. The mean inter-observer error for tooth crown height measurements is low at $n = 110$, 2.9%, 0.24 mm (Steele 2002, 167; see also Morrison and Whitridge 1997), thus measurements can be combined. C. Wolf's 170 specimens plus my 56 mandibles brings the known-age sample to 226 individuals (Fig. 1, male: $n = 79$, female: $n = 129$, unknown: $n = 18$). Although most of the specimens are still under 72 months (6 years), this expanded sample increases the number of individuals in the 78–104 months (6.5–8.5 years) age category from what was available in previous studies. The oldest age classes are still underrepresented, because these animals are rare in most mammal populations (Caughley 1966; Deevey 1947). The older individuals in this sample are primarily females, because adult males are less numerous in the population due to extermination earlier in life by human hunters (K. Hamlin, pers. comm.).

Measuring Tooth Crown Height

Following Klein and Cruz-Uribe (1984, 46–47), crown height was measured on all specimens as the minimum distance between the occlusal surface and the line separating the enamel of the crown and the dentine of the root (enamel-dentine junction) on the buccal-most surface of the anterior lobe of the tooth. Some researchers measure tooth crown height as the distance from the enamel-dentine junction to the “saddle” between the protoconid and hypoconid peaks on the buccal surface of a mandibular tooth (e.g. Gifford-Gonzalez 1991; Lowe 1967; Spinage 1971). This often is done when the cusps are damaged and cannot be measured (Gifford-Gonzalez 1991; Lowe 1967). Unfortunately, this “saddle” measurement may be biased, because it is not affected by wear until the peaks of the cusps of the tooth are worn. By not recording the early wear on the tooth, individuals might be recorded as younger than their actual age. Other researchers measure crown height on the lingual side of

<i>age cohorts years (months)</i>	<i>total</i>	<i>m1</i>	<i>males (m1)</i>	<i>females (m1)</i>
0.5 (5–10)	42			
1.5 (17–20)	41	21	9	11
2.5 (27–33)	36	36	15	15
3.5 (40–44)	33	33	7	23
4.5 (53–57)	25	25	6	17
5.5 (65–68)	15	15	4	9
6.5 (77–79)	6	6		5
7.5 (89–92)	8	8		8
8.5 (101–104)	10	10		8
9.5 (113–114)	3	3		3
10.5				
11.5 (138)	1	1		1
12.5 (150–156)	2	2		2
13.5				
14.5 (173)	1	1		1
15.5 (185)	2	2	1	1
16.5				
17.5				
18.5				
19.5				
20.5				
21.5 (260)	1			
<i>total</i>	<i>226</i>	<i>163</i>	<i>42</i>	<i>104</i>

Fig. 1. The number of known-age elk in the total sample, and the number of both sexes, males, and females in each age cohort with measurable m1 crown heights. Sex was not known for some specimens.

a mandibular tooth as the minimum distance between the occlusal surface (the metaconid or entoconid peaks) and the enamel-dentine junction (e.g. Koike and Ohtaishi 1985; Lister 1981). I expect that lingual crown height measurements have a comparable relationship with age as buccal crown height measurements, because metaconid height is highly correlated to protoconid height, i.e. $n = 47$, $r = 0.97$ (Steele 2002). The lingual surface of a mandibular tooth is fairly flat so the lingual measurement is harder to define consistently than the buccal measurement, particularly once the cusps have worn flat. Also, the lingual measurement is awkward to take on comparative material when the hemi-mandibles are still articulated. The crown height measurement described by Klein and Cruz-Uribe (1984, 46–47) is preferable to the other measurements, because it is easy to define (i.e. has a low inter-observer measurement error), easy to take, and has become standard practice in zooarchaeology (e.g. Gaudzinski 1995; Hoffecker, Baryshnikov, and Potapova 1991; Morrison and Whitridge 1997; Pike-Tay 1991; Pike-Tay, Morcomb, and O'Farrell 2000; Slott-Moller 1990; Walker 2000).

Measurements were taken on dp4, p4, m1, m2, and m3. The right mandible was measured unless it was missing or damaged (lefts measured: $n = 14$), and pathological specimens were omitted. In this initial investigation into the relationship between crown height and age, I analyzed only the measurements on m1,

because this tooth had the largest sample size (Fig. 1, $n = 163$). The first molar could not be measured on the youngest individuals, because the tooth had not yet erupted enough to expose the enamel-dentine junction, nor on the oldest individual (260 months), because the crown was completely worn away and only roots remained.

One difficulty with using m1 to estimate age-at-death in fossil specimens is that in many ungulate species, it can be difficult to separate isolated m1s from m2s, as they are morphologically similar. Klein *et al.* (1981) addressed this problem in their initial investigation into the utility of mathematical equations to estimate age-at-death from tooth crown heights in *C. elaphus*. They found that length and particularly breadth measurements clearly separated m1s from m2s with minimal overlap, supporting the visual impression that m2s are more massive than m1s. These results were similar whether the teeth were isolated or in mandibles. Investigations into my own fossil and modern data confirm these results. Because the size difference is relative, measurements will not help identify m1s versus m2s when only a few teeth are present, but small samples cannot provide meaningful mortality profiles regardless. Thus, isolated teeth from an archaeological sample can be visually compared and measured to separate m1s from m2s when samples are large enough to create mortality profiles. An alternative is to use m3s to create mortality profiles, because they are more readily identifiable due to their third lobe. However, to make a complete mortality profile, deciduous teeth (often dp4) need to be considered in conjunction with adult teeth. Although m3 erupts at about the same time dp4 is shed (Brown and Chapman 1991; Lowe 1967; Quimby and Gaab 1957), m3 crown height is not measurable until well after the dp4 is shed, because the enamel-dentine junction is not visible until approximately 54 months (Steele, personal observation). Because of this, there would be a gap from approximately 26 months to 54 months in a mortality profile created from the combination of dp4 and m3. However, m3 can be used to examine age distributions in older individuals.

Tooth wear rates may vary between individuals and populations, possibly because of differences in diet (Flook 1970; Hewison *et al.* 1999; Skogland 1988) or degree of enamel mineralization (Kierdorf and Becher 1997). However, as Spinage (1973) suggested, teeth are critical for survival; it would be surprising if they varied widely in efficiency in a single species, because animals acquire energy by using their teeth to eat. Lowe (1967) found that teeth of *C. elaphus* from German forests had similar wear per age patterns as *C. elaphus* from Rhum, Scotland, although the climate, habitat, and management were very different. Any method of assessing age from wear on teeth, either by coding stages or measuring crown heights, assumes that individual and between population variation in timing of eruption and rate of wear is limited. They assume that individual variation is random, and the

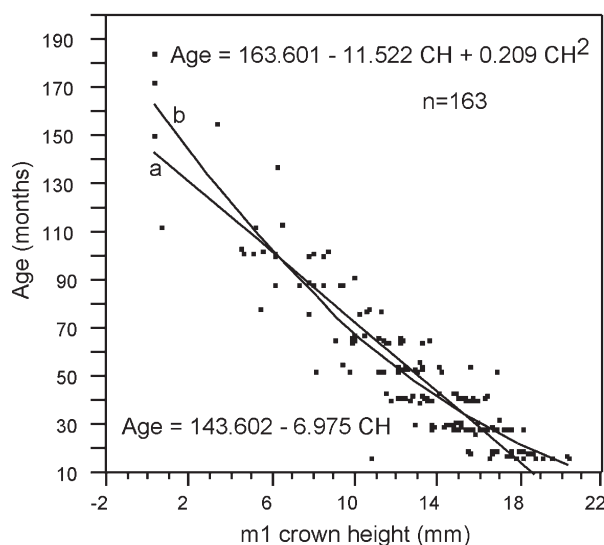


Fig. 2. Linear (a) and quadratic (b) regressions of age on crown height for the known-age sample of elk. Summary statistics are provided in Fig. 3.

method must not consistently over- or under-estimate the ages of animals (Spinage 1973). Because of potential for variation, age-at-death estimates based on wear cannot accurately assign age to narrow age classes, however, this study investigates their utility in assigning specimens to broader age classes, such as 10% of life span.

The Relationship Between Crown Height and Age

In order to determine the nature of the relationship between crown height and age, I performed both linear and quadratic regressions of age in months on tooth crown height for m1 (Fig. 2). There is discussion in the literature about whether inverse or classical calibration should be used to estimate an unobservable quantity (e.g. age-at-death, stature) from observable dental or skeletal measurements (Aykroyd *et al.* 1999; Aykroyd *et al.* 1997; Dapson 1980; Konigsberg *et al.* 1998). As the purpose of this study is to adjust the theoretical equation used in the QCHM and not direct predictions from the regression equation, I chose to use inverse calibration because it produces a quadratic equation that is directly comparable to the QCHM equation.

The quadratic regression provides a slightly better fit to the data than the linear regression (Fig. 3). Pike-Tay *et al.* (2000) also found that quadratic regression lines better fit their large sample ($n = 999$) of known-age barren-ground caribou (*Rangifer tarandus*, Linnaeus 1758). In Morrison and Whitridge's (1997) study of known-age barren-ground caribou from the same

sample information	m1
sample size (n)	163
mean age (months)	53.5
standard deviation of age (months)	33.1
mean crown height (mm)	12.9
standard deviation of crown height (mm)	4.3
<i>linear regression</i>	
coefficient of determination (r^2)	0.84
standard error of estimate (months)	13.26
y-intercept	163.6
<i>quadratic regression</i>	
coefficient of determination (r^2)	0.87
standard error of estimate (months)	12.09
y-intercept	143.6

Fig. 3. Summary of regressions of age on crown height.

population as Pike-Tay *et al.*'s (2000) sample, they found that linear equations adequately predicted age, but this discrepancy is possibly due to smaller sample size ($n = 78$). However, Morrison and Whitridge (1997) suggest that the quadratic equation may be "overly precise" for semi-hypsodont caribou, and therefore, the linear equation is sufficient. These results support Spinage's (1971) proposal that teeth will start wearing rapidly, but then the wear rate will decelerate as the occlusal surfaces become smooth. The magnitude of the standard error suggests that it should be possible to estimate age-at-death within approximately ± 1 year. Klein *et al.* (1983) had similar results in their study of the original known-age elk sample.

Assessing Differences in Toothwear Between Males and Females

One potential source of error when estimating age-at-death from tooth wear is a different wear rate between males and females. I investigated this by regressing m1 crown height on age as in Fig. 2, but I calculated separate regression lines for males ($n = 42$) and females ($n = 104$; Fig. 4). When 95% confidence intervals are defined for each line, they overlap for their entire length. This indicates that differences in wear rates between males and females cannot be detected in this sample. This is fortunate because sex usually cannot be identified in fossil *C. elaphus* dental remains.

The lack of differences between the sexes in this sample of elk is supported by studies of caribou and white-tailed deer (*Odocoileus virginianus*, Zimmermann 1780). In Pike-Tay *et al.*'s (2000) large sample of known-age caribou, they found no differences in wear rates between the sexes. In contrast, when Morrison and Whitridge (1997) regressed age on m1 crown height for their sample of caribou, they obtained different linear regression lines for the sexes, although they did not provide statistical results. By examining the data they provided in an

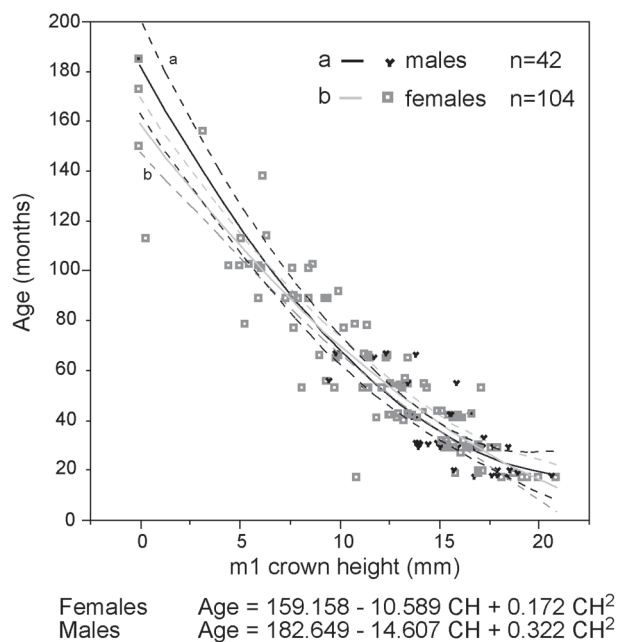


Fig. 4. When quadratic regression equations are calculated for males (a) and females (b) of known-age elk separately, the confidence intervals around the two regression lines overlap, indicating that differences in wear rates between males and females cannot be detected.

Appendix to their paper, I was able to determine that the slopes of the male and female regression lines are different and this difference in wear rates holds even when the confidence intervals around the lines are considered. It is unclear why Pike-Tay (2000) and Morrison and Whitridge's (1997) results differ. Van Deelen *et al.* (2000) studied white-tailed deer ($n = 100$) from Illinois, United States whose age-at-death had been assigned by counting cementum annuli. They measured crown height as the maximum height from the occlusal surface to the stains at the tooth gum line, and they found no differences in degree of wear between m1s of males and females.

Estimating Age-at-Death

I assessed the ability of the regression equations to predict age-at-death by plotting residual values against known ages for the known-age sample of elk (Fig. 5). I calculated the residuals by subtracting the age assigned by the regression equation from the known age for each specimen. A residual of '0' is a perfect estimation, while a positive value shows that age has been underestimated and a negative value shows that age has been overestimated. In Fig. 5, the width of the correct 10% of life span age class (19.2 months and centered on residual = 0) is darkly shaded and the adjacent two 10% of life span

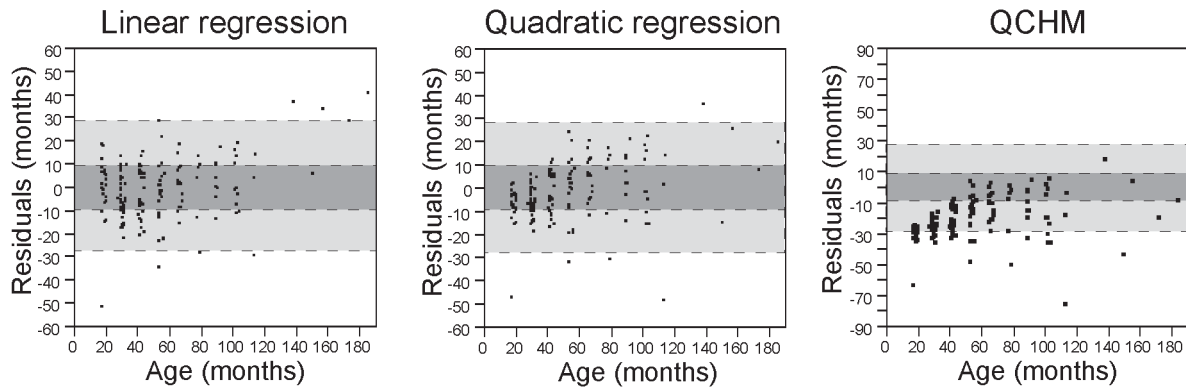


Fig. 5. Known-age plotted against known-age minus the estimated age. Age was estimated using three equations: linear regression, quadratic regression, and the QCHM. Positive values are under-estimates and negative values are over-estimates. The darkly shaded regions approximate ± 9.6 months (one 10% of life span age class), while the lightly shaded regions approximate the adjacent 10% of life span age class.

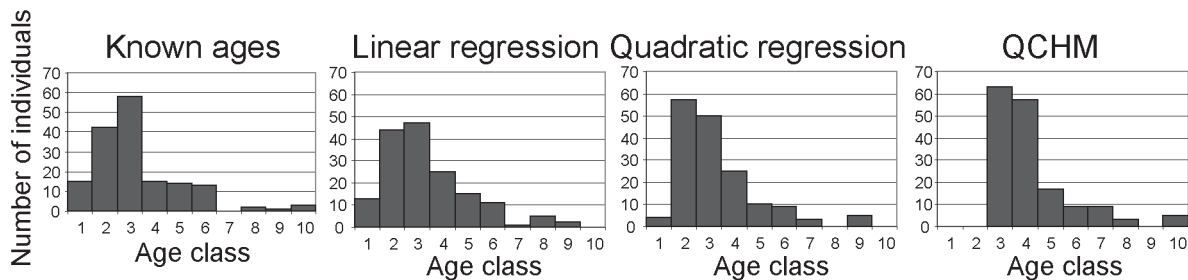


Fig. 6. Histograms comparing the number of individuals in each age class using multiple methods of estimating age. The Kolmogorov-Smirnov test was used to see if the distributions created from the estimation techniques were similar to the known age distribution. The histograms of the linear and quadratic regressions were not significantly different from the known-age histogram, but the QCHM histogram was.

ages classes are lightly shaded. This allows assessment of how well the regression equations estimate age. While there is a large amount of variation present at each age, age is almost always assigned to either the correct age class or to an adjacent one, as is suggested by the standard error of estimates. I created histograms of 10% of life span age classes using the age estimates from the linear and quadratic equations and compared them to a histogram of the known-age specimens (Fig. 6). Neither histogram based on age estimates was statistically different from the known-age histogram using the Kolmogorov-Smirnov test (linear: $K = 0.61$, $p = 0.95$; quadratic: $K = 0.61$, $p = 0.95$).

The regression equations appear to adequately estimate age from crown height in this sample of known-age Rocky Mountain elk. If age estimates were needed only for elk with the same sized teeth, then the regression equations are sufficient. However, faunal analysts need to assign ages in a variety of populations whose teeth and life histories may have different parameters. This is especially

true for *C. elaphus* whose body and tooth size vary across space and through time. The regression equations are only suitable for populations with teeth the size of Rocky Mountain elk, one of the largest subspecies of elk (Geist 1998, 349–350). Enloe and Turner's (in this volume) study of reindeer (*R. tarandus*) confirmed that initial unworn crown heights need to be population specific and therefore that general regression equations are not adequate for estimating age-at-death in species whose tooth size varies. Because of this variation, it is desirable to have a theoretical formula in which initial crown heights and other values can be sample specific.

The Quadratic Crown Height Method

Spinage (1971) first proposed a wear model for using crown heights to estimate age-at-death of hypsodont ungulates. It has been tested with known-age samples of Rocky Mountain elk by Klein and colleagues (Klein,

Allwarden, and Wolf 1983; Klein and Cruz-Uribe 1983; Klein *et al.* 1981), bison (*Bison bison*, Linnaeus 1758) by Gifford-Gonzalez (1991), and barren-ground caribou by Pike-Tay *et al.* (2000). The technique, now known as the Quadratic Crown Height Method (QCHM), employs a set of quadratic formulae based on a variable rate of wear that can be used to predict age-at-death from tooth crown height when the unworn tooth crown height and the age when tooth crown height reaches '0' are known. Unlike the eruption and wear methods, the QCHM is easy to replicate, is objective, and can be utilized with isolated teeth.

Spinage's model (1971; 1972; 1973) is based on the observation that when crown height is plotted against age, wear rate is not linear but actually slows with age. This may be because the opposing occlusal surfaces m1 become smoother, and friction thus decreases, and as m2 and m3 begin to wear, friction on anterior surfaces further decreases (Spinage 1971). The QCHM assumes that when the permanent teeth are worn completely away (crown height equals '0'), the animal dies. Ideally the age when crown height equals '0' would be calculated for each tooth from large known-age samples, but these data are unavailable for most species. Instead, the age of potential ecological longevity must be used as an approximation. Potential ecological longevity is not the mean life span for the species, but the maximum age that a wild individual can reasonably obtain.

The QCHM formulae are (from Klein, Allwarden, and Wolf 1983, 49):

$$\begin{array}{ll} \text{For deciduous teeth:} & \text{AGE} = \text{AGEs} [(CH-CH_0)/CH_0]^2 \\ \text{For permanent teeth:} & \text{AGE} = (\text{AGE}_{\text{pel}} - \text{AGE}_{\text{e}}) [(CH-CH_0)/CH_0]^2 + \text{AGE}_{\text{e}} \end{array}$$

Equations are calculated by substituting the appropriate values for each tooth. AGEs is the age at which the deciduous tooth is shed, AGEe is the age at which the permanent tooth erupts, and AGEpel is the potential ecological longevity of individuals of the species. CH₀ is the mean initial unworn crown height for each tooth type for the sample under study, and CH is the crown height of the specimen for which age is being assigned. Ages are measured in months, and crown heights are measured in millimeters.

The appropriate values for Rocky Mountain elk can be obtained from wildlife biology. The potential ecological longevity for individuals of this population is 192 months (Houston 1982), and m1 erupts through the gum at 6 months (Quimby and Gaab 1957). These two variables appear to be consistent across subspecies (Brown and Chapman 1991; Lowe 1967; Lowe 1969), so they can be used for populations where these ages cannot be directly ascertained. Average unworn tooth crown height needs to be determined for each sample, and for Rocky Mountain elk the measurement is 27.0 mm (Klein and Cruz-Uribe 1984, 49). Tooth crown height is determined for each

specimen. I used these values in the QCHM formula to estimate age-at-death from m1 crown height measurements on the known-age sample of elk.

I tested the ability of the QCHM to adequately estimate age-at-death by plotting the residuals and creating a histogram in the same manner as with the regression estimates. It is apparent that the QCHM overestimates the age-at-death of the specimens, and this bias occurs more frequently for younger individuals (Fig. 5). The histogram of the ages estimated with the QCHM is significantly different from the histogram of known-ages ($K = 3.16$; $p < 0.001$). As formulated, the QCHM did not satisfactorily estimate age-at-death.

Adjustments to the QCHM

Because there is still a need for a flexible equation that can be used to estimate age-at-death in archaeological specimens, I examined the QCHM equation further to determine if it could be adjusted to provide more reliable estimates of age-at-death. Following Pike-Tay *et al.* (2000), I investigated two aspects of the equation: 1) AGEpel, the age of potential longevity, and 2) the degree of curvature of the line created by the equation.

One reason for discrepancies between the theoretical formulae and regression equations is that tooth crown height does not always equal '0' when an animal reaches the age of potential ecological longevity. For m1, teeth can be worn past the crown-root junction before the animal dies (Spinage 1972; Steele, personal observation). The known-age elk sample has one 150-month-old individual with an m1 crown height of '0'; all individuals 173 months and older ($n = 4$) have m1 crown heights of '0', and one 156-month-old individual still has a measurable crown height. In all of these cases, p4, m2, and m3 still have crown remaining. Only one 260-month-old individual has m2 and m3 crown heights of '0'; m1 is completely worn away, but p4 still has a measurable crown. Based on these data, AGEpel should be changed in the QCHM formulae to the age at which the crown height of each tooth type reaches '0', as suggested by Klein *et al.* (1983). This value can be considered the average age of the tooth's potential longevity (AGEtpl). At the moment, the known-age data set has too few older animals to obtain AGEtpl empirically, so I calculated the y-intercept values, i.e. the ages when crown height reaches '0', from the quadratic regressions. For m1, the y-intercept is 163.6 months.

I substituted AGEtpl (163.6 months) for AGEpel in the QCHM's formula for estimating age from m1 crown height. All other values stayed the same. The resulting equation is shown in Fig. 7, along with a plot of the residuals for the estimated ages. The adjusted formula estimates age within the correct 10% of life span age class for the majority of m1s, and all but a few are within

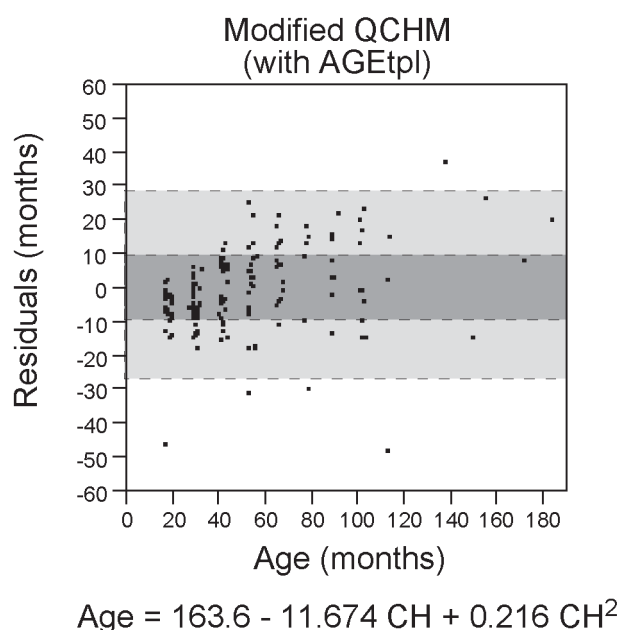


Fig. 7. Known age plotted against known age minus the age estimated for m1s in the known-age elk sample. Age was estimated using a modified QCHM equation where AGEtpl, the y-intercept value of the regression equation, was substituted for AGEpel. The y-intercept value predicts the age at which m1 crown height will reach '0', here 163.6 months. The darkly shaded region approximates ± 9.6 months (one 10% of life span age class), while the lightly shaded regions approximate the adjacent 10% of life span age classes (life span is still considered to equal AGEpel or 192 months)

one adjacent age class; changing AGEpel to AGEtpl greatly increased the reliability of the theoretical formula. Importantly, the histogram constructed with the new theoretical formula is not statistically different from the histogram of the known-age individuals ($K = 0.56$; $p = 0.999$; Fig. 8).

Klein *et al.* (1983) also argued that AGEpel needed to be adjusted in the QCHM to equal the age when crown height reaches '0', but they decided that their known-age sample size was too small to accurately adjust the formula. They had to assume that when tooth crown height equals '0', the animal dies, and therefore the maximum age reached by wild individuals would approximate the age at which tooth crown height equals '0' for any tooth (see also Spinage 1973). The increased sample size presented here allows for more confidence in the adjustments. The more accurate predictions – granted that the predictions are on specimens that provided the adjustment – seem to justify changes to the AGEpel. In their study of known-age caribou, Pike-Tay *et al.* (2000) changed AGEpel to AGEmax, the average maximum life span, which they use for all teeth. This value is the same age in months as

the potential ecological longevity, but they were trying to clarify what that variable represented.

Adjusting the value of animal potential longevity to tooth longevity presents an additional problem for m1. The age of tooth longevity (163.6 months) is lower than the age of animal longevity (192 months), so when estimating age from m1, no specimens will ever be assigned an age above 163.6 months. This means that when creating mortality profiles based on 10% of life span, no m1 specimens will be placed in Age Class 10. If this bias is consistent across all samples, it should not interfere with interpretations of the data.

I also investigated if a quadratic equation provides the most accurate description of the relationship between crown height and age; it is possible that a line with a different shape may better fit the data. By modelling the QCHM equation as the allometric growth curve, it is possible to empirically determine the best exponent for the equation (Steele 2002). The allometric growth equation has been used successfully to model many biological relationships, so it is logical to apply it to toothwear. When I did this for the known-age elk sample, the resulting exponent was 1.99 (95% confidence interval of 1.84–2.14). The exponent of 2 in the QCHM, as traditionally formulated, is right in the middle of the confidence interval. This confirms that a quadratic equation is appropriate for m1.

Comparisons with Other Cervids

I compared the m1 wear rates of three species of cervids: the elk sample studied here (Klein, Allwarden, and Wolf 1983; Klein and Cruz-Urbe 1983; Klein *et al.* 1981; Steele 2002), barren-ground caribou (Morrison and Whitridge 1997), and white-tailed deer (unpublished data collected by C. Wolf). Visual comparisons of these three species supports species-specific adjustments to the QCHM formulae (Fig. 9). Caribou m1s wear more slowly than elk m1s, because caribou have lower crowned teeth than elk but the two species have similar maximum life spans. In their adjustment of the QCHM for caribou, Pike-Tay *et al.* (2000) changed the degree of curvature to reflect this. They found that an exponent of 1.6 provided a better fit to the data than an exponent of two. Caribou and white-tailed deer have similar initial unworn crown heights, but it appears that white-tailed deer teeth initially wear more rapidly than caribou teeth. Further investigation into the white-tailed deer sample will allow the parameters of the QCHM equation to be adjusted to this species.

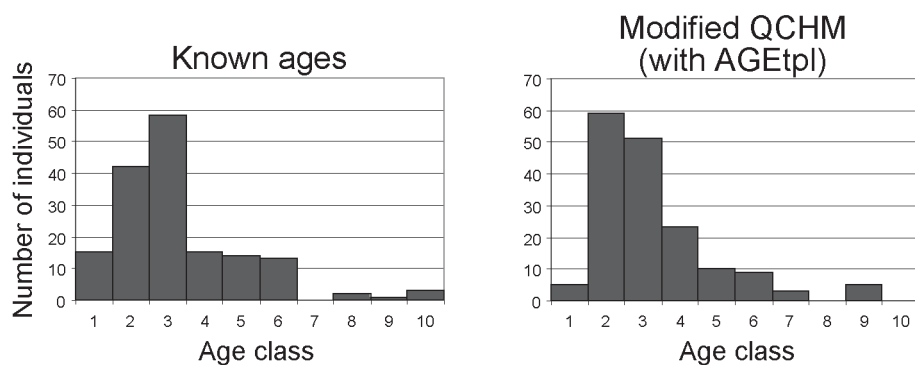


Fig. 8. Histograms comparing the known-age distribution to the distribution of individuals in each age class using the modified QCHM equation for *m1*. When age classes are calculated using AGEtpl, the histogram does not differ significantly from the histogram based on known ages.

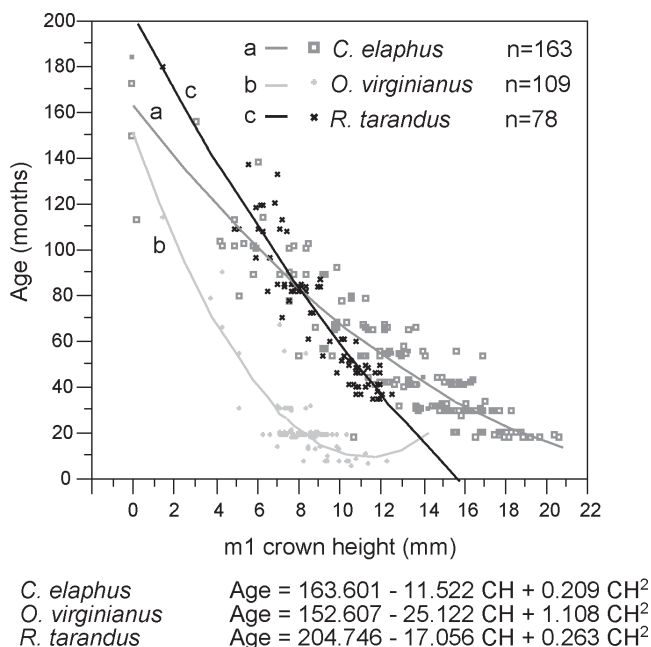


Fig. 9. Quadratic regressions of age in months on *m1* crown height for three species: *C. elaphus* (a; Klein, Allwarden, and Wolf 1983; Klein and Cruz-Urbe 1983; Klein et al. 1981), *O. virginianus* (b; unpublished data collected by C. Wolf), and *R. tarandus* (c; Morrison and Whitridge 1997, 1105–6).

Conclusions

Tooth crown heights provide an objective and replicable way to assess the degree of wear on a tooth. They can be used to estimate age class, but not narrow age estimates. For accurate age-at-death estimations for species whose size changes through time and across space, population-

specific parameters need to be used instead of a generic species-specific regression equation. This can be done with the QCHM, where unworn tooth crown height for each population can be substituted into the equations. However, the appropriateness of the equation for each species under consideration should be investigated using known-age specimens of that species, because as originally formulated, the QCHM did not predict satisfactorily age-at-death for a known-age sample of *C. elaphus*. Using large known-age samples, it is possible to adjust the equations to fit species-specific parameters. The adjusted equations can be applied to archaeological samples with the assumption that what we know about modern animals will also be true of prehistoric animals. Adjustments such as those discussed here are not feasible for extinct species, but parameters from closely related species might be adequate. For more accurate estimations, the age of potential ecological longevity (AGEpel) should be changed to the average age of the tooth's potential longevity (AGEtpl). AGEtpl needs to be empirically determined for each tooth type for each species using known-age samples. For the known-age elk sample, I estimated AGEtpl from the y-intercept of the quadratic regression of crown height on age. Using the adjusted equation, age class is more accurately estimated from tooth crown heights. In addition, using the known-age sample, I was able to confirm that a quadratic equation can be used to describe the relationship between *m1* and age.

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