

RED DEER: THEIR ECOLOGY AND HOW THEY WERE HUNTED BY  
LATE PLEISTOCENE HOMINIDS IN WESTERN EUROPE

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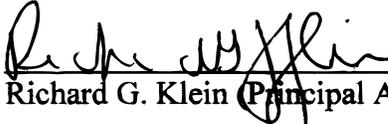
DOCTOR OF PHILOSOPHY

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## **Abstract**

Fossil hominid morphology, archaeology, and genetics indicate that in Europe 30,000-40,000 years ago, anatomically modern humans and their Upper Paleolithic industries replaced Neandertals and their Middle Paleolithic tools. Neandertals had thrived for hundreds of thousands of years, so why were they replaced? One possibility is that modern humans were able to extract more resources from the environment. This dissertation tests this explanation by assessing variation present in ancient hunting practices and investigating the relationship between Late Pleistocene hominids, tool industries, and hunting. I examined the hunting of one species, red deer (*Cervus elaphus*), through time and across space using prey age-at-death as an indicator of hunting strategy. In the process, I evaluated the ability of the Quadratic Crown Height Method to accurately assign age-at-death; compared how well histograms, boxplots, and triangular graphs reconstruct mortality profiles from fossil assemblages; and developed a novel method for statistically comparing samples on triangular graphs.

My results show that Neandertals and modern humans did not differ significantly in their ability to hunt prime-age red deer. None of the mortality distributions from the archaeological samples resemble the distribution constructed from elk killed by wolves in Yellowstone National Park, Wyoming. Like other carnivores, wolves usually take young, old, and infirm prey. Nevertheless, the samples included in this study show a shift in prey age-at-death during the Middle Paleolithic approximately 50 kya. Young adult prey are more abundant in recent assemblages than in more ancient assemblages. Over 25 archaeological samples from western Europe contribute to these conclusions, making this

dissertation the most comprehensive study of Pleistocene hunting to date. More well-dated samples are needed, however, to confirm these results.

Because red deer skeletal and tooth size fluctuated across my samples, I investigated the relationship between climate and *C. elaphus* size to determine if body size could indicate paleoclimates. In modern North American specimens, distal metatarsal breadth has a good relationship with climate, and tooth breadth has a similar but weaker relationship. The modern European data do not relate clearly to climate. Fossil red deer are larger during glacials than interglacials, but additional data are needed to better define patterns.

*to my parents  
Gary and Nancy Steele  
and  
my grandmother  
Helen Steele*

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## Table of Contents

|  |      |
|--|------|
| <b>Abstract</b> .....  | iv   |
| <b>Acknowledgements</b> .....  | vii  |
| <b>Table of Contents</b> .....   | x    |
| <b>List of Tables</b> .....  | xv   |
| <b>List of Illustrations</b> .....   | xvii |
| <b>Chapter 1: Introduction, background, and research objectives</b> .....        | 1    |
| The Neandertals .....  | 2    |
| Modern human origins .....   | 4    |
| <i>The evidence for replacement</i> .....  | 6    |
| <i>Evidence against a complete replacement</i> .....                             | 11   |
| <i>The origins of modern behavior</i> .....                                      | 12   |
| How did this replacement occur?.....   | 14   |
| <i>Evidence for and against differences in resource extraction</i> .....         | 14   |
| <i>Evidence for and against differences in population density and size</i> ..... | 22   |
| This study .....   | 25   |
| <i>Prey age-at-death as an indicator of hunting strategies</i> .....             | 26   |
| <i>Objectives of this study</i> .....  | 28   |
| <b>Chapter 2: <i>C. elaphus</i> ecology</b> .....                                | 30   |
| Evolutionary history.....  | 31   |
| Diet and habitat preferences .....   | 34   |
| Social behavior.....   | 35   |
| <i>C. elaphus</i> body size variation.....                                       | 38   |
| Ethnographic examples of methods used to hunt <i>C. elaphus</i> .....            | 39   |

|   |    |
|---|----|
| <b>Chapter 3: Samples and data collection</b> .....                         | 41 |
| Research samples .....  | 41 |
| <i>Modern samples</i> .....   | 41 |
| <i>Fossil samples</i> .....   | 43 |
| Data collection .....   | 44 |
| <i>Metric data</i> .....  | 44 |
| <i>Non-metric data</i> .....  | 46 |
| Analyses.....   | 48 |
| <b>Chapter 4: Methods of age determination</b> .....                        | 50 |
| Teeth as indicators of age .....  | 50 |
| Age determination by eruption and wear .....                                | 52 |
| The Quadratic Crown Height Method.....                                      | 58 |
| <i>Spinage's model</i> .....  | 58 |
| <i>Testing the model with known-age elk</i> .....                           | 60 |
| <i>Additional investigations into the QCHM</i> .....                        | 62 |
| <i>Ways of measuring tooth crown height</i> .....                           | 64 |
| Expanded known-age sample .....   | 66 |
| <i>Regression analysis</i> .....  | 66 |
| <i>Potential differences in wear rates between the sexes</i> .....          | 68 |
| <i>Further testing of the QCHM with known-age elk</i> .....                 | 70 |
| <i>Adjusting the QCHM formulas</i> .....                                    | 72 |
| Summary and conclusions .....   | 79 |
| <b>Chapter 5: Methods of mortality profile construction</b> .....           | 81 |
| Using mortality profiles to interpret ancient behavior .....                | 81 |
| <i>Model age structures</i> .....   | 81 |
| <i>Interpreting age structures</i> .....                                    | 83 |
| <i>Differences between human and non-human hunting</i> .....                | 83 |
| <i>Assumptions that are fundamental to mortality profile analysis</i> ..... | 85 |
| <i>Pre- and post-depositional processes</i> .....                           | 88 |
| Samples with known age structures .....                                     | 90 |

|   |     |
|---|-----|
| Histograms .....  | 91  |
| <i>The human and wolf-killed samples</i> .....  | 93  |
| <i>Advantages of histograms</i> .....   | 94  |
| <i>Disadvantages of histograms</i> .....  | 95  |
| Boxplots.....   | 96  |
| <i>The human and wolf-killed samples</i> .....  | 97  |
| <i>Advantages of boxplots</i> .....   | 97  |
| <i>Disadvantages of boxplots</i> .....  | 98  |
| Triangular graphs .....   | 100 |
| <i>The human and wolf-killed samples</i> .....  | 101 |
| <i>Advantages of triangular graphs</i> .....  | 102 |
| <i>Disadvantages of triangular graphs</i> .....                                       | 103 |
| Modified triangular graphs .....  | 103 |
| <i>The human and wolf-killed samples</i> .....  | 106 |
| <i>Advantages of modified triangular graphs</i> .....                                 | 106 |
| <i>Disadvantages of modified triangular graphs</i> .....                              | 107 |
| Summary and conclusions .....   | 107 |
| <b>Chapter 6: Size variation in modern and fossil <i>Cervus elaphus</i></b> .....     | 110 |
| Previous research on size variation in <i>C. elaphus</i> .....                        | 110 |
| Modern samples and climatic parameters .....  | 113 |
| Fossil samples and climatic parameters .....  | 114 |
| Modern <i>C. elaphus</i> tooth breadth and climate.....                               | 115 |
| Fossil <i>C. elaphus</i> tooth breadth and climate.....                               | 117 |
| <i>All of western Europe through time</i> .....                                       | 117 |
| <i>The Mediterranean coast, northern Spain and northern Europe through time</i> ..... | 119 |
| <i>During each Oxygen Isotope Stage</i> .....   | 120 |
| Modern <i>C. elaphus</i> metatarsal breadth and climate.....                          | 121 |
| Fossil <i>C. elaphus</i> metacarpal breadth and climate.....                          | 124 |
| Discussion.....   | 125 |
| Summary and conclusions .....   | 127 |

|   |     |
|---|-----|
| <b>Chapter 7: Mortality profiles in paleolithic western Europe</b> .....          | 130 |
| First analysis: Samples with more than twenty-five individuals .....              | 131 |
| <i>Sample definition</i> .....  | 131 |
| <i>Histograms</i> .....   | 132 |
| <i>Boxplots</i> .....   | 135 |
| <i>Modified triangular graphs</i> .....   | 137 |
| <i>Summary</i> .....  | 139 |
| Second analysis: Grouped samples .....  | 140 |
| <i>Sample definition</i> .....  | 140 |
| <i>Histograms</i> .....   | 141 |
| <i>Boxplots</i> .....   | 142 |
| <i>Modified triangular graphs</i> .....   | 143 |
| <i>Summary</i> .....  | 144 |
| Third analysis: Many samples .....  | 145 |
| <i>Boxplots</i> .....   | 145 |
| <i>Bivariate plots</i> .....  | 147 |
| Discussion.....   | 150 |
| <i>Variation in the number of juveniles</i> .....                                 | 150 |
| <i>Hunting during the Upper Paleolithic</i> .....                                 | 151 |
| <i>Comparison of the Middle to the Upper Paleolithic</i> .....                    | 154 |
| Summary and conclusions .....   | 157 |
| <b>Chapter 8: Summary and conclusions</b> .....                                   | 158 |
| Significance of this research.....  | 158 |
| Future research directions.....   | 161 |
| Conclusions.....  | 164 |
| <b>Appendix A Tables</b> .....  | 166 |
| <b>Appendix B Illustrations</b> .....   | 192 |
| <b>Appendix C Archaeological sites that provided samples for this study</b> ..... | 234 |

|  |     |
|--|-----|
| <b>Appendix D Data on each layer of each site included in this study</b> ..... | 240 |
| <b>Bibliography</b> .....  | 248 |

## List of Tables

|   |     |
|---|-----|
| Table 3.1 Interobserver measurement error for tooth crown height and breadth .....  | 167 |
| Table 3.2. Eruption and wear stages recorded in this study .....  | 167 |
| Table 4.1 Summary of elk specimens with known ages .....  | 168 |
| Table 4.2 Summary of regressions of age on crown height in the known-age elk<br>sample .....  | 169 |
| Table 4.3 Summary of regressions of age on crown height the known-age white-tailed<br>deer sample.....  | 169 |
| Table 4.4 Values used in the Quadratic Crown Height Method.....   | 170 |
| Table 4.5 Comparison of regression and theoretical equations .....  | 170 |
| Table 5.1 Model life table .....  | 171 |
| Table 5.2 Data used to compare methods of reconstructing age distributions .....  | 172 |
| Table 5.3 Data used to describe the modified triangular graph.....  | 173 |
| Table 5.4 Properties of the four methods for summarizing mortality profiles discussed<br>in this study .....  | 174 |
| Table 6.1 Modern specimens used in the study of size variation in <i>C. elaphus</i> .....   | 175 |
| Table 6.2 Climate data for the locations of the modern comparative specimens used<br>to investigate the relationship between <i>C. elaphus</i> size and climate.....        | 176 |
| Table 6.3 The relationship between M <sub>1</sub> tooth breadth and climate .....   | 178 |
| Table 6.4 Data on Late Pleistocene red deer M <sub>1</sub> breadths for studying size variation ...   | 179 |
| Table 6.5 Comparisons of M <sub>1</sub> breadth by Oxygen Isotope Stage.....  | 181 |
| Table 6.6 The relationship between metatarsal breadth and climate .....   | 182 |
| Table 6.7 Data on Late Pleistocene red deer metacarpal breadths for studying the<br>relationship between size and climate .....   | 183 |
| Table 7.1 First analysis: Individual samples with more than twenty-five measurable<br>dP <sub>4s</sub> and M <sub>1s</sub> .....  | 184 |
| Table 7.2 First analysis: Results of the Kolmogorov-Smirnov test for individual<br>samples with more than twenty-five measurable dP <sub>4s</sub> and M <sub>1s</sub> ..... | 185 |

|  |     |
|--|-----|
| Table 7.3 First analysis: Summary statistics for the modified triangular graphs for the individual samples. ....   | 186 |
| Table 7.4 Second analysis: Grouped samples with more than twenty-five measurable $dP_{4s}$ and $M_{1s}$ .....  | 187 |
| Table 7.5 Second analysis: Results of the Kolmogorov-Smirnov test for grouped samples with more than twenty-five measurable $dP_{4s}$ and $M_{1s}$ ..... | 188 |
| Table 7.6 Second analysis: Summary statistics for the modified triangular graph for the grouped samples .....  | 189 |
| Table 7.7 Third analysis: Grouped samples with ten or more measurable $M_1$ crown heights.....   | 190 |
| Table 7.8 Third analysis: Individual samples with ten or more measurable $M_1$ crown heights.....  | 191 |

## List of Illustrations

|   |     |
|---|-----|
| Figure 1.1 Later Pleistocene climatic and cultural stratigraphy .....   | 193 |
| Figure 2.1 Global distribution of <i>C. elaphus</i> .....   | 194 |
| Figure 3.1 Map of fossil sites included in this study .....   | 195 |
| Figure 3.2 Dental measurements used in this study.....  | 196 |
| Figure 3.3 <i>C. elaphus</i> tooth nomenclature.....  | 197 |
| Figure 3.4 Postcranial measurements used in this study.....   | 198 |
| Figure 4.1 Regression of age on crown height for elk .....  | 199 |
| Figure 4.2 Regression of age on crown height for white-tailed deer .....  | 200 |
| Figure 4.3 Comparison of wear rates between elk, white-tailed deer, and reindeer.....   | 201 |
| Figure 4.4 Residuals of age predictions using the regression equations.....   | 202 |
| Figure 4.5 Differences in wear rates between male and female elk .....  | 204 |
| Figure 4.6 Residuals of ages predicted using the Quadratic Crown Height Method.....   | 205 |
| Figure 4.7 Comparisons of the two age estimation methods.....   | 206 |
| Figure 4.8 Adjusted method for estimating age from M <sub>1</sub> s .....   | 207 |
| Figure 5.1 Model age structures.....  | 208 |
| Figure 5.2 Differences in prey age-at-death between human and wolf hunters .....  | 208 |
| Figure 5.3 First method: Histograms .....   | 209 |
| Figure 5.4 Second method: Boxplots .....  | 210 |
| Figure 5.5 Third method: Triangular graphs .....  | 211 |
| Figure 5.6 Modified triangular graphs .....   | 212 |
| Figure 5.7 The effects of sample size in modified triangular graphs.....  | 213 |
| Figure 6.1 Sexual dimorphism in <i>C. elaphus</i> .....   | 214 |
| Figure 6.2 The relationship between M <sub>1</sub> tooth breadth and climatic variables in<br>modern <i>C. elaphus</i> .....                    | 215 |
| Figure 6.3 The relationship between M <sub>1</sub> tooth breadth and climatic variables in<br>modern <i>C. elaphus</i> from North America ..... | 216 |

|  |     |
|--|-----|
| Figure 6.4 The relationship between M <sub>1</sub> tooth breadth and climatic variables in modern <i>C. elaphus</i> from western Europe .....  | 217 |
| Figure 6.5 The relationship between tooth breadth and glacial/interglacial climates in fossil red deer .....                                   | 218 |
| Figure 6.6 The relationship between fossil red deer tooth breadth and glacial/interglacial climates in various regions of western Europe ..... | 219 |
| Figure 6.7 Variation in fossil red deer M <sub>1</sub> breadth during different Oxygen Isotope Stages .....                                    | 220 |
| Figure 6.8 The relationship between distal metatarsal breadth and climatic variables in modern <i>C. elaphus</i> from North America .....      | 221 |
| Figure 6.9 Variation in fossil red deer distal metacarpal breadth during different Oxygen Isotope Stages.....                                  | 222 |
| Figure 7.1 First analysis: Histograms of individual samples.....   | 223 |
| Figure 7.2 First analysis: Boxplots of individual samples .....  | 224 |
| Figure 7.3 First analysis: Boxplots of individual samples .....  | 225 |
| Figure 7.4 First analysis: Modified triangular graphs of individual samples.....   | 226 |
| Figure 7.5 Second analysis: Histograms of grouped samples .....  | 227 |
| Figure 7.6 Second analysis: Boxplots of grouped samples .....  | 228 |
| Figure 7.7 Second analysis: Boxplots of grouped samples .....  | 229 |
| Figure 7.8 Second analysis: Modified triangular graphs of grouped samples.....   | 230 |
| Figure 7.9 Third analysis: Boxplots of small grouped samples.....  | 231 |
| Figure 7.10 Third analysis: Bivariate plot of median crown height by time.....   | 232 |
| Figure 7.11 Third analysis: Bivariate plots of median crown height by environment....  | 233 |

## **Chapter 1: Introduction, background, and research objectives**

Fossil hominid morphology, archaeology, and genetics all indicate that anatomically and behaviorally modern humans (*Homo sapiens sapiens*) originated about 50,000 years ago (kya), most likely in East Africa. These modern humans spread out of Africa, populated western Asia, Europe, and the Far East, and eventually reached Australia and the Americas. In this range expansion, they appear to have replaced the archaic people who preceded them. The evidence for replacement is clearest in Europe, where the paleoanthropological record documents that 30-40 kya modern humans and their Upper Paleolithic industries replaced the archaic people of Eurasia, the Neandertals (*Homo neanderthalensis* or *H. sapiens neanderthalensis*), and their Middle Paleolithic industries (as summarized in Klein, 1999; Mellars, 1996; Stringer & Gamble, 1993). Excavations in western Europe have been ongoing for the past 150 years, providing a rich fossil and archaeological record, including genetic sequences from ancient Neandertals, that allows the exploration of the fate of the Neandertals.

The Neandertals persisted through many climatic changes for hundreds of thousands of years, yet they were replaced by modern humans in a few thousand years. Although the fate of the Neandertals has captured the attention of paleoanthropologists for generations, researchers still are trying to determine how and why neandertals were replaced. One hypothesis is that modern humans were able to acquire more resources from the environment than the Neandertals. More calories could have allowed the modern humans to have increased fertility and survivorship (Kaplan & Hill, 1992), and

therefore, increased population sizes or densities, which in turn could have led to the continuation of modern humans and not Neandertals. The goal of this research is to examine the similarities and differences in the hunting strategies of Neandertals and early modern humans in an effort to understand how they extracted resources from their environment. This study asks the question: Were modern humans better big game hunters than Neandertals? From this research, I hope to contribute data addressing why Neandertals ultimately went extinct and, therefore, provide a better understanding of the pattern of human evolution.

### **The Neandertals**

Since the first recognition of Neandertals in 1856, much of the research into human prehistory has focused on the fate of these ancient people. Neandertals are a distinct group of archaic humans that inhabited Europe and western Asia from approximately Oxygen Isotope Stage 6 (OIS; Figure 1.1) until 30-40 kya. Their remains are documented throughout western Europe; in southern central Europe; in the Caucasus Mountains and Crimea of southern European Russia; in western Asia in what is today Iran, Iraq, Israel, Syria, and Turkey; and as far east as Uzbekistan (Klein, 1999).

The earliest well-documented hominids found in western Europe are specimens of *H. antecessor* from the Gran Dolina, Atapuerca, Spain and are from just over 780 kya (Falgueres *et al.*, 1999). However, Europe was continuously occupied by hominids only after about 500 kya, as shown by the marked increase in well-supported sites after this time (Roebroeks, 2001). From 500 kya until their demise 30-40 kya, these archaic humans in Europe accumulated morphological features that distinguish them from all other Old World populations. Hublin (1998) formulated this trend into the “accretion

model” where the Neandertal’s unique morphology resulted from an accretion process driven by population crashes and expansions caused by Pleistocene glacial cycles. By 74 kya, the Neandertals acquired their characteristic “classic” skeletal morphology: long, low brain cases that end with a bun on the back of the head; receding foreheads with large browridges and protruding faces; mandibles lacking chins with large spaces behind the third molars; and short, robust limb bones. These “classic” specimens were the first described and are the most abundant in the fossil record, so the name Neandertal primarily applies to specimens from OIS 3-5. European hominid fossils pre-dating OIS 6 are commonly considered *H. heidelbergensis*, but their taxonomic status really remains unresolved (Hublin, 1998; Klein, 1999).

Throughout their geographic range, Neandertals most frequently are associated with the Mousterian stone tool industry, which defines the Middle Paleolithic of Europe, the Near East, and northern Africa. The Mousterian likely evolved out of local Acheulean industries during OIS 6 or 7 (130-244 kya, Klein, 1999:408). The Mousterian contains a variety of tools, such as points, side scrapers, denticulates, backed knives, and used flakes, and it is distinguished from the preceding Acheulean by lacking large hand axes. Microscopic and chemical analyses of lithic artifacts from the Near East show that some of these tools were hafted and that they were used on wood, flesh, bone, and hide (Boëda *et al.*, 1996; Shea, 1989). While Neandertals were fully capable flint-knappers, their tools were highly variable and are difficult to classify into discrete categories. However, some unique variations existed during the Middle Paleolithic, such as the stemmed points that distinguish the Aterian (e.g. Tixier, 1967). Within the Mousterian, there is little evidence

that Neandertals regularly worked antler, bone, or ivory into formal tools or art items, such as figurines, pendants, or beads.

There is no evidence that Neandertals had bows and arrows or spear throwers, but three 400-ky-old wooden spears from Germany provide some evidence of ancient hunting technology and wood-working (Thieme, 1997). All three spears have a similar shape of being approximately 2 m long, having maximum weight at the end sharpened to a point, and being long and tapered at the opposite end. This morphology resembles modern javelins, and therefore Thieme (1997) concludes that the spears were for throwing and not thrusting. Polish and mastic residue on stone tool surfaces and impact fractures on stone tool tips suggest that Middle Paleolithic people living in the Near East mounted points, usually made with the Levallois technique, onto shafts to make thrusting spears (Shea, 1989; Shea, 1998; Shea *et al.*, 2001). These thrusting spears would have been used at a close range, perhaps after an animal had been captured in a pit-trap or surround, but the wound caused by the stone point likely would have disabled the prey adequately.

### **Modern human origins**

During much of the mid-20<sup>th</sup> century, paleoanthropologists debated the general pattern of modern human origins, and consequently the relationship of Neandertals to modern humans. Discussion centered on two alternate hypotheses for the overall pattern of human evolution: Multiregional Evolution and Out of Africa. The Multiregional Evolution model postulates that after an initial expansion out of Africa 1 to 1.8 million years ago, *H. erectus* colonized eastern Asia and eventually Europe. Once in place, these populations remained one species through gene flow and each eventually evolved into

behaviorally and morphologically fully modern *H. sapiens sapiens*, although not necessarily simultaneously (e.g. Wolpoff, 1989; Wolpoff *et al.*, 2000; Wolpoff *et al.*, 1984). In this model, Neandertals are designated as a subspecies, *H. sapiens neanderthalensis*, and as such they either evolved *in situ* into modern humans or were capable of interbreeding with fully modern humans arriving into Europe, although they did not necessarily do so (Wolpoff *et al.*, 2000). The proponents of this model suggest that Neandertals and modern humans shared many skeletal features and were part of one population that continued through time in western Europe (Fruyer, 1992), central Europe (Wolpoff *et al.*, 2001), and Israel (Kramer *et al.*, 2001). Under this model, Neandertals would be capable of the same behaviors that are characteristic of modern humans.

The Out of Africa model also begins with *H. erectus* leaving Africa 1 to 1.8 million years ago, but in this model, fully modern *H. sapiens sapiens* did not originate until 50-60 kya and only in Africa. They subsequently spread out of Africa and into Asia and Europe, replacing the archaic hominids already living in these areas (e.g. Klein, 1999; Klein, 2000a; Lahr & Foley, 1998; Stringer & Andrews, 1988; Stringer & Gamble, 1993). The Out of Africa Model was formulated from fossil hominid (Bräuer, 1989; Rightmire, 1989) and archaeological data (Klein, 1992), but genetic studies greatly advanced the idea (Cann *et al.*, 1987; Vigilant *et al.*, 1991). The genetic, fossil, and archaeological evidence for this model is clearest in western Europe, where data strongly suggest that modern humans replaced the Neandertals by 30-40 kya. A complete replacement means that Neandertals did not contribute significantly to the modern human gene pool, and thus they would be considered a separate species, *H. neanderthalensis*. Some intermediate models do allow for higher levels of interbreeding (Bräuer, 1989).

Duarte *et al.* (1999) recently suggested that the remains of a 4-year-old child buried 24.5 kya in what is now Portugal show evidence of hybridization because of their mosaic of supposed-Neandertal and modern skeletal features, but others have questioned the interpretation of the remains (Tattersal & Schwartz, 1999). The Out of Africa model has gained the support of most paleoanthropologists, and some form of it is likely the most accurate reconstruction of modern human origins.

### ***The evidence for replacement***

#### *Morphology*

In Europe, hominid fossil morphology abruptly changes from Neandertal to anatomically modern humans 30-40 kya, indicating a replacement of populations and not a gradual transition of Neandertal to modern morphology. Modern human crania look quite different from Neandertal crania, because they have vertical foreheads; rounded braincases; small to absent browridges; faces that are tucked under their braincases; no spaces behind the mandible's third molar; and prominent chins (Klein, 1999). Fossil remains older than 30-40 kya have Neandertal characteristics, while those after 30-40 kya resemble modern humans, indicating a population replacement. Frayer (1992) identified cranial features that appeared in both Neandertals and modern humans in Europe, and he used these features to argue for population continuity. When Lahr (1994) studied all Old World populations, she found that cranial features used to argue for continuity frequently occur, often in high incidences, outside of the regions where they are expected, and therefore the continuity of features described by Frayer (1992) could be due to chance. Before these features can be used to determine phylogeny, researchers must be sure that

they are homologous between Neandertals and modern humans (Lieberman *et al.*, 2000) and that they are genetically and not functionally determined (Moran & Chamberlain, 1997).

Limb-proportions provide strong support for the replacement of Neandertals by modern humans. Neandertals, who lived in glacial Europe, had body proportions that are characteristic of recent modern humans living in cold environments. The modern humans that replaced the Neandertal had significantly different limb proportions, ones that are characteristic of people living in warm environments, providing an indication of the early modern humans' African origin (Holliday, 1997; Trinkaus, 1981).

The human paleontological record shows that the transition from archaic to modern morphology is visible only in Africa, and fossils with features unique to modern humans appear approximately 127 kya (Bräuer, 1989; Rightmire, 1989). Rightmire (1976) recognized the Middle and Late Pleistocene hominid fossils from Africa as being distinct from the Neandertals, and Hublin (1998) documented a gradual accumulation in Europe of unique Neandertal cranial features that distinguish the Neandertals from their African contemporaries and modern humans. Hominid fossils document the African origin of anatomically modern humans, and fully modern human morphology does not appear outside of Africa until after 50 kya.

### *Archaeology*

By at least 32-35 kya, the stone tools of western Europe exhibit a distinct change (Mellars, 1999), and a new industry called the Aurignacian appears, which marks the beginning of the Upper Paleolithic in Europe. Mellars (1996:393-400) characterizes the Aurignacian as having the following: more sophisticated technology for making blades (=

flakes that are twice as long as they are wide); new forms of stone tools that can be classified into types easily, including end-scrapers and burins; bone, antler, and ivory fashioned into tools, including the Aurignacian “index fossil” – split-base points; personal ornaments, art, and decoration; and expanded distribution and trading networks. Early Upper Paleolithic people made a much higher percentage of their stone tools on exotic raw materials, while Neandertals primarily used local sources to make their Mousterian industry (Mellars, 1996). Whether the stone reached the site through the movements of the people who lived in the site or through trade is not yet known, but the evidence indicates that Middle and Upper Paleolithic people differed in their settlement patterns, social organization, or both (Klein, 1999:449).

Only about a dozen of the earliest Aurignacian assemblages in Europe have yielded human fossil remains, but where they are found, the fossils show traits that are undeniably characteristic of modern human morphology (Churchill & Smith, 2000; Gambier, 1989). Hoffecker (1999) also concluded that the earliest Upper Paleolithic in eastern Europe, which was different from the Aurignacian of western Europe, is associated only with modern humans. Neandertals have been associated with early Upper Paleolithic industries in Vindija Cave, Croatia (Karavanic & Smith, 1998), but d’Errico *et al.* (1998) question the integrity of this assemblage. The weight of the evidence suggests that anatomically modern humans are associated with the Aurignacian.

Most archaeologists support the model that modern humans and the Aurignacian dispersed concurrently across Europe, providing evidence of replacement of Neandertals by modern humans instead of an *in situ* evolution of Neandertals into modern humans. Mellars (1996:405-411) offers these lines of evidence for the colonization of one

population: the Aurignacian industry is remarkably uniform across western Europe and very distinct from the preceding Mousterian industries; there is scant evidence for an *in situ* evolution of the industry; and the industry shows unique inventions in stone, bone, and antler working and symbolism that are unlikely to be independent inventions. While the chronology is not fully worked out, the Aurignacian industry appeared in temporal clines across Europe (Bar-Yosef, 2000; Bocquet-Appel & Demars, 2000a; Mellars, 1996:410; Zilhão & d'Errico, 1999). Bar-Yosef (see also Ambrose, 1998; 2000; Hoffecker, 1999; Kuhn *et al.*, 2001) documented an east-west trend in the earliest appearance of Upper Paleolithic industries which began in east Africa approximately 50 kya, exited northeastern Africa 47-45 kya, entered the region east of the Mediterranean 38-45 kya, moved north into eastern and central Europe 40 kya where they diversified, and finally appeared as the characteristic Aurignacian in western Europe 36-41 kya. While most researchers agree with this characterization, some scholars find evidence for continuity between Mousterian and Aurignacian stone tools and a lack of uniformity in the earliest Aurignacian, indicating *in situ* evolution of the Aurignacian from the local Mousterian (Cabrera *et al.*, 2000).

### *Genetics*

The genetic evidence that emerged in the past two decades provides the strongest evidence for the replacement of the Neandertals in western Europe and an Out of Africa model for modern human origins. Although analyses of mitochondrial DNA sequences supplied the earliest clear evidence of a recent common origin in Africa for all living humans (Cann *et al.*, 1987; Vigilant *et al.*, 1991), more recent studies of Y chromosome sequences provided the most concordant evidence. Y chromosome variation shows that

the genetic diversity in people living outside of Africa is a subset of the diversity within Africa (Underhill *et al.*, 2001; Underhill *et al.*, 2000), and a sample of 43 Y chromosome sequences coalesce about 59 kya (with a 95% confidence interval of 40-140 kya), suggesting that Y chromosomes in living men share a common ancestor that lived at this time (Thomson *et al.*, 2000). Estimates of the ages of certain Y chromosome mutations suggest that people migrated out of Africa approximately 47 kya (with a 95% confidence interval of 35-89 kya; Thomson *et al.*, 2000). Although the confidence intervals around these dates are large, it is important that they are in tens of thousands of years and not hundreds of thousands of years. Further sampling of 12,000 Y chromosomes focusing on East Asia show no evidence of contributions from archaic humans in living men, disputing Multiregional Evolution in the area where the morphological evidence is strongest (Ke *et al.*, 2001). Recent mitochondrial DNA data show a concordant pattern of high genetic diversity within Africa, coalesce about 52 ( $\pm 27.5$ ) kya, and show an expansion out of Africa approximately 38.5 kya (Ingman *et al.*, 2000). Autosomal DNA evidence provides further support by showing a low level of sequence divergence, particularly outside of Africa, which suggests a recent origin of all living people and no significant genetic contributions from pre-modern-human populations (Knight *et al.*, 1996; Tishkoff *et al.*, 1996).

In addition, short sequences of ancient mitochondrial DNA have been extracted from multiple Neandertal fossils (Krings *et al.*, 2000; Krings *et al.*, 1999; Krings *et al.*, 1997; Ovchinnikov *et al.*, 2000). These sequences are similar to each other and different from all living humans, and they coalesce with modern lineages about 465 kya, with a 95% confidence interval of 317-741 kya (Krings *et al.*, 1999). While these data do not

necessarily indicate a complete replacement (Nordborg, 1998), they suggest that Neandertals and modern humans were potentially two separate lineages during the Middle Pleistocene.

### ***Evidence against a complete replacement***

One complication to the Out of Africa model is evidence that Neandertals performed some of the behaviors that are characteristic of Upper Paleolithic people (Klein, 1995; Klein, 1999; Klein, 2000a). A handful of assemblages exist in central and southwestern France and northern Spain that contain typical Mousterian tools, side-scrapers, notches, and denticulates, but they also have unique knives, end-scrapers, and burins that are characteristic of the Aurignacian (Harrold, 1989). The assemblages are characterized by curved, steeply backed knives called Châtelperron points, so they are collectively known as the Châtelperronian industry. One assemblage, Grotte du Renne, Arcy-sur-Cure in north-central France, also contains worked bone and ivory and personal ornaments of pierced animal teeth and ivory rings (d'Errico *et al.*, 1998; Hublin *et al.*, 1996). These features make the Châtelperronian industry an Upper Paleolithic industry, but in two sites, Saint-Césaire and Grotte du Renne, the assemblages have been firmly linked to Neandertal remains (Hublin *et al.*, 1996; Lévêque & Vandermeersch, 1980). The Saint-Césaire assemblage has been dated using thermoluminescence to  $36.3 \pm 2.7$  kya, and the Grotte du Renne was radiocarbon dated to approximately 33.5 kya, which makes these Neandertals among the youngest known, acknowledging that the radiocarbon date is uncalibrated and probably a minimum age (Mercier *et al.*, 1993). These dates overlap with the earliest Aurignacian in the area (Zilhão & d'Errico, 1999), and researchers are still trying to determine if the earliest Châtelperronian industries pre-

date the earliest Aurignacian in the same areas (d'Errico *et al.*, 1998; Mellars, 1999; Mellars, 2000; Zilhão & d'Errico, 1999). Similar industries with unique tools, but no ornaments, have been identified in Italy as the Uluzzian and in eastern Europe as the Szeletian, but questions about their significance remain (Mellars, 1989; Mellars, 1996).

Currently, there are two hypotheses to explain the early Upper Paleolithic assemblages that were manufactured by Neanderthals (d'Errico *et al.*, 1998). The Neandertals were either in the process of their own Middle to Upper Paleolithic transition when modern humans arrived (d'Errico *et al.*, 1998; Rigaud, 2000) or copied the behaviors from modern humans in a form of acculturation (Mellars, 1999; Mellars, 2000; Stringer & Gamble, 1993). Another possibility is that the Neandertals developed the Châtelperronian independently, but in response to the arriving modern humans. This is an active area of current research, and resolving the issue is dependent on refining the chronology of the region. Given that the Châtelperronian and Aurignacian potentially co-occur for only a few thousand years and the margins of error around all the dating techniques, this will be a difficult task. Once the sequence of events is adequately determined, researchers may meaningfully ask what these Upper Paleolithic-like behaviors seen in Neandertals indicate about Neandertal cognitive ability and social systems.

### ***The origins of modern behavior***

Assessing Neandertal cognitive capabilities is critical for understanding the origins of modern human behavior. While most paleoanthropologists agree that anatomically and behaviorally modern humans left Africa approximately 50 kya, recent research has focused on the events preceding 50 kya in Africa that lead to this geographic

expansion. Two alternative scenarios are being discussed. The first, described most fully by McBrearty and Brooks (see also Deacon, 1989; Henshilwood *et al.*, 2001; Henshilwood *et al.*, 2002; 2000) argues that modern behaviors appeared incrementally during the Middle Stone Age (MSA, the African equivalent of the Middle Paleolithic) from the need to have novel solutions to problems resulting from population growth and environmental deterioration, and therefore McBrearty and Brooks extend the roots for modern human behavior back to the earliest appearance of the MSA, about 250-300 kya. The features that they identify as indicative of modern human behavior include (McBrearty & Brooks, 2000:530): blade manufacture, use of grindstones, pigment processing, stone points, consumption of shellfish, long distance exchange, fishing, working bone into tools, manufacturing barbed points, mining, incised pieces, microliths, beads, and images. These new behaviors continued to lead to new technologies and increased long-distance exchange, which in turn resulted in increased survivorship and population growth. One difficulty with this model is that the Middle Paleolithic Neandertals were also doing many of the “modern” behaviors that McBrearty and Brooks identified in the MSA (d'Errico *et al.*, 2002; d'Errico & Soressi, 2002), and some Neandertals were able to make the Upper Paleolithic Châtelperronian. The fact that the Mousterian and MSA people were behaving similarly and the Neandertals were replaced argues for a more recent origin of modern humans. It also suggests that the behaviors identified by McBrearty and Brooks (2000) as modern are not actually diagnostic of modern humans.

The alternate view to a gradual accumulation of modern behaviors during the MSA is that all truly modern behaviors originated simultaneously in Africa

approximately 50 kya. This “behavioral revolution” allowed these fully modern humans to spread throughout the world and replace the archaic people, including the contemporaneous non-modern MSA people (Klein, 1999; Klein, 2000a; Mellars, 1996; Stringer & Gamble, 1993). The challenge with this model is to explain the sudden and simultaneous appearance of all these behavioral traits. Most explanations are vague and often postulate changes in population density, social organization or language (Gamble, 1999:350; Mellars, 1996:419; Tattersal, 2001). Klein (1999; 2000a) hypothesized that a significant cognitive change, the product of a genetic mutation, could have caused the behavioral revolution by promoting the ability to innovate, thus behavior could rapidly change; this would be the origin of modern human capacity for culture. This ability to innovate would have conveyed such an advantage that modern human population size grew rapidly, and modern humans subsequently left Africa.

### **How did this replacement occur?**

The current paleoanthropological evidence implies that fully modern humans and their Upper Paleolithic tool industries were able to replace Neandertals in Europe 30-40 kya. The question remains, how did this replacement occur? What advantage did the modern humans have over Neandertals? One possible explanation is that modern humans were able to extract more resources from the environment. This may have allowed them to support larger population sizes and densities.

### ***Evidence for and against differences in resource extraction***

Middle Paleolithic archaeological assemblages are notably devoid of botanical remains, although there is sparse evidence of residues on stone tools that indicate that

Neandertals were exploiting plants (Hardy *et al.*, 2001). Thus, discussions of Neandertals' ability to extract resources must focus on acquiring meat. The first comparison of Middle and Upper Paleolithic large mammal exploitation in Europe must address to what degree Neandertals were hunting or scavenging. Binford (1985; 1988) proposed that early Neandertals from the Mousterian assemblage of Couche VIII, Grotte Vaufrey in southwestern France (OIS 6 or 7) were scavengers, while the later Neandertals from Combe-Grenal, also in southwestern France (OIS 4 and 5), were competent hunters. His argument for scavenging was based on carnivore-chew versus human-cut marks, bone breakage patterns, skeletal part representation, mortality profiles, and the horizontal distribution of the remains. Based on sites from west-central Italy, Stiner made similar arguments that earlier Neandertals (older than approximately 45 kya) scavenged more while later Neandertals hunted more, because the earlier assemblages had higher proportions of old prey and head and foot skeletal parts than the more recent assemblages (Stiner, 1990; Stiner, 1994).

Grayson and Delpech (1994) carefully reanalyzed Binford's data, along with their own data on the Couche VIII fauna, in light of Binford's research, and they firmly refuted his proposal. They found many more stone-tool cut marks, including disarticulation and filleting marks, than Binford identified. They also found that his own skeletal part representation data and spatial distribution data did not support his arguments for Neandertal scavenging. Grayson and Delpech's research suggests that Neandertals were capable hunters who regularly captured large game.

Subsequent scholars have also systematically investigated the possibility of consistent scavenging in Middle Paleolithic assemblages, but they conclude that

Neandertals were most likely able to regularly hunt large game (Chase, 1986; Chase, 1989; Marean, 1998; Marean & Kim, 1998; Speth & Tchernov, 1998; Stiner, 1990; Stiner, 1991a; Stiner, 1991b). This is not to say that Neandertals never scavenged. Occasional scavenging is not necessarily an indicator of ineffective foraging, and contemporary hunter-gatherers steal carcasses from other predators when given the opportunity (O'Connell *et al.*, 1988).

Middle Paleolithic assemblages across Europe contain a variety of prey, including red deer (*Cervus elaphus*), reindeer (*Rangifer tarandus*), fallow deer (*Dama dama*), roe deer (*Capreolus capreolus*), horses (*Equus caballus*, *E. hydruntinus*), ibex (*Capra ibex*), bison (*Bison priscus*), and aurochs (*Bos primigenius*). Early studies by Mellars' (1973; 1982) found that Upper Paleolithic assemblages in southwestern France were usually dominated by one species, reindeer. He proposed that specialization in hunting one game species was characteristic of the Upper Paleolithic and, therefore, modern human behavior. Subsequent studies have shown that the proportion of sites with a great abundance of one species does not differ between the Middle and Upper Paleolithic in southwestern France (Grayson & Delpech, 2002) or Europe as a whole (Chase, 1989; Gamble, 1999:235, 340-341), so specialized hunting does not distinguish Upper from Middle Paleolithic hunting.

Ungulate species abundance in both Middle and Upper Paleolithic assemblages apparently reflects the local environment at the time of deposition and not the prey choice of the occupants (Chase, 1989; Grayson & Delpech, 1998; Grayson *et al.*, 2001; Klein, 1999:453; Stiner, 1994). Mellars (1973; 1982) formed his hypothesis of reindeer specialization using data from southwestern France. But this region experienced dramatic

climatic changes during the Late Pleistocene (van Andel & Tzedakis, 1996), and the faunal community changed in response. Bordes and Prat (1965) demonstrated that in the Middle Paleolithic sequences from Combe-Grenal in southwestern France, red deer and reindeer fluctuated in direct response to the glacial cycles with more red deer in the warm phases and more reindeer during the cold periods. During the Upper Paleolithic of southwestern France, reindeer abundance increased with decreasing temperatures during OIS 3 and 2 leading up to the Last Glacial Maximum (Grayson *et al.*, 2001). This trend culminated in the Magdalenian “Age of the Reindeer” just subsequent to the Last Glacial Maximum (c.a. 18 kya). In conclusion, the abundance of reindeer in Upper Paleolithic assemblages, when it happens, is most parsimoniously explained by increasing reindeer abundance as a result of decreasing summer temperatures and not by intentional specialization in reindeer hunting by modern humans (Grayson *et al.*, 2001).

Many Mousterian sites have a high abundance of one species, and sites dominated by steppe bison and aurochs have received a great deal of attention, likely because of obvious comparisons with North American bison (*Bison bison*) deposits (e.g. Speth, 1997). The large bovids in these assemblages are often 85-99% of the ungulates present (Gamble, 1999:235, 340-341; Jaubert & Brugal, 1990). While there are only about ten of these sites, they have a wide geographic distribution spanning southwestern and northern France, Germany, and the northern Caucasus (Gaudzinski, 1995; Gaudzinski, 1996). These sites are earlier assemblages, mostly from 190-60 kya, and they are predominately open-air deposits, often along river valleys or in sinkholes (Gaudzinski, 1995; Hoffecker *et al.*, 1991; Jaubert & Brugal, 1990). The composition of the deposits suggests that a few animals were killed at the site during each hunting episode, and that the sites were

repeatedly used for hundreds of years (Farizy *et al.*, 1994; Gaudzinski, 1995; Hoffecker *et al.*, 1991; Jaubert & Brugal, 1990). There is an abundance of prime adult animals in all of the systematically analyzed assemblages, although the number of juvenile remains varies, possibly biased by pre- and post-depositional destruction and excavation techniques (Brugal & David, 1993; Farizy *et al.*, 1994; Gaudzinski, 1995; Hoffecker *et al.*, 1991; Jaubert & Brugal, 1990). This suggests that small herds, possibly family groups, may have been trapped at once. Killing just a few large bovids at once would generate large amounts of meat, yet there is no evidence of food storage during the Middle Paleolithic (Gamble, 1999:230). Meat could have been dried, however, and leave little archaeological evidence. The abundance of bones at these sites indicates that even early Neandertals were quite capable hunters, and the geographic positioning of the deposits suggests that the Neandertals were exploiting the species' natural movements and the local topography to hunt game. The extent to which these sites were exclusively kill sites or habitation sites is unknown. If they are only kill sites, then the extent to which the Neandertals exploited other species also remains unknown; these assemblages only indicate that the Neandertals could hunt large bovids, but do not necessarily indicate specialization in bovid hunting.

Researchers frequently cite seasonal exploitation of faunal resources as an indicator of hunting abilities, arguing that seasonality implies pre-planning and detailed knowledge of the prey's ecology. Changes in seasonality could indicate changes in land use, resource procurement and group mobility patterns (Pike-Tay *et al.*, 1999:284). Many of the large deposits of large bovids show seasonal deaths. The steppe bison of Mauran in southern France were consistently killed during the end of the summer and in autumn,

indicating that the animals were deposited during seasonal hunting episodes when the animals may have been positioned on the landscape such that they were easier to capture or drive (Farizy *et al.*, 1994). The steppe bison deposit of Coudoulous, in southwestern France also indicated seasonal hunting, but during the end of winter through summer with a peak during the end of spring and beginning of summer, the likely time of steppe bison rutting, which possibly made the animals more vulnerable (Brugal & David, 1993). The nearby site of La Borde, dominated by aurochs, contained animals killed during all seasons of the year (Slott-Moller, 1990). This non-seasonal hunting could be investigated in light of differences in behavior between steppe bison and aurochs. In Cantabrian Spain, Pike-Tay *et al.* (1999) demonstrated that at three sites, El Castillo, Cueva Morín, and El Pendo, Middle Paleolithic people were seasonally targeting red deer, roe deer, large bovids, and horse. These deposits also contained early Upper Paleolithic remains, and the seasonal signal of hunting is the same. These data show that Neandertals were exploiting the seasonal patterns of prey species and that they did not differ from modern humans in this respect, but seasonality data are difficult to interpret. They need not imply the targeting of a certain prey species during a specific season, but seasonal hunting could be a by-product of a stationary group of humans exploiting animals that happen to be local during only one season.

The age-at-death of prey in a faunal assemblage also provides information about hunting abilities. Non-human predators take the youngest, oldest, and weakest members of an ungulate herd (Carbyn, 1983; Kunkel *et al.*, 1999; Mech, 1970; Mech *et al.*, 1998; Mech *et al.*, 2001; Smith *et al.*, 2000), while only humans are able to consistently hunt prime adults, too (Boyd *et al.*, 1994; Klein, 1982b; Stiner, 1990; Stiner, 1991b; Stiner,

1994). The hunting of healthy adult animals likely indicates that the humans used either complex tools, such as bows and arrows or spear throwers, or built traps and surrounds where animals of all ages were equally likely to be captured. Stiner (1990; 1994) compared the age-at-death of cervids and aurochs in six sites in west-central Italy that span the Middle to Upper Paleolithic transition. She found that the more ancient Mousterian sites (older than 45 kya) contained more old prey, while the more recent Mousterian (younger than 45 kya) and Upper Paleolithic prey ages resembled modern hunters by containing many prime-aged individuals. Pike-Tay *et al.* (1999) compared age-at-death of the cervids, equids, and large and small bovids in three northern Spanish sites that span the Middle to Upper Paleolithic transition. They found no difference in the ages of the animals hunted during the two time periods, and the majority of the animals were prime adults. The Neandertals' ability to capture prime animals is attested by the large number of prime animals found in all of the large bovid sites discussed above (Brugal & David, 1993; Farizy *et al.*, 1994; Gaudzinski, 1995; Hoffecker *et al.*, 1991; Jaubert & Brugal, 1990). Finally, Levine (1983) studied the mortality profiles of horses in Lower (Acheulean), Middle, and Upper Paleolithic assemblages in southwestern France. Their mortality profiles clustered into different groups, but these groups contained assemblages associated with all tool industries. The patterning in her data did not reflect the chronology of the sites, and Middle and Upper Paleolithic people were taking animals of similar ages. Most of the assemblages that she studied contained many prime adult individuals, indicating that Neandertals were capable of obtaining prime-aged horses.

Pike-Tay (1991) studied the age-at-death of red deer in seven Upper Paleolithic sites from southwestern France. Four were early Upper Paleolithic from the Upper

Perigordian (ca. 26 kya) and three were later Upper Paleolithic from the Final Magdalenian and Azilian (ca. 11 kya). Although Pike-Tay was not studying the Middle to Upper Paleolithic transition, her results are relevant for studying Neanderthals' ability to hunt. The mortality profiles from the Upper Perigordian samples contained the same proportion of ages as a living herd, while the more recent assemblages had a bias towards juveniles. Pike-Tay (1991:108) hypothesized that the difference was due to differences in technology. The Magdalenian and Azilian people were hunting with spear-throwers, which allowed individuals or small groups of hunters to take the least wary and slowest prey, the youngest individuals. The Upper Perigordian people lacked projectile technology, so Pike-Tay (1991:108) suggested that they used organized, cooperative hunting to intercept and detain the prey, along with traps, snares, pits, stalking, and ambush. She hypothesized that these strategies would take animals of different ages in equal abundance to their presence on the landscape, and therefore there would be many prime animals in the fossil assemblages. Based on this study, I expect that the mortality profiles of red deer in Mousterian assemblages would more closely resemble those of the Upper Perigordian samples, because both groups hunted without projectile technology. This assumes that Neandertals hunted in a cooperative fashion, similar to the modern humans. If they did not, I expect that prey mortality profiles from their sites would resemble those accumulated by non-human carnivores.

Although there is no difference between the Middle and Upper Paleolithic in the degree of specialization in hunting large ungulates, the proportion of taxa in faunal assemblages does change through time. Upper Paleolithic assemblages have much higher amounts of smaller animals in them, including fish, birds, and lagomorphs (rabbits and

hares; Klein, 1999:459; Stiner *et al.*, 1999). Although all of these taxa are present in Middle Paleolithic deposits, particularly lagomorphs, they are more abundant in later assemblages (Chase, 1986; Stiner *et al.*, 1999; Straus, 1977). Increased faunal diversity in the more recent sites is mirrored in Africa where the MSA assemblages have fewer small animals than the Late Stone Age (LSA, African equivalent of Upper Paleolithic) sites (Klein, 1994). The ability to readily acquire fish and birds, particularly airborne species, is significant, because hunting them required more sophisticated non-lithic technology, such as harpoons, fish hooks, gorges, which were made out of bone and ivory, and nets. There is no evidence for such implements in the Middle Paleolithic or MSA (Klein, 1999).

#### ***Evidence for and against differences in population density and size***

Despite the apparent similarities between Neandertal and modern human hunting strategies, the early Upper Paleolithic people must have been extracting more resources from the environment, because they appear to have sustained denser, larger populations. Estimating population densities and sizes using the archaeological record is notoriously difficult; there are preservation biases against older assemblages and different settlement patterns may generate different numbers of sites. Aurignacian sites outnumber Mousterian sites even though the Middle Paleolithic had a much longer duration. Clark and Straus (Clark & Straus, 1983:146) counted the number of deposits in each time period in Cantabrian Spain; they recorded 13 Mousterian sites spanning 65,000 years or 0.2 sites per thousand years, and 18 early Upper Paleolithic sites spanning only 15,000 years or 1.2 sites per thousand years. This pattern is mirrored in southwestern France where there are about five Upper Paleolithic sites for every one Mousterian site, and

again, the Mousterian spans much more time (Mellars, 1982). White (1982) criticized analyses such as these for counting sites and not layers within sites and discussed how different settlement systems could place sites more or less in the open-air or in rock shelters, biasing the number of preserved and excavated sites. Even though population density is difficult to quantify, the impression is of more people living in Europe in the early Upper Paleolithic than in the Middle Paleolithic.

The intensity of occupation in a site provides another line of evidence for population densities (Mellars, 1982). Mousterian caves and rock shelters appear to have been much more ephemerally inhabited, because the density of artifacts and faunal remains in the deposits is lower than in most Upper Paleolithic sites (although see Speth & Tchernov, 1998 and Stiner & Tchernov, 1998 for an exception). Many Middle Paleolithic assemblages show evidence of carnivore activity, such as carnivore remains, coprolites, and chewing and gastric acid etching on ungulate remains, indicating that humans did not always occupy the sites (Boyle, 1998; Speth & Tchernov, 1998). The number of large carnivores found in Upper Paleolithic sites is greatly reduced, although small carnivores are more abundant, possibly because they were hunted for their fur (Klein, 1999:535-6).

The density of occupation in a region can also be inferred from the size of small animal remains, particularly tortoises and limpets (Clark & Straus, 1983; Klein, 1998; Klein, 2000b; Klein *et al.*, 1999:472-3; Klein & Cruz-Urbe, 1984; Stiner *et al.*, 2000; Stiner *et al.*, 1999). Both tortoises and limpets grow continuously throughout their life, and human foragers have a natural tendency to collect the largest, therefore the oldest, individuals. As a result, the mean age of the population decreases, and so the mean body

size of individuals in the population also decreases. A small mean size of a sample likely indicates that the source population was experiencing elevated predation pressure, although care must be taken to control for changes in paleoclimate, site function, and the season of site use (Speth & Tchernov, 2002). Unfortunately, few known assemblages with abundant small animals span the Middle to Upper Paleolithic transition in Europe. The sequence of Riparo Mochi, Liguria, Italy provided a series of limpets, *Patella caerulea*, in the Upper Paleolithic sequences that showed a marked size change between 19 and 24 kya (Stiner *et al.*, 2000). The Middle Paleolithic levels in this site provided a few specimens, and although they were too fragmented to measure, they were large, suggesting minimal pressure on the population (Stiner *et al.*, 2000). In the assemblages from Nahal Meged in Israel, the mean size of tortoises (*Testudo graeca*) in the Middle Paleolithic was statistically larger than the early Upper Paleolithic samples, and a similar pattern was noted in the nearby Kebara and Hayonim Caves (Stiner *et al.*, 2000; Stiner & Tchernov, 1998). In both the Nahal Meged and Hayonim assemblages, the most recent Mousterian deposits had tortoises that were similar in size to the Aurignacian deposit just above, but their sample sizes were small. The possible effects of changes in paleoenvironment must be carefully considered in these studies (Speth & Tchernov, 2002), but the increase in the number of small animals as well as the decrease in the size of the small animals suggests that the earliest Upper Paleolithic people in these two regions were harvesting these animals more intensely than during the Middle Paleolithic.

During the Middle Paleolithic, many northern regions apparently were abandoned or sparsely populated during peak cold times, as evidenced by their lack of archaeological sites; the Neandertals probably experienced population crashes and survived in refugia

(Hoffecker, 1999; Hublin, 1998). Unlike Neandertals, modern humans lived in the central eastern European Plain during glacial times (Dolukhanov *et al.*, 2001; Hoffecker, 1999:137). The oldest, northern-most site is possibly Mamontovaya Kurya at 66° N near the polar Urals of Russia at the Arctic Circle and is approximately 36 kya, but the material was in redeposited layers (Pavlov *et al.*, 2001). Additional sites in the area are needed to confirm this remarkable find. An incredibly rich site of Sungir' (approximately 25-30 kya) is located at 56° N and provides firm evidence of modern humans living in territories never previously occupied (Hoffecker, 1999). The early modern humans moving into northern latitudes had body proportions typical of people living in Africa today (Holliday, 1997; Trinkaus, 1981). They were able to survive under harsh conditions because of their cultural adaptations; they built complex structures and manufactured bone and ivory awls and needles, probably to sew clothing (Hoffecker, 1999). These eastern European sites also provided the first evidence of systematic fur trapping (as in Klein, 1999:535-6).

### **This study**

Comparisons between Middle and early Upper Paleolithic subsistence strategies and ways of life often focus on single, narrowly defined geographic regions. Differences may be identified, but it is difficult to know if the pattern is robust when one or two sites are considered. In this study, I wanted to assess the variation present in Middle and Upper Paleolithic hunting practices so that I could investigate differences and similarities in behavior between the two groups. To best control for prey behavior, I studied the hunting of only one prey species, *C. elaphus*, red deer in Europe and elk or wapiti in North

America\*, across space and time. *C. elaphus* is geographically widespread and persisted through many climatic fluctuations. By holding the prey species constant, I can more easily consider prey behavior, such as predator avoidance tactics, the ability to be driven, and herd structure, in order to determine hunting strategies (Frison, 1991a). I investigate variation in how Late Pleistocene humans hunted red deer by examining prey age-at-death. Detailed data exist on how prey-at-death indicates hunting strategies in both human and non-human predators, making it a good parameter for assessing variation in hunting strategies.

### ***Prey age-at-death as an indicator of hunting strategies***

The prey choice model, as known as the diet breadth model, of Optimal Foraging Theory guides my investigations into Late Pleistocene subsistence ecology (Kaplan & Hill, 1992; Smith & Winterhalder, 1992; Stephens & Krebs, 1986). This model assumes that hunters, both human and non-human, make decisions about which prey to pursue by considering which individuals will provide the highest return rate, usually calories, per unit of time or energy spent foraging (Stephens & Krebs, 1986). Prey availability is a factor in this decision, because the search-time to find a certain prey is included in the “cost” of that prey. In addition to calories, predators need to consider the risks involved in hunting, such as the likelihood that a prey target will injure the hunter, and for humans, the number of hunting implements that might be broken or lost. Consequently, the prey that hunters capture informs on hunting abilities and strategies or prey choice.

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\*Throughout this study, I will refer to *C. elaphus* as “red deer” when I exclusively mean animals living in Europe, either in the present or during the Late Pleistocene. I will call exclusively North American individuals “elk”. When I am referring to animals from both Europe and North America, I will use their common species name, *C. elaphus*.

For example, hunters may choose to pursue the more abundant species, the more docile species, or the species that provides the most meat. They may also choose a species that is more amenable to being herded or driven. The age and sex of the prey are also potential factors influencing prey choice, because meat, marrow and organ quantity and quality changes with age and sex, as does the vulnerability or dangerousness of the prey. The season will affect prey choice, because migrations affect species availability and abundance and the quantity and quality of meat, marrow, and organs. Herd structure changes with season, so that a certain age or sex may be targeted depending on the season. Human hunters may move beyond their fundamental caloric needs and choose their prey based on sex, if they desire antlers for tools or trophies, or on hide quality, which can change with age, sex or season. In sum, the behavioral ecology of each species greatly affects a predator's hunting strategy.

As the largest individuals of a population, adult male ungulates may provide the most calories, but risks are involved that may make this prey unobtainable or best avoided. These risks may dictate the hunting of more vulnerable individuals, such as the diseased, injured, senile, or young. Consequently, age-at-death data provide information about how readily a hunter can take the strongest or prime animals versus the weakest or most vulnerable individuals, usually the young and old. Hunters of prime animals must be stronger, faster, or better armed (meaning technologically sophisticated in the case of humans) than their prey to reduce the risks of injury and increase the probability that the animal will be taken. Cooperative hunting also increases the potential of obtaining desirable prey.

Age-at-death data for prey assemblages can be acquired from field observations, skulls of deceased wild animals, or the archaeological and fossil record. For many species, relative prey age-at-death is readily estimated from fossil and archaeological assemblages. Teeth continuously change throughout an individual's life by erupting in a predictable sequence and wearing as the animal eats, and, therefore, assessing the amount of wear on a tooth provides a means of estimating age. Teeth also preserve well in the archaeological record, which increases the number of assemblages that can be compared and reduces some biases produced by post-depositional destruction. Age-at-death data can be compiled to create frequency distributions, or mortality profiles, that show the proportion of individuals that died in each age class. These profiles reveal one aspect of hunting strategy by showing the proportions of juvenile, prime, and old individuals that the predator acquired.

### ***Objectives of this study***

I have four objectives for this study:

1. Investigate the methods used to estimate the age-at-death of archaeological specimens of *C. elaphus* and to construct mortality profiles for fossil assemblages. Based on my results, I will provide recommendations for future researchers.

2. Describe variation in the age-at-death of red deer in archaeological sites spanning the last 200,000 years in western Europe. I will investigate these data to see if they indicate differences in hunting ability between Neandertals and early modern humans.

3. Assess *C. elaphus* body-size changes through time and across space. The large dataset that I collected for studying age-at-death also allows me to investigate the

relationship between climate and mean body size in *C. elaphus*. If I can establish a relationship in modern populations or in fossil samples, Late Pleistocene red deer body size will be useful as a paleoclimatic indicator.

4. Suggest directions for future research that address how modern humans were able to replace the Neandertals. Answering this question will further the understanding of modern human origins.

## Chapter 2: *C. elaphus* ecology

In this study, I focus on red deer for three reasons. First, *C. elaphus* existed historically throughout Eurasia and North America and was a common human prey species whenever the two co-occurred in prehistory (Appendix C and D and Figure 2.1 and 3.1). The rich zooarchaeological record of *C. elaphus* facilitates comparisons between many sites from different geographic locations and time periods. Second, *C. elaphus* persists today in Europe and North America as a big game animal, so wildlife biologists on both continents have devoted vast amounts of resources to understanding the ecology of this species (Clutton-Brock & Albon, 1989; Clutton-Brock *et al.*, 1982; Houston, 1982; Murie, 1951; Thomas & Toweill, 1982). Importantly for my study, much of this research has focused on the demographics of hunted populations to ensure that the herds maintain viable numbers of reproductive individuals. Wildlife biologists have collected known-age specimens to develop techniques for determining the age-at-death of *C. elaphus* individuals (Brown & Chapman, 1991a; Brown & Chapman, 1991b; Hamlin *et al.*, 2000; Lowe, 1967; Quimby & Gaab, 1957). This makes *C. elaphus* one of a few species where the relationship between tooth wear and chronological age has been well defined (Klein, 1978; Klein *et al.*, 1983; Klein & Cruz-Urbe, 1983; Klein *et al.*, 1981, but see Chapter 4 for further refinements). Finally, *C. elaphus* body size fluctuates through time (i.e. Dixon & Lyman, 1996; Lister, 1981; Lister, 1984; Lister, 1993; Mariezkurrena & Altuna, 1983; Straus, 1981; Walvius, 1961) and space (i.e. Clutton-Brock & Albon, 1983; Clutton-Brock & Albon, 1989; Clutton-Brock *et al.*, 1982;

Langvatn & Albon, 1986; Lister, 1984; Walvius, 1961), indicating that the mean body size in *C. elaphus* populations may be a useful environmental indicator.

### **Evolutionary history**

The detailed research of A. M. Lister is primarily responsible for our understanding of the evolution of Quaternary cervids in Europe, and much of the description here is taken from his work (Lister, 1981; Lister, 1984; Lister, 1986). The species *C. elaphus*, identified by the antlers' double lower tine, is first recognized in Europe during the Cromerian Interglacial Complex in Britain, which is probably equivalent to OIS 13 (Schreve, 2001) and therefore approximately 475 – 505 kya (Bradley, 1999:212). This first species is *C. elaphus acornatus*, so named because the distal end of their antlers ended in a simple, two-pointed fork. By the Hoxnian Interglacial, now correlated to OIS 11 (Schreve, 2001) between about 347 – 421 kya (Bradley, 1999:212), red deer evolved distinctive many-pointed crowns or cups at the end of their antlers, and this new form is *C. elaphus elaphus*. The potential to develop these crowns is still present in the red deer of western Europe today, and so they also belong to the subspecies *C. elaphus elaphus*, as described by Linnaeus in 1758. The oldest fossils included in my study are from approximately 200,000 years ago, so all the fossil specimens considered are *C. elaphus elaphus*.

Prat and Suire (1971) noted that red deer from the OIS 5 deposits of Combe-Grenal in southwestern France were very small, and Guadelli (1996) described these specimens as a new species, *C. simplicidens*. Their identification is primarily based on size and tooth morphology, particularly that of the lower fourth premolar, P<sub>4</sub>. However, P<sub>4</sub>s are variable in morphology and, therefore, are not good taxonomic indicators (Janis &

Lister, 1985). These small specimens also co-occur with other mammal species that are indicative of temperate, wet forests, while the larger individuals from the site are associated with a colder climate (OIS 4, Guadelli, 1996). Climatic, and not taxonomic, reasons could explain the differences in body size. Until further research is conducted on *C. simplicidens*, I include these specimens in my analysis as *C. elaphus*, although the particular samples containing these individuals are indicated in Appendix D.

The fossil evidence for the spread of *C. elaphus* into North America from Eurasia is not as clear as the evidence for their history in Europe. According to Bryant and Maser (1982), *C. elaphus* first appeared in Alaska during the Illinoian glacial stage (OIS 6). These early elk arrived across Beringia from Siberia, but were isolated in an Alaskan refugium during this glacial period. They apparently did not disperse fully into North America until the succeeding Sangamonian interglacial (OIS 5). Isolation during the Wisconsin glaciation (OIS 4-2) was probably responsible for the geographic distribution seen in elk today (Bryant & Maser, 1982). Geist (1998:186) had a contradicting view, because he concluded that *C. elaphus* was rare in North America during the Illinoian and Sangamonian and was reliably identifiable throughout North America only after 11.5 kya; he hypothesized that the species did not become abundant until the late Pleistocene mega-faunal extinctions opened up many new niches.

Researchers agree that North American elk originally derived from Eurasian ancestors, but the taxonomic status of the modern groups is currently in dispute. Although considered separate species (*C. elaphus* in Europe and *C. canadensis* in North America) since 1780, in the early 1900's it became apparent that individuals of both "species" introduced into New Zealand readily interbreed (Bryant & Maser, 1982). This

ability to interbreed warranted the two being placed into the same species in the 1950's, following the biological species-concept where "species are groups of interbreeding natural populations that are reproductively isolated from other such groups" (Mayr, 1970:12). Wilson and Reeder (1993:385-386) consider all the North American and Eurasian populations to be *C. elaphus*. More recent researchers claim that the New Zealand population is not a "natural" population. Geist (1998) found the European and North American taxa morphologically and behaviorally distinct and claimed that the hybrid offspring have reduced fitness, such as having intermediate, therefore ineffective, predator avoidance strategies. Viable interbreeding would mean that the offspring are able to survive in the "natural" state, but the New Zealand hybrid offspring can only survive in a semi-domesticated state where there are no predators. *C. elaphus* is documented to freely hybridize with *C. nippon* where the sika deer has been introduced, and the offspring survive so well that wildlife managers are concerned about maintaining the integrity of local *C. elaphus* populations (Geist, 1998; Lister, 1984).

For my study, the exact taxonomic definition of the European and North American groups is not important. I primarily draw upon North American elk for a known-age sample that I use to determine the relationship between tooth crown height and age. Red deer and elk teeth are identical except for size (personal observation). There is no reason to suppose that the wear rates differ more between North American and European populations than they do within the populations, although wear rates are correlated with diet. Ideally, I would use crown height measurements on known-age European populations, but these were not yet available to me.

## Diet and habitat preferences

The close management of extant *C. elaphus* herds in both Europe and North America offers abundant opportunities for studies of red deer habitat preferences, population dynamics, and interactions with human and non-human predators (e.g., Clutton-Brock & Albon, 1989; Clutton-Brock *et al.*, 1982; Houston, 1982; Murie, 1951; Thomas & Toweill, 1982). From studies of living animals, researchers know that *C. elaphus* is an ecologically plastic species that is adaptable to a wide range of climatic, topographic, and vegetation zones (Markova *et al.*, 1995; Straus, 1981). Although red deer often are considered to be a woodland species, they actually thrive in a variety of habitats, from mixed forests in Poland's Bialowieza Primeval Forest to open Scottish highlands. Geist (1998:1) described deer as filling the niche of opportunistic foraging, and as reviewed by Straus (1981) red deer and elk eat browse, forbs, grasses, and even seaweed. A carbon and nitrogen stable isotope study of 27 red deer remains from Paglicci cave (32.6-13.2 kya) in southern Italy suggested that these deer were eating mainly C<sub>3</sub> plants, or browse, in an open environment (Iacumin *et al.*, 1997). *C. elaphus* digestive anatomy and tooth morphology suggests that they are adapted to both browsing and grazing (Clutton-Brock *et al.*, 1982). Their range is limited more by the need to have protection from the snow and wind than by dietary constraints, and either trees or topographic relief can provide this protection (Lister, 1984; Straus, 1981). For this reason, *C. elaphus* never dispersed to the far northern regions that are dominated by reindeer. They can tolerate steppe environments, but not tundra. Ideal *C. elaphus* habitat is probably patchy wooded areas that provide a protective forest cover and openings with good grazing and browsing opportunities (Harpole & Lyman, 1999; Lister, 1984).

The fossil record for red deer is consistent with the modern, wide distribution of red deer. Lister (1984) documented red deer remains in Britain associated with mammals species that are characteristic of cold, open environments, such as reindeer, woolly rhinoceros (*Coelodonta antiquitatis*), mammoth (*Mammuthus primigenius*), and horse, but he also found them associated with warm oak forest species, such as fallow deer, and with hippopotamus (*Hippopotamus amphibius*). In Britain, red deer were present, but never abundant, during the warm interstadials and absent during glacial periods (Bordes and Prat, 1965; Lister, 1984). As Britain warmed after the Last Glacial Maximum, red deer became quite abundant there and were common prey of Mesolithic hunters living approximately 9,000 years ago (Clutton-Brock & Albon, 1989; Lister, 1984). In southern France, red deer were abundant during the warm interglacials, but during the cold stages, they were replaced by reindeer, although never completely (Delpech, 1996). In northern Spain, red deer were always quite abundant, even during the Last Glacial Maximum when arboreal pollen counts were low, suggesting an open environment (Straus, 1981).

### **Social behavior**

Modern behavioral studies provide data on how red deer herds are organized on the landscape. The discussion below is primarily based on Clutton-Brock and colleagues' work on red deer in Scotland (Clutton-Brock & Albon, 1989; Clutton-Brock *et al.*, 1982) and research on Rocky Mountain elk (Geist, 1982). Throughout most of the year, the males are separated from the females. Geist (1982) hypothesized that this is because females compromise forage quality and abundance by congregating into herds for protection, while in the summer, males seek higher quality forage, singly or in groups, in order to build up reserves for the fall rut. Observations of elk in Yellowstone National

Park, Wyoming contradict Geist's hypothesis, because the open meadows were females and their young congregate provide high quality forage, while the males are eating lower quality forage in the forests (E. Hadly, personal communication). During the rut, herds of one to more than twenty females are defended by a single dominant male, and this is the only time adult males and females exist as a group. Non-harem holding males, usually young adults and old individuals, are peripheral to the group and may challenge the harem-holder. During the winter, stags weakened by the rut may congregate for protection in male herds away from the females, or they may solitarily seek higher quality forage. Old males are often alone. Males that have survived the rut with sufficient fat stores might remain in close proximity to the females. In the spring, calving herds consist of the adult females, their newborns, and juveniles of both sexes and are separated from the fully adult males. For both males and females, individual party composition is always fluid, although females have a limited territorial range and tend to associate in mother-daughter and sister-sister groups (Clutton-Brock *et al.*, 1982). Males leave their maternal herd to seek mates in other territories (Clutton-Brock *et al.*, 2002). Party size is often small, approximately five to ten individuals, although it can reach into the thousands depending on the environmental conditions (Boyle, 1990). There is also a general trend for deer species living in open landscapes to congregate into larger groups than those living in more closed habitats, likely to avoid predators, although it may also be due to the nutritional quality of the vegetation (Clutton-Brock *et al.*, 1982).

Throughout different *C. elaphus* populations, variation exists in the prevalence of seasonal migration. McCullough (1969) argues that migrations do not occur in *C. elaphus*, but the herds do have localized movements in response to local conditions. The

majority of seasonal movement is usually in altitude and in response to food availability and decreasing snow cover, and therefore the animals usually move to higher elevations in the summer (Adams, 1982). Red deer and elk are frequently found in snow as deep as approximately 46-76 cm, but they can tolerate deeper snow if it loose and not crusted (citations in: Adams, 1982; Lister, 1984). Insect infestation also encourages *C. elaphus* herds to seek higher altitudes during summer months (Adams, 1982; Clutton-Brock *et al.*, 1982). Long distance migrations that are characteristic of reindeer herds are never seen in *C. elaphus*.

*C. elaphus* seasonal behavior may affect hunting strategies in a variety of ways. Males are often alone or in loosely associated groups seeking better forage or mates, which makes them vulnerable to predation because of the lack of a herd help warn them of imminent danger. Isolated males are vulnerable, because often they are older males unable to form a harem during the rut or are prime males weakened by the rut and seeking high quality forage to restore their reserves for the winter. Females may be more vulnerable, because they are smaller and lack formidable antlers. However, because they are usually in herds, at least one female will be alert and will warn the rest of the herd if danger approaches. Females have well defined home ranges (Clutton-Brock *et al.*, 2002; Clutton-Brock *et al.*, 1982), which makes them easier for hunters to locate. Their anti-predator strategy is to stay in a group and run from disturbance (Geist, 1982), which probably makes this species amenable to hunting by driving the animals. Frison (1991b:261-263) finds elk to be easily confused; if a hunter can sneak in close before startling the group, they scatter in confusion and are easier to kill. Given proper warning, the herd runs off to safety in a tight group.

Calving is synchronous, and more so in higher latitudes where the growing season is short (Geist, 1982). Newborn elk and red deer have a “hider” anti-predator strategy where the newborn stays hidden for most of the day away from the herd while the mother forages nearby; in the face of danger the calf freezes, while the mother assesses the situation (Geist, 1982). This behavior may last from one to three weeks (Geist, 1982). During this time, the calf has not fully developed its running ability, and this, along with its small size, makes the calf very vulnerable to predation. Even once the calf is fully mobile, the mother still flees with the calf trailing behind, leaving the juvenile very vulnerable to predation. Shortly before the newborn calf is born, the previous year’s offspring segregate from their mothers. The females often stay within their mother’s group, but the males often wander on their own, seeking other males or a group of females (Geist, 1982). These young males may be vulnerable to predation, because they are solitary and inexperienced.

### ***C. elaphus* body size variation**

As described above, *C. elaphus* thrive in many different habitats, so their presence in a fossil assemblage is not a good indicator of the surrounding environment during deposition (Lister, 1986). Throughout these different habitats, however, red deer body size is highly variable and therefore might be a useful indicator of environment. Modern *C. elaphus* adult male lean weight ranges from 110-478.6 kg (Geist, 1998:349-350), and paleontologists have recorded significant fluctuations in fossil body size through time (Delpech, 1983; Lister, 1981; Lister, 1993; Mariezkurrena & Altuna, 1983). Lister (1989) has also documented decreased body size in island populations. In northern Spain, red deer were largest during the last glaciation, and their body size has decreased to historic

times (Mariezkurrena & Altuna, 1983). These changes might reflect either Bergmann's "rule" where cold climate selects for survival of larger body sizes, or they might reflect differences in available resources under various environmental conditions (see full discussion in Chapter 6). Studies by Langvatn and Albon (1986) and Walvius (1961) suggest that body size changes in response to climate related changes in available vegetation. If the relationship between body size and certain climatic parameters can be determined, then red deer body size might be useful as a paleoclimatic indicator.

### **Ethnographic examples of methods used to hunt *C. elaphus***

Ethnographic data collected by early explorers and ethnographers in North America provide information on methods commonly used to hunt elk. Although never really the dominant prey species of any Native American group, elk were hunted in small quantities by almost every group that overlapped their range (McCabe, 1982:88). Elk were commonly hunted only in the southern Pacific Northwest and the Columbia River basin area, although they were still second to fish in dietary importance (McCabe, 1982:88). McCabe (1982) provides a thorough review of early accounts of elk hunting, and what follows is a summary of his report. I excluded hunting techniques that involved horses, dogs, or firearms.

Elk were commonly hunted with snares or pitfalls set along commonly used trails. Nets were also used on occasion to capture an animal. Occasionally elk were driven along these trails to ensure that an animal fell prey to the trap. Native Americans were also able to successfully hunt elk with ambushes from blinds alongside game trails. One hunter would chase an animal so that it passed by another hunter in hiding, and the second hunter would then spear the animal. Deep snow and rivers were often used to

slow the elk so hunters could get close enough to dispatch the animals. Elk would be chased into snow banks by hunters on snowshoes or chased into rivers, sometimes covered by thin ice, and killed by hunters waiting in the water or in canoes. Multiple hunters could also chase the elk to exhaustion, as well. There are a few descriptions of elk being driven over cliffs or into surrounds, but these are rare. Single hunters or small groups could accomplish all of these hunting methods, and there is little archaeological evidence for large organized communal hunting, as is often seen with bison (Frison, 1987). Most hunting methods rely on elk's natural tendency to flee from danger, and while they do not stampede, they can be driven.

Unfortunately, each of these Native American hunting strategies is from ethnographic documentation, and associated archaeological signatures are unknown. The ethnographic literature does provide some information on the preferred animals:

“These Indians...concentrated on yearlings, whose meat was more tender than bison or older elk. Elk cows were hunted shortly after the calving season, because their hides were most pliant at that time” (as in McCabe, 1982:72).

“When there was a choice between sex and age classes of elk, the Indians invariably killed mature bulls. The amount of meat that an animal provided was of paramount importance” (as in McCabe, 1982:72).

These comments confirm that age-at-death of prey in archaeological assemblages should provide data on ancient hunting strategies. Combining this age data with sex data would maximize information, but it is difficult to reliably reconstruct the proportions of each sex in a fossil assemblage of red deer (Klein & Cruz-Urbe, 1994; Mariezkurrena & Altuna, 1983).

## Chapter 3: Samples and data collection

### Research samples

#### *Modern samples*

I used modern specimens of *C. elaphus* in multiple contexts: to compare human and wolf hunting strategies, to refine age determination techniques, to compare different methods for reconstructing mortality profiles, and to study body size variation. The data for these studies came from three sources: human-hunted elk with associated known ages, wolf-killed elk with associated cementum annuli ages, and comparative specimens from multiple zoological collections. For comparative purposes, I also used a sample of known-age white-tailed deer (*Odocoileus virginianus*), measured by C. Wolf.

The human-hunted sample is of Rocky Mountain elk (*C. elaphus nelsoni*) from Montana just north of Yellowstone National Park, Wyoming. These specimens were all marked as calves and were subsequently retrieved at hunter checkpoints, and therefore they have known ages in months associated with them. Data on this sample were collected twice. Quimby and Gaab (1957) accumulated the original known-age specimens for their wear-stage study, and C. Wolf measured this sample's tooth crown heights in the late 1970's with the purpose of developing a technique that could be used to assign age to fossil *C. elaphus* specimens (Klein *et al.*, 1983; Klein & Cruz-Uribe, 1983; Klein *et al.*, 1981). In the summer of 2000 I re-examined this collection, which is housed at Montana State University (Bozeman, Montana). I collected additional data and compared my measurements with the Wolf's measurements of the same specimens. In

addition, I collected supplementary data on known-age Rocky Mountain elk from the same general population in Montana that were housed at the Montana Department of Fish, Wildlife, and Parks (Bozeman, Montana). A team from this institution tagged the specimens as calves from 1972-97 and collected the mandibles at hunter checkpoints as part of a study comparing estimates of age using wear stages to incisor cementum annuli counts (see Hamlin *et al.*, 2000 for a complete description of the sample and their study). I combined these two samples into one known-age sample (n = 226), which I used to refine the Quadratic Crown Height Method (QCHM) for estimating age in fossil *C. elaphus* (Chapter 4) and as a sample with a known age distribution to compare methods of reconstructing mortality profiles (Chapter 5). I also used this sample to compare patterns of sexual dimorphism (most specimens were also of known sex) and body size variation (Chapter 6) and as an example of human hunting (Chapter 7).

The wolf-kill sample is of Rocky Mountain elk from Yellowstone National Park, Wyoming. Since wolf (*Canis lupus*) reintroduction into Yellowstone in 1995 and 1996, park biologists have been tracking the wolves as part of larger behavioral studies to understand the new predators' impact on the Yellowstone ecosystem. During the winter months when snow cover makes tracking easiest, biologists collected data on each wolf kill, including mandibles for age determination by incisor cementum annuli and metatarsals for inferring the condition of the animal from their marrow quality (Mech *et al.*, 2001). The primary prey of the wolves was the local elk (Mech *et al.*, 2001; Smith *et al.*, 2000). I studied the mandibles and metatarsals of the elk that were killed by wolves in 1999, the largest complete sample available at the time. D. Smith provided cementum annuli ages from incisors for all of these specimens, and because Hamlin *et al.* (2000)

demonstrated the reliability of the cementum annuli technique in modern specimens, I consider the cementum annuli ages to be known-ages. I used these wolf-killed elk ( $n = 98$ ) as a sample with a known age distribution to compare methods of reconstructing mortality profiles (Chapter 5) and to compare patterns of sexual dimorphism (many specimens were of known sex) and body size variation (Chapter 6). Finally, the wolf-kill sample provided a good comparison of how wolves and humans hunt animals of different ages.

My third modern sample is composed of many comparative specimens from zoology museums and zooarchaeology laboratories in the United States and western Europe. In the United States, I collected data at the California Academy of Sciences (San Francisco, California), Montana Department of Fish, Wildlife, and Parks (Bozeman, Montana), Montana State University (Bozeman, Montana), Museum of Vertebrate Zoology (Berkeley, California), National Park Service (Yellowstone National Park, Wyoming), and the Philip L. Wright Zoological Museum (Missoula, Montana). In Europe, I measured comparative specimens in the British Natural History Museum (London, United Kingdom), Römisch-Germanisches Zentralmuseum (Neuwied, Germany), Sdad. de Ciencias Aranzadi (Donostia/San Sebastián, Spain), Universität Tübingen (Tübingen, Germany), and Université Bordeaux I (Talence Cedex, France). I used these specimens to study sexual dimorphism and the relationship between mean body size of a population and various environmental parameters.

### ***Fossil samples***

The 64 fossil localities used for my study are shown in Figure 3.1, with the names, locations, excavators, where the assemblages were housed, and references for

each site listed in Appendix C. Appendix D provides detailed information about each layer within each site: associated tool industry, red deer abundance by NISP, OIS, date, and climatic data. Some data are not available for some sites and assemblages. My data collection focused on determining the age-at-death of the specimens and taking measurements for tooth and body size. All of the other data points, including full faunal lists and counts, dates, and climatic information, were taken from the references listed in Appendix C and discussions with the museum curators and site excavators.

My sampling strategy for the fossil assemblages was to pick a few large, well-documented sites, travel to the museums that housed those collections (listed in Appendix C), measure the red deer specimens in those collections, and then measure other red deer available in the museum. The larger, target assemblages included Arago, Combe-Grenal, Gabasa, La Riera, Lazaret, Piegu, and Urtiaga. R. G. Klein allowed me to use his data on many large samples from northern Spain: Altamira, El Castillo, El Juyo, and Majolicas. K. Cruz-Urbe provided data on the Star Carr, England sample. These large samples formed the basis of my study on Late Pleistocene hunting by humans, and I included the smaller samples in my study of body size changes through time and space.

## **Data collection**

### ***Metric data***

On teeth, I measured mandibular deciduous fourth premolar (dP<sub>4</sub>), the fourth molar (P<sub>4</sub>), and the first (M<sub>1</sub>), second (M<sub>2</sub>), and third (M<sub>3</sub>) molars, as shown in Figure 3.2.A, and the analogous maxillary teeth. I took the same measurements on isolated teeth and teeth in their mandibles. Crown height and breadth were taken on the anterior two

lobes of each tooth, along with occlusal length and basal length (see Figure 3.3 for a description of nomenclature). Following Klein and Cruz-Urbe (1984:46-47), crown height was measured as the minimum distance between the occlusal surface and the line separating the enamel of the crown and the dentine of the root. For mandibular teeth, crown height was measured on the buccal-most surface; for maxillary teeth, the lingual-most surface was measured. Tooth breadth was defined as the maximum buccolingual dimension, and basal tooth length was the anteroposterior dimension of the tooth at the crown base, just above the crown-root junction (Klein and Cruz-Urbe 1984:176). Occlusal length was taken as the maximum anteroposterior length of the tooth on the occlusal surface (Driesch, 1976:56). When complete dental rows were preserved, I measured premolar, molar, and total row length according to von den Driesch (1976:37, 56) and Figure 3.2.B.

For a body size proxy, I measured distal metacarpal and metatarsal mediolateral and anteroposterior diameters according to von den Driesch (1976:92), Klein and Cruz-Urbe (1984:20) and Figure 3.4.A and B. Anteroposterior diameter was taken on the medial condyle. When complete bones were present, I also measured maximum length (Klein & Cruz-Urbe, 1984:20).

I took all measurements with Mitutoyo digital extended point jaw calipers (965 Corporate Blvd., Aurora IL, 60504; [www.mitutoyo.com](http://www.mitutoyo.com)) and recorded them to the nearest hundredth of a millimeter. I collected all data directly into a spreadsheet using a SmartCable (7403 Lakewood Drive #14, Lakewood, WA 98499; [www.smart-cable.com](http://www.smart-cable.com)) that connected the calipers to the computer. I used the DigiCal software interface (written as shareware by Gary Rensberger and available at <http://life.bio.sunysb.edu/morph/soft->

dataacq.html) which converted the SmartCable's modem-like signals into text that was inputted directly into JMP statistics software (SAS Institute Inc., JMP Software, SAS Campus Drive, Cary, NC 27513; www.jmpdiscovery.com).

R. G. Klein provided data taken by himself on comparative and fossil material and by C. Wolf on known-age specimens. In order to ensure that all measurements were comparable when combining samples, I calculated the percentage of interobserver error following White and Folkens (1991:292) for measurements that were taken both by others and myself on the same specimens. I compared my measurements with C. Wolf's on the Quimby and Gaab known-age collection, and my measurements with R. G. Klein's on comparative material housed in the British Museum of Natural History (Table 3.1). A pooled sample of breadth measurements on all tooth types has a mean interobserver error of 2.5% (0.36 mm), and the error of tooth crown height measurements on the same specimens is 2.9% (0.30 mm). These errors are small enough that data can be shared between researchers, and they confirm the replicability of these measurements.

### *Non-metric data*

I coded the eruption and wear stage for each tooth that I measured as shown in Table 3.2. Stages of eruption were identified as the following: "E1" when the tooth was still in the crypt (the bone that surrounds the growing tooth in the maxilla or mandible; Hillson 1986:178) so that none of it had emerged above the gum line; "E2" when the tooth was only half erupted; "E3" when the tooth was over half erupted but the cusps were still not in occlusion; and "E4" when the tooth was in occlusion, as evidenced by the cusps being worn, but the crown height was not measurable because the base of the crown had not emerged above the alveolar bone. For E2-E4, I measured the tooth height

from the alveolar bone to the occlusal surface, although these measurements were not included in the current analyses. When crown height was measurable, either because the tooth was fully erupted from the mandible or it was isolated from its mandible, I coded wear as the following: “UW” when a tooth was completely unworn; “VEW” when there was only a very slight amount of wear on the edge of the cusp and the crown height represented the height of an unworn tooth; “LW” when the occlusal surface has high peaks and the dentine bands are narrow; “MW” when the occlusal peaks are muted to no longer existent and dentine bands are wide; “HW” when the occlusal surface is flat and the crown is more than 50% worn away; and “VHW” when the crown is completely worn away. In *C. elaphus*, the crown-root junction is visible on a tooth in its mandible only after the tooth has come into occlusion. Therefore, the stages of E3 and E4 exclusively describe teeth in the mandible, and UW primarily identifies isolated teeth. It is very rare, if not impossible, to obtain an unworn crown height for a tooth still in its mandible.

These wear stage data were taken primarily to supplement and confirm my measurements, and they have had only a secondary role in the subsequent analyses. There are two exceptions. First, the identification of the “UW” and “VEW” teeth was necessary to determine the unworn crown height of a given sample. This measurement is used to help estimate age-at-death, because it makes it possible to quantify the amount of wear on other teeth from the same sample. Second, in some analyses I needed to include the total number of dP<sub>4s</sub> present, not just the measurable teeth (meaning the tooth had erupted enough so that the crown-root junction was visible). For these analyses, I included dP<sub>4s</sub> coded with all eruption and wear stages.

I also noted any peculiarities, such as a pathology or unusual wear. Unusual teeth were omitted from subsequent analyses if the relevant measure would be affected. Finally, I recorded the state of epiphyseal fusion for the metapodials. All unfused epiphyses were omitted from the analyses.

## **Analyses**

All bivariate plots, regressions, and correlations were calculated in JMP, and all boxplots were created in DataDesk (Data Description, Inc., P.O. Box 4555, Ithaca, NY 14852; [www.datadesk.com/](http://www.datadesk.com/)). R. G. Klein provided his Smirnov program to run Kolmogorov-Smirnov tests for the histograms. As described in Chapter 5 and by Steele and Weaver (2002), a statistical test was developed for the triangular graph as part of this project, and T. D. Weaver wrote the Triangle program that employs the new method. The Triangle program is available is available by contacting the author.

In my fossil analyses, I did not distinguish between right and left teeth or metapodials. For teeth, the actual number of mandibles represented by the sample is somewhere between the number of rights or lefts, which ever is larger, and the sum of the two. For example, Lazaret E has 13 right  $M_1$ s and 9 left  $M_1$ s for a total sample of 22 measurable  $M_1$ s. The minimum number of individuals present in the sample is 13, but up to twenty-two individuals could be represented. Of course, more mandibles may have been deposited during ancient times, but only a subset of them survived to the present. Given the number of isolated teeth in each fossil sample, I assumed that teeth from either side of the jaw were independent. Examination of the coefficients of variation (C.V.) in some of my larger samples reinforces this assumption. The C.V. provides a measure of the homogeneity of a sample. If the variance is low, the sample is more homogenous. If

many of the rights and lefts of my samples are from the same individuals, the C.V. of tooth crown heights of a combined sample should be lower than the variation found in either rights or lefts, because many of the teeth will be mirrors of each other. Fortunately, this is not the case. For Lazaret E, the C.V. of  $M_1$  crown heights is 49.97 for the rights, 46.39 for the lefts, and 47.37 for the total sample. I performed the same comparison for eleven of my larger samples, and the differences are always small. When the C.V.s for the groups of right teeth are compared to the C.V.s for the total groups of teeth, there is no significant difference (Wilcoxon test:  $p = 0.6694$ ; Median test:  $p = 0.6770$ ). The same is true of the lefts (Wilcoxon test:  $p = 0.6936$ ; Median test:  $p = 0.6770$ ). The lack of increased homogeneity in the combined samples of rights and lefts allows me to analyze both rights and lefts as one sample. In my modern specimens, I measured only one mandible, metacarpal or metatarsal for each individual, so there is no chance of counting these individuals twice.

## **Chapter 4: Methods of age determination**

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 so easy. Numerous methods exist for assessing age at death of archaeological specimens (for reviews see Amorosi, 1989; Morris, 1972; Pike-Tay, 2000; Wilson *et al.*, 1982), yet epiphyseal fusion, tooth cementum annuli, and tooth eruption and wear remain the most reliable and frequently applied methods (Klein & Cruz-Uribe, 1984; O'Connor, 2000; Reitz & Wing, 1999). In this study I rely on measuring tooth crown heights so that I can objectively determine the amount of wear on the tooth and perform statistical analyses on the results. In this chapter I review previous studies on determining age in *C. elaphus* by tooth eruption and wear. Using a larger sample of known-age *C. elaphus*, I follow Klein *et al.* (1983) to re-evaluate the utility of the Quadratic Crown Height Method (QCHM) to estimate age-at-death in fossil populations of red deer. Finally, I offer adjustments to the theoretical quadratic formula, which I then use in my subsequent analyses.

### **Teeth as indicators of age**

One of the primary goals of my study is to determine the ratio of prime to old individuals. Although important for discussing juvenile to adult ratios, epiphyses are fused once adulthood is reached and, therefore, are not useful for determining ratios of prime to old individuals. Thus, I used teeth, which continually change throughout an animal's life, to estimate age-at-death of the fossil specimens. Minerals, primarily

hydroxyapatite, constitute 96-97% of tooth enamel (Scott & Symons 1974 as in Hillson, 1986), so teeth are more resistant than bone to organic decomposition and mechanical erosion. Consequently, teeth are the most common mammalian fossils found. The same tooth type (P<sub>4</sub>, M<sub>1</sub> etc.) of different ages should preserve equally well. Unlike many post-cranial elements, teeth are almost always identifiable to species, reducing the possibility that a mortality profile might actually be a mix of two or more similar-sized species. Two methods for determining animal age-at-death from teeth have received the most attention: counting annually deposited cementum increments and assessing tooth eruption and the degree of wear.

Studies demonstrate that age-at-death in modern *C. elaphus* specimens can be successfully estimated by counting the number of seasonal bands of cementum, known as cementum annuli, that are deposited on the roots of a tooth (Hamlin *et al.*, 2000; Keiss, 1969; Lowe, 1967; Mitchell, 1967; Pike-Tay, 1991). Pike-Tay (1991; Pike-Tay *et al.*, 1999) applied this method to fossil red deer. Two types of bands are identified: “annuli” which are narrow and dense and represent periods of slow growth corresponding to winters, and “zones” that are wider and less dense and represent periods of rapid growth corresponding to summer (Pike-Tay, 1995:274). The formation of these bands is influenced by the quality of the diet and biomechanical stress resulting from mastication (Lieberman, 1993). Because these bands are deposited seasonally, cementum annuli often are examined to determine prey season-at-death (Burke, 1995; Lieberman & Shea, 1994; Pike-Tay, 1991; Pike-Tay *et al.*, 1999). To employ the method (as described by McKinley & Burke, 2000; Pike-Tay, 1995), teeth are embedded in epoxy and cross-sectioned down the mesial-distal midline of a molar. The exposed tooth is polished and

attached to a glass slide. The tooth is sectioned again parallel to the slide, and this thin section is ground and polished to a thickness of 30-50  $\mu\text{m}$ . The thin section is viewed under polarized transmitted light, and in ungulates other than horses, the annuli are counted on the root just below the crown-root junction. In horses, the cementum annuli are counted on the folds of the crown, because the roots form at an advanced age (McKinley & Burke, 2000). The amount of time represented before the cementum annuli began to form on the adult tooth (i.e. time elapsed while the deciduous precursor was in place) must be added to the number of annuli to obtain an estimated age-at-death.

Cementum annuli studies have their limitations. In modern specimens teeth are often decalcified before being cross-sectioned (Hamlin *et al.*, 2000), but fossil teeth usually do not retain enough organic matter to survive this process (Pike-Tay, 1991:62). Also, incisors are the most often studied element in modern specimens (as in Hamlin *et al.*, 2000), but they are fragile and difficult to identify when isolated in an archaeological context. Counting cementum annuli requires specialized equipment and training to accurately execute, which limits the method's general utility. However, the greatest limitation for zooarchaeologists is that this method requires large numbers of irreplaceable fossils to be cross-sectioned to generate one mortality profile. For these reasons, I chose to determine age in my samples by examining tooth eruption and wear.

### **Age determination by eruption and wear**

Age can be estimated in complete mandibular rows by determining which deciduous teeth have erupted and been shed and by evaluating the amount of wear on the adult teeth. The premise is that teeth erupt and are replaced in a predictable and timed sequence, and once in place, mastication wears down a tooth's surface at a rate that is

related to age and diet. Investigators can estimate the degree of wear by comparing the sample in question to known-age samples, previously sequenced samples, written descriptions, photographs, or measurements. These can be used to assign developmental or relative ages, but comparisons using a method based on samples with known ages are essential for establishing chronological ages (i.e. age-at-death in months or years).

Quimby and Gaab (1957) published a pioneering study on determining the age-at-death of *C. elaphus* mandibles using a known-age reference sample. Wildlife biologists tagged newborn Rocky Mountain elk from Montana in the vicinity north of Yellowstone National Park and collected a sample of 168 known-age mandibles. This study showed that calves, yearlings, and 2-year olds could be assigned to age class using the state of shedding of their deciduous teeth and eruption of their permanent teeth. Once the complete adult dentition was in place, age was more difficult to determine and the difficulty increased with age. This study involved comparisons of the known-age specimens to a jaw board of specimens assigned to age by previous comparison to the known-age specimens, determined key presence/absence characters that described each age class, and measured tooth height from the gums to the occlusal surface. Quimby and Gaab found that comparison to the jaw board was more accurate than comparison to written characteristics, particularly when the specimen was older. They also found that tooth crown heights were indicative of wear, but difficult to measure in the field on hunters' kills and dependent on the gum line being intact. They concluded that the best method for determining the age of their unknown sample of elk was comparison with the known-age mandibles. Following that was comparison to assigned-age mandibles, and finally comparison with good drawings or photos of known-age mandibles. Not

surprisingly, the level of experience of the examiner also determined the accuracy of the age assignments. Luckily, when errors occurred, they were unbiased – specimens were equally likely to be over or under aged. One limitation of Quimby and Gaab’s study is that although the sample was large, it was skewed toward younger individuals with only a few specimens represented in the older age classes. The difficulty in assigning age to older specimens might be resolved if additional older specimens with known ages were available.

Lowe (1967) used a sample of 34 known-age Scottish red deer (*C. elaphus scoticus*) mandibles from the island of Rhum, Scotland to investigate four methods of age determination: tooth and jaw measurements; dentine increments inside the incisor crown; annuli in cementum deposits on the root pad of M<sub>1</sub>; and tooth eruption and wear stages. He found that comparing tooth eruption, shedding, and wear of unknown specimens to known-age specimens was the most reliable method, although he also provided a list of characters and photographs describing each age group. In measuring his mandibles, Lowe found that the best age estimator was a linear function that depended on the distance between the third molar and the posterior margin of the angular process, jaw depth below the first molar, and the minimum crown height of the first molar. This function assigned correct ages for half of the specimens, and with one exception, all other mandibles were predicted within plus or minus a year. Lowe acknowledged that although individuals of the same age often exhibit variability in crown height, maximum crown height (as measured in my study) might actually be a better predictor of age than the minimum crown height he measured (measured from the “saddle” of the tooth or the lowest point between the two cusps). This is because the cusps of the tooth are actually in occlusion

and wearing for a period of time before the “saddle” wears (before minimum crown height begins to record a decrease in size). Another limitation of Lowe’s study was the small sample size and young ages of the known-age individuals. The oldest specimen is 96 months (8 years) old whereas *C. elaphus* individuals can live to be 192 months (16 years) and older (Houston, 1982; Lowe, 1969).

In more recent studies, Brown and Chapman developed scoring schemes for determining the age of juvenile (Brown & Chapman, 1991a) and adult (Brown & Chapman, 1991b) Scottish red deer mandibles. To do this, they used 113 mandibles from Richmond Park, Surrey, England that had known ages ranging from 1 month to 138 months (11.5 years). They used X-rays of the 82 juvenile mandibles to identify stages of tooth development and eruption, such as evidence of the crypt and degree of crown and root formation. In total, they identified 10 juvenile stages. Each tooth in the mandibular row was given a score that represented the stage, and all of the scores for the row were summed so that the scores became higher as the individuals became older. The regression equation of age on score provided a method of predicting ages (with 95% confidence intervals) for mandibles of unknown age. Using this method, age was predicted for the known-age juveniles to within  $\pm 4.7$  months or less (Brown & Chapman, 1991a:93).

Brown and Chapman (1991b) developed a similar scoring technique for wear features on adult dentitions ( $n = 111$ ) using the same known-age Scottish red deer sample as in their study described above. They identified 20 zones for  $M_1$  and  $M_2$ , and 25 for  $M_3$ . A score of 0, 1 or 2 was given for each of these zones based on the degree of wear, and the scores were added for the molar row. They regressed age on score to obtain a curvilinear regression equation that they could use to predict age for unknown mandibles.

As scores increased with age, the width of the 95% confidence intervals also increased. The maximum interval was  $\pm 30.5$  months for the oldest individuals. Their study showed a large range of ages during which a particular wear pattern, or overall wear pattern, appeared in older individuals, and, therefore, they found that scoring individual features accounted for all aspects of the wearing phenomenon by accumulating data on wear locations. Brown and Chapman (1991b) found their method to be good because using the scoring system increased the objectivity of recording wear patterns. It also gave a quantified value with confidence intervals that could be used in statistical analyses, unlike coded wear stages. The scores also accounted for variation in wear patterns of animals with the same age. In addition, coding should reduce the need for a known-age reference sample or jaw board to assist with accurate wear assessments, as recommended by Quimby and Gaab (1957).

There are limitations in using tooth eruption and wear to estimate age from mandibles of *C. elaphus* or any other species. One is that wear may vary from population to population due to diet differences. This variation will affect estimates of age using both wear stages and crown height measurements. If an animal is eating more grasses or there is more sand and grit in the diet, the teeth may wear faster and make a specimen look older than its chronological age. Spinage (1973:183) suggested that teeth are critical for survival; it would be surprising if they varied widely in efficiency in a single species, because this is how animals acquire energy. This is particularly true because consistent wear (not too much or too little) is necessary to maintain a healthy mouth in wild populations (Spinage, 1973). Lowe (1967) found that teeth of red deer from German forests had similar wear per age patterns as red deer from Rhum, although the climate,

habitat, and management were very different. Spinage and Brown (1988) reached the same conclusion when they studied the wear on two geographically separated subspecies of African buffalo (*Syncerus caffer*) that differ in climate, diet, and body size. Important for my study of Late Pleistocene red deer, they concluded that “tooth wear is relatively constant within species despite wide differences in bodily size and environment” (Spinage & Brown, 1988:227). Many of the studies cautioning differences in wear rates between populations have included domesticated animals or other populations where, at least for part of the year, humans supplemented the animals’ diet (Gifford-Gonzalez, 1991; Spinage, 1973:174), although the problem has also been noted in wild populations (Flook, 1970). No one has devised a reliable method to account for differences between populations in rates of wear, and more research is needed on this problem. For the moment, age-at-death assessments using wear on teeth must assume a consistent rate of wear between individuals separated in space and time.

Individual variation may also reduce the accuracy of age determination methods. There may be variation in the ages at which teeth erupt and are shed. Chapman and Brown’s (1991b:525) review of the literature on these ages combined with Lowe’s (1967) and Quimby’s (1957) studies suggests that in *C. elaphus*, variation in the ages at which teeth erupt is likely to be minor. Other factors, including favoring one side of the jaw, are more likely to increase the variation within one population. Kierdorf and Becher (1997) suggested that individual variation may be due to differences in the degree of enamel mineralization. They recommended measuring enamel hardness along with degree of wear, but acknowledge that this requires specialized, expensive equipment and is labor intensive.

A major limitation to using tooth eruption and wear to estimate age is that the methods described above are best used on complete dental rows. Unfortunately, these are rare in fossil samples, and zooarchaeologists need a method of age estimation that can be used in the absence of a reference sample and on isolated teeth. Measuring tooth crown heights to assess the amount of wear provides an objective, easy to replicate, non-destructive technique that can be applied to both isolated teeth and teeth in mandibles, making it ideal for archaeological assemblages. The interobserver error for this measurement is low, 2.9%, thus demonstrating its replicability (Table 3.1).

### **The Quadratic Crown Height Method**

#### ***Spinage's model***

Spinage (1971) first proposed a wear model for using crown heights to age hypsodont ungulates. Klein and colleagues (Klein *et al.*, 1983; Klein & Cruz-Uribe, 1983; Klein *et al.*, 1981) tested this model on a sample of known-age elk. The technique now is known as the Quadratic Crown Height Method (QCHM) and employs a set of quadratic formulas based on a variable rate of wear that can be used to predict age-at-death from tooth crown height when the beginning and end points are known. Unlike the eruption and wear methods, the QCHM is easy to replicate, is objective, and can be utilized with isolated teeth. Unfortunately, the method is subject to the same variations in individual and populational wear rates as other tooth wear methods. To use these methods, individual variation must be random, and the method must not consistently over- or under-estimate the ages of animals (Spinage, 1973).

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, as the opposing occlusal surfaces  $M_1$  become smoother, friction decreases and as  $M_2$  and  $M_3$  begin to wear, friction on anterior surfaces further decreases (Spinage, 1971). Although Spinage found that using known-age comparative specimens was the most reliable way to accurately determine the age-at-death of an unknown individual, the conceptual wear model was satisfactory in "predicting the mean age of samples, and not the age of individuals" (Spinage, 1973:183).

The QCHM assumes that when the permanent teeth are worn completely away (crown height equals '0'), the animal dies. Because  $M_1$  erupts before  $M_2$ ,  $M_1$  will wear to '0' before  $M_2$ . 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, including *C. elaphus*. Instead, the age of potential ecological longevity must be used. 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 formulas are (from Klein *et al.*, 1983:49):

$$\text{For deciduous teeth: } AGE = AGE_s [(CH-CH_0)/CH_0]^2$$

$$\text{For permanent teeth: } AGE = (AGE_{pel} - AGE_e) [(CH-CH_0)/CH_0]^2 + AGE_e$$

Equations are calculated by substituting the appropriate values for each tooth.

$AGE_s$  is the age at which the deciduous tooth is shed,  $AGE_e$  is the age at which the permanent tooth erupts, and  $AGE_{pel}$  is the potential ecological longevity of the species. In this study, age is measured in months.  $CH_0$  is the mean initial unworn crown height for each tooth type for the sample under study, and  $CH$  is the crown height, measured in millimeters, of the specimen for which age is being assigned.

### ***Testing the model with known-age elk***

Spinage had reasonable success with his model for assigning age in impala (*Aepyceros melampus*, Spinage, 1971) and zebra (*Equus burchelli boehmi*, Spinage, 1972), but he lacked large samples of known-age specimens with which he could fully test his model. Klein and colleagues (Klein *et al.*, 1983; Klein & Cruz-Uribe, 1983; Klein *et al.*, 1981) tested Spinage's wear model with Quimby and Gaab's (1957) known-age sample, plus a few specimens that had been added since the 1950's. Their sample consisted of 170 mandibles with ages ranging from 5 months to 260 months (21.7 years, Table 4.1, Klein *et al.*, 1983). The majority of the specimens were collected at hunter checkpoints, so the month of death was mainly from October to January. Because Rocky Mountain elk in this region give birth around June 1<sup>st</sup> each year, the specimens formed discrete clusters around the half-year mark. Until 5.5 years, the sample was an even mix of males and females, however, after this age, the sample was primarily females and "unknowns" that were probably males whose antlers were removed (Klein *et al.*, 1983). Although, the oldest individual was 260 months (21.7 years) old, 90% of the sample was younger than 72 months (6 years) old. These studies used the same crown height measurement that I describe in Chapter 3.

Klein *et al.* (1983) first regressed age on tooth crown height for the known-age elk sample. They found that for all tooth types, the coefficients of determination ( $r^2$ ) were larger than 0.80 for both linear and quadratic regressions, indicating that in general, crown height was a good predictor of age, because there was a good relationship between crown height and age. However, examination of the standard errors of estimate, which were high, indicated that individual crown heights were not a very accurate predictor of

individual ages. Analyses of the residuals showed that crown height could accurately predict broader age classes, such as those defined as 10% of potential ecological longevity, and that when an individual was not assigned to the correct age class, it was assigned to an adjacent one. Klein *et al.* (1983) also found that although the linear and quadratic regression formulas predicted age equally well for the deciduous fourth premolar, the quadratic formula was preferable for the molars. The linear formula was more likely to underestimate the ages of old individuals. The quadratic fit followed Spinage's suggestions from the early 1970s. Klein *et al.* (1983) thought that the quadratic regression formulas would have fit their data even better if their sample had included a larger number of older individuals.

The next step of Klein *et al.*'s (1983) analysis was to compare the theoretical formulas proposed by Spinage to the regression equations derived from their known-age sample. They found that, in general, the two formulas corresponded well and that the main difference was in the age at which the tooth crown height reaches '0'. The theoretical formula has tooth crown height in M<sub>1</sub>, M<sub>2</sub>, and M<sub>3</sub> reaching '0' at the same time (age of potential ecological longevity) and in life, this is not the case. The first molar is the first to erupt and the lowest crowned, therefore it often reaches a crown height of '0' before the animal dies. The authors found that the quadratic theoretical formula was the best age estimator for M<sub>1</sub> and that more data on M<sub>2</sub> and M<sub>3</sub> were needed for older individuals in order to make corrections for these teeth. They concluded that, until the sample could be expanded, the theoretical quadratic formulas should be used, because they reflected a variable rate of wear that was not figured into the linear formulas. For dP<sub>4</sub>, the authors offered a "corrected" theoretical formula that acknowledged that crown

height would only reach '0' if the tooth remained in the mouth beyond the age that it is generally shed. They set the "corrected" age of shedding (the age at which dP<sub>4</sub> crown height would reach '0') to 25% longer than the actual age at which dP<sub>4</sub> is shed.

In sum, Klein *et al.* (Klein *et al.*, 1983; Klein & Cruz-Urbe, 1983; Klein *et al.*, 1981) found a strong relationship between tooth crown height and age. They concluded that Spingale's theoretical formulas, now known as the Quadratic Crown Height Method (QCHM), could not adequately estimate age within a month or two to isolated teeth, but they were adequate to assign 10% of life-span age classes ( $\pm 19.2$  months) in *C. elaphus*. These age classes are sufficient to study of overall shape of an age distribution, which is the goal of most faunal analyses.

#### ***Additional investigations into the QCHM***

Gifford-Gonzalez (1991) tested the QCHM with two samples of known-age North American bison (n = 65 and 52). She was particularly interested in the predictive value of the equations at the ends of the distribution, because her studies of Neolithic cattle mandibles suggested that initial wear on M<sub>1</sub> and M<sub>2</sub> was slow compared to the rapid wear predicted by the QCHM. Her study of the known-age bison samples supported this, although she measured known-age crown heights as the distance from the crown-root junction to the "saddle" between the cusps on the lingual side of the mandible (similar to Lowe, 1967). She concluded that this did not affect her results, because her Neolithic cattle sample showed the same pattern when crown height was measured to the metaconid peak. This initial slow attrition meant that when age was assigned with the QCHM, young specimens were underestimated and old specimens were overestimated. She also was concerned that while the QCHM may be able to effectively predict 10% of

life span age class, this may not be enough resolution to test some hypotheses, particularly in studies of domestication where fine resolution is needed or in studies of long-lived species where 10% of life-span covers a long period of time. Finally, Gifford-Gonzalez (1991) concluded that measurements of tooth crown height are a useful way to assess the degree of wear on a tooth, and species-specific regression formulas derived from large samples of known-age individuals may better predict age than a generalized quadratic equation. Although this is an ideal goal, known-age animals are currently unavailable for most species, and regressions will be inaccurate if tooth size varies through time or space as it does in *C. elaphus*. Model formulas where population specific values can be inserted will better estimate age in these types of species.

Pike-Tay *et al.* (2000) tested the QCHM using a large sample of 999 known-age barren-ground caribou (*R. tarandus groenlandicus*) from the Kaminuriak population of Canada. They found that the mean crown height for the two lobes had the best relationship with age and is useful because it can help accommodate fragmented teeth. Their data generally supported a quadratic correlation between crown height and age, as assumed by the QCHM. They found that crown height does not equal '0' at the age of potential ecological longevity, and they suggested using the average maximum life span of the population calculated independent of tooth wear; this is discussed in more detail below in the section "Adjusting the QCHM – AGEpel." In general, Pike-Tay *et al.* (2000) found that the QCHM failed to approximate the wear patterns of their sample, but by modifying the formula to fit species-specific patterns of wear, the QCHM would be useful for estimating age-at-death in samples of fossil reindeer.

### ***Ways of measuring tooth crown height***

There are multiple ways to measure tooth crown height. I follow Klein and colleagues (Klein, 1978; Klein *et al.*, 1983; Klein & Cruz-Uribe, 1983; Klein & Cruz-Uribe, 1984) and measured crown height as the minimum distance between the occlusal surface and the crown-root junction taken on the buccal-most surface of a lower tooth (Figure 3.2). Measuring the buccal-most surface means that the measurement includes the protoconid or hypoconid peaks. This has become the standard crown height measurement for ungulate teeth and is taken by many researchers (e.g. Gaudzinski, 1995; Hoffecker *et al.*, 1991; Morrison & Whitridge, 1997; Pike-Tay, 1991; Pike-Tay *et al.*, 2000; Slott-Moller, 1990; Walker, 2000). Some researchers measure crown height on the lingual side of a mandibular tooth as the minimum distance between the occlusal surface (the metaconid or entoconid peaks) and the crown-root junction (e.g. Koike & Ohtaishi, 1985; Lister, 1981). The buccal and lingual measurements are very similar to each other. I would expect that they have equally strong relationships with age, because metaconid height is highly correlated to protoconid height ( $n = 47$ ,  $r = 0.97$ ). The lingual surface of a mandibular tooth is fairly flat, so I find the lingual measurement harder to consistently define than the buccal measurement, particularly once the cusps have worn flat. In addition, the lingual measurement is awkward to take on comparative material when the mandibular rami are still articulated. For these reasons, I chose to measure crown height on the buccal-most surface of mandibular teeth.

When using these tooth measurements, some researchers have chosen to average the heights of the two cusps on the buccal side (Morrison & Whitridge, 1997; Pike-Tay *et al.*, 2000). The justification for doing this is that specimens that are missing either their

anterior or posterior cusp or have asymmetrical wear can be included in the sample.

Taylor (1988) carried this idea one step further by averaging the crown height measurements on all four peaks of the M<sub>1</sub>s in his sample.

Some researchers have measured tooth crown height as the distance from the crown-root 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 is done when the cusps are damaged and cannot be measured (Gifford-Gonzalez, 1991; Lowe, 1967). This measurement is biased, because it is not affected by wear until the peaks or cusps of the tooth are worn. By not recording the early wear on the tooth, individuals will be recorded as younger than their actual age.

Variation also is present where the base of the crown height is measured. Spinage (1972) measured crown height of zebra from the occlusal surface to the “saddle” of the root, not the crown-root junction. This measurement cannot be used widely, because it cannot be taken on teeth still in the mandible. Wildlife biologists commonly measure tooth height from the bone or gum line to the occlusal surface, because it can be taken on living animals or unmacerated specimens (Quimby & Gaab, 1957; Severinghaus, 1949; Van Deelen *et al.*, 2000). This measurement is very problematic, because crown height may not change if a tooth is erupting and wearing at the same rate. This measurement does avoid one problem with measuring crown height from the crown-root junction, which is the masking of this junction by the bony alveolus. Often, the crown-root junction is not visible until an animal is many years old, a problem in very hypsodont bovids. This can be handled a few ways. These specimens can either be excluded from analyses or included based on their wear stage. The bone can be cut away to reveal the

crown-root junction. Finally, X-rays of the mandibular ramus can be taken, which will reveal the junction because enamel and dentine have different densities (Klein *et al.*, 1981). Fortunately, for many fossil assemblages, teeth are often found in isolation so that the crown-root junction is readily visible.

### **Expanded known-age sample**

I expanded Klein and colleagues' sample of known-age elk to 226 individuals by collecting data on 56 additional specimens (Table 4.1). These individuals are from the same general population of Rocky Mountain elk as Klein and Cruz-Uribe's sample. Although 70% of the new specimens are still under 72 months (6 years), this additional sample expands the number of individuals in the 78-90 months (6.5-7.5 years) age category so that prime-aged individuals are better represented. The potential ecological longevity, or the average maximum life span, of *C. elaphus* is 192 months, so the oldest age classes are still underrepresented. The older individuals are still primarily females, because adult males could not always be identified directly (the frontals had been removed, presumably to retrieve antlers) and are less numerous in the population due to extermination earlier in life by human hunters (K. Hamlin, personal communication).

### ***Regression analysis***

In order to determine the nature of the relationship between crown height and age, I regressed age in months on tooth crown height in millimeters for each tooth type. Both linear (a) and quadratic (b) regression lines are plotted in Figure 4.1 and listed in Table 4.2. All of the regressions are highly significant. The quadratic regressions provide better fits to the data, as shown by the slightly higher coefficients of determination ( $r^2$ ) and

lower standard errors of estimate. This confirms Spinage's (1971) proposal that teeth will start wearing rapidly, but then the wear rate will decelerate as the occlusal surfaces become smooth. The standard errors of estimate show that it should be possible to estimate age-at-death within approximately  $\pm 1$  year. Klein *et al.* (1983) had similar results in their study of the original know-age elk sample, and Pike-Tay *et al.* (2000) also found that quadratic regression lines better fit their large sample ( $n = 999$ ) of known-age barren-ground caribou. In Morrison and Whitridge's (1997) study of known-age barren-ground caribou from the same population as Pike-Tay *et al.*'s sample, they found that linear equations adequately predicted age, but this discrepancy is most likely due to their much smaller sample size ( $n = 78$ ).

I analyzed unpublished measurements taken by C. Wolf on known-age white-tailed deer from New Jersey and New York. This sample of 124 individuals contains animals ranging from only a week old through 114 months (9.5 years), which is about the maximum life span of individuals of this species (Severinghaus, 1949). I performed linear (a) and curvilinear (b) regressions of age on crown height for  $dP_4$ ,  $M_1$ ,  $M_2$ , and  $M_3$ , (Figure 4.2 and Table 4.3). As with as with elk and caribou, the quadratic regressions provide a better fit than the linear regressions, supporting a non-linear rate of wear. The different rates of wear for the three species are visible in the quadratic regressions of  $M_1$  for each species (Figure 4.3; data from Klein & Cruz-Urbe, 1983; Morrison & Whitridge, 1997:1105-6, and this study).

I assessed the ability of the regression equations to predict age by plotting residual values against known ages for the known-age sample of elk (Figure 4.4). 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 Figure 4.4, 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 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 in each age class, age is almost always assigned to either the correct age class or to one adjacent, as is suggested by the standard error of estimates. To varying degrees, all regressions exhibit a tendency to underestimate age as the specimens get older. This suggests that at the "old" end of the distribution of crown height, neither a linear or quadratic line correctly fit the data, although the quadratic provides a better fit. When I tried cubic regressions, the results were very similar to those for the quadratic regression, suggesting that the quadratic equation adequately described the relationship. This lack of fit in the older age classes is possibly due to small sample sizes of older individuals, although wear stage studies show that variation in wear increases with age. Possibly, teeth do not wear more slowly with age as Spinage assumed. Finally, when the tooth has worn below the crown-root junction, its crown height must be recorded as '0', which compounds the problem in older individuals by creating a wide spread of ages when crown height equals '0'.

### ***Potential differences in wear rates between the sexes***

Any method of assessing age from wear on teeth assumes that individual variation in timing of eruption and rate of wear is limited. One potential source of variation is differences in wear rates between males and females. I investigated this possibility in the

M<sub>1</sub>s of the known-age elk sample. Age in months was regressed on M<sub>1</sub> crown height the same as in Figure 4.1, but I calculated separate regression lines for males (n = 42) and females (n = 104; Figure 4.5). When 95% confidence intervals are defined for each line, they overlap for the entire area of interest. This indicates that differences in wear rates between males and females cannot be detected and therefore separating the sexes before determining the age of specimens is not necessary. This is fortunate because sex cannot be identified in fossil *C. elaphus* teeth; tooth size is not sexually dimorphic (see Figure 6.2).

The lack of differences between the sexes in this sample of *C. elaphus* is supported by studies of caribou and white-tailed deer. When Morrison and Whitridge (1997) regressed age on M<sub>1</sub> crown height for their sample of 78 known-age caribou mandibles, they obtained different linear regression lines for the sexes, although they do not provide statistical results. By examining the data they provided in an Appendix to their paper, I was able to determine that after approximately 70 months, the confidence intervals for these two lines do not overlap, supporting their conclusion of different wear rates for males and females, at least at advanced ages. In Pike-Tay *et al.*'s (2000:147) substantially larger sample of caribou (n = 999) from the same population as Morrison and Whitridge's sample, they found no differences in wear between the sexes. This suggests that Morrison and Whitridge's difference may be due to inadequate sample size.

Van Deelen and colleagues (2000) studied a sample of 100 white-tailed deer from Illinois whose age-at-death had been assigned by counting cementum annuli. Although they measured crown height as the maximum height from the occlusal surface to the stains at the tooth gum line, they found no differences in degree of wear between male

and female  $M_1$ s, although  $M_3$  may show some differences. In the sample of known-age white-tailed deer described above, there is a difference in wear rates between males and females in  $M_1$ . When age is regressed on  $M_1$  crown height, the confidence intervals for the sex specific regression lines do not overlap at approximately 25 months and older. These results should be considered with caution, because although males outnumber females in the sample (males:  $n = 69$ , females:  $n = 35$ ), no male is over 31 months while the oldest female is 90 months.

### ***Further testing of the QCHM with known-age elk***

The regression equations appear to adequately estimate age from crown height in the sample of known-age Rocky Mountain elk. If age estimates were needed for this population only, then the regression equations are quite 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 size and tooth size vary across space and through time. Initial unworn crown heights that are different from the specimens used in the regression analysis would cause errors in age estimation in a new sample, so it is still desirable to have a theoretical formula in which initial crown heights and other values can be sample specific. For this reason, I tested the ability of the QCHM to estimate the ages of the expanded known-age elk sample. To do this, I inserted the tooth and life history parameters presented in Table 4.4 into the theoretical formulas presented above.

In general, the coefficients in theoretical formulas are similar to those obtained in the regression equations (Table 4.5). In each case, the most noticeable difference is in the age when crown height equals '0', which for adults is considered the potential ecological

longevity for individuals of this species and for juveniles is the age at which the deciduous tooth is shed. This value in both  $M_1$  regressions and the  $M_2$  linear regression is lower than in the theoretical equations, but for all the other tooth types, the regression value is higher.

Using the theoretical formulas listed in Table 4.5, I estimated age for each specimen and plotted the residuals for each tooth type in Figure 4.6 exactly how I plotted the regression equation residuals in Figure 4.4. Examination of the residuals shows that although ages were consistently underestimated for  $dP_4$ , the estimated ages all fall within the correct 10% of life span age class. Ages for  $P_4$ ,  $M_2$ , and  $M_3$  were consistently underestimated and the amount of underestimation increases as the individuals get older. Ages for  $M_1$  were overestimated, and younger individuals were more likely to be overestimated. These results support Klein *et al.*'s (1983) suggestion that crown height equals '0' at different age for different teeth, and therefore, age of potential ecological longevity may not adequately estimate this parameter.

To further test the QCHM for each tooth type, I created mortality profiles using 10% of life span age classes based on the known ages, the ages estimated from the regression equation, and the ages estimated from the QCHM (Figure 4.7). I statistically compared the quadratic regression and QCHM profiles to the known-age profiles using the Kolmogorov-Smirnov test, which compares the cumulative distributions of two histograms. In all cases the profiles based on the regressions are not statistically different from the known ages. The  $dP_4$  profile based on the QCHM is not different from the known ages, but the QCHM profiles for the permanent teeth are all different from the profiles created from the known ages. It is expected that the regression equations would

be good at assigning ages, because they are estimating age for the sample from which they are derived. But the QCHM does not adequately estimate age in adult teeth and requires further examination as to why. Two possible explanations come to mind.

### *Adjusting the QCHM formulas*

#### *AGE<sub>pel</sub>*

One reason for discrepancies between the theoretical formulas and regression equations is that tooth crown height does not always equal '0' when an animal reaches the age of potential ecological longevity, or for  $dP_4$ , the age when the tooth is shed. For  $M_1$ , teeth can be worn past the crown-root junction before the animal dies (Spinage 1972; personal observation on the wolf-kill sample). The known-age sample has one 150-month-old individual with an  $M_1$  crown height of '0'; all individuals 173 months and older ( $n = 4$ ) have  $M_1$  crown heights of '0', and one 156-month-old individual still has a measurable crown height. In all of these cases,  $P_4$ ,  $M_2$ , and  $M_3$  still have crown remaining. Only one 260-month-old individual has  $M_2$  and  $M_3$  crown heights of '0';  $M_1$  is completely worn away, but  $P_4$  still has a measurable crown. Based on these data,  $AGE_{pel}$  should be changed in the QCHM formulas to the age at which each tooth type reaches '0', as suggested by Klein *et al.* (1983). This value can be considered the age of the tooth's potential longevity or  $AGE_{tpl}$ . For this study, estimates of  $AGE_{tpl}$  are taken from the quadratic regression equations, but ideally these estimates should be determined using large samples of known-age individuals with completely worn teeth. At the moment, the known-age data set has too few older animals, so y-intercept values, i.e. the ages when crown height reaches '0', must be calculated from the quadratic regressions.

For  $M_1$ , the y-intercept is 163.6 months. As described above for the known-age sample, the age when  $M_1$  crown height reaches '0' is between 150 and 173 months, so the value from the regression equation is consistent with the known-age data. For known-age  $M_2$ s, tooth crown height reaches '0' between 185 and 260 months, which is consistent with a y-intercept of 218.5 months.  $M_3$  crown height also reaches '0' between 185 and 260 months in the known-age sample, so the y-intercept of 224.2 months is also a reasonable estimate of the age at which  $M_3$  crown height reaches '0'. For  $dP_4$ , the y-intercept is 33.9 months, suggesting that  $dP_4$  crown height has not reached '0' by the time the tooth is shed when an animal is approximately 26 months old. In the known-age sample, the oldest animals to have their  $dP_4$ s in place are 29 months old ( $n = 2$ ).

I substituted  $AGE_{tpl}$  for  $AGE_{pel}$ , 163.6 months, into the QCHM's formula for estimating age from  $M_1$  crown height. All other values stayed the same. The resulting equation is shown in Figure 4.8.A, 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  $M_1$ s, and all but a few are within one adjacent age class; changing  $AGE_{pel}$  to  $AGE_{tpl}$  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 (Figure 4.8.B). This suggests that there is no bias in the age estimates. For  $M_2$  and  $M_3$ , substituting the calculated ages of when crown height will equal '0' for potential ecological longevity improves the accuracy of age estimates from these teeth, but there is still a strong tendency to underestimate the ages of individuals in older age classes. Performing a similar substitution for  $P_4$  does not greatly improve the performance of the theoretical equations. When the y-intercept value is

substituted into the equation for dP4, the predictions improve, but ages of young specimens are overestimated and the ages of older specimens are underestimated (graphs not shown).

Klein *et al.* (1983:54) also argued that AGEpel needed to be adjusted in the QCHM, but they decided that their known-age sample size was too small to accurately adjust the formula. 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) also chose to manipulate AGEpel so that age predictions using the QCHM were more similar to those produced by the regression equations. They changed AGEpel to the average maximum life span, which is still the same for all teeth. It is unclear how average maximum life span differs from the age of potential ecological longevity (they do not offer an adjusted value in their paper).

Klein *et al.* (1983) reasoned that AGEpel should equal the age when crown height reaches '0' for each tooth, but data on large known-age samples were not available to test this assumption. They had to assume that when tooth crown height equals '0', the animal died, 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). Pike-Tay *et al.*'s (2000) reformulation of AGEpel to average maximum life span appears not to be a reformulation but a repetition of Klein *et al.*'s (1983) assumption. I argue here that tooth crown height reaches '0' at different ages for different teeth, and therefore a different value is needed for each tooth type for the most accurate age estimates (see also

Klein & Cruz-Uribe, 1983:54). These values should be derived from known-age samples whenever possible.

Adjusting the value of potential longevity to tooth longevity presents an additional problem for  $M_1$ . The age of tooth longevity (163.6 months) is lower than the age of animal longevity (192 months), so when estimating age from  $M_1$ , 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  $M_1$  specimens will be placed in the 10<sup>th</sup> age class. In my study, I have chosen to compare histograms composed of nine age classes, and thus this bias against Age Class 10 is consistent across all samples. In future work, it may be possible to code for teeth worn past '0', and they could all be placed in Age Class 10. For this study, these teeth were recorded as having crown heights equaling '0' and were assigned to Age Class 9.

#### *Fitting a line*

A second methodological consideration is whether or not a quadratic curve best describes the relationship between crown height and age. I used linear and quadratic regressions in this study, because they are readily calculated by most standard statistical software packages. But there is no a priori reason to expect that teeth wear at either linear or quadratic rates, and a different shaped line may better fit the data. The form of the relationship between crown height and age can be adjusted mathematically by changing the exponent of the QCHM equation. A lack of fit between the data and a quadratic curve may be why changing the value of potential ecological longevity does not greatly improve the ability of the  $M_2$  and  $M_3$  theoretical equations to estimate age. Changing the exponents could provide better estimations of age using these teeth. Pike-Tay *et al.*

(2000) also adjusted exponents in their assessment of the QCHM using known-age caribou.

To investigate this issue, I performed transformations of the QCHM formula to determine empirically if a quadratic equation best describes the relationship between crown height and age. The quadratic crown height equation can be written as follows:

$$(1) \quad AGE = (AGE_{tpl} - AGE_e) [(CH-CH_0)/CH_0]^m + AGE_e$$

Note that the exponent of 2 has been replaced by  $m$ , because this is the constant under investigation. This equation was transformed to the following equation by subtracting  $AGE_e$  from both sides of the equation:

$$(2) \quad AGE - AGE_e = (AGE_{tpl} - AGE_e) [(CH-CH_0)/CH_0]^m$$

This equation is equivalent to the allometric growth curve,  $Y = aX^b$ , where  $Y = AGE - AGE_e$ ,  $a = (AGE_{tpl} - AGE_e)$ ,  $X = [(CH-CH_0)/CH_0]$ , and  $b = m$  (Sokal & Rohlf, 1995:533-535). Because tooth wear may be described by the allometric growth curve, transforming both variables to the logarithmic scale makes the curve described by this relationship become straight (Sokal & Rohlf, 1995:533). The regression equation of the transformed data is  $\log Y = \log a + b \log X$ . I used this regression equation to solve for  $b$ , the exponent of the QCHM equation and the constant that determines the shape of the curve. To transform the QCHM equation to the same form as this regression equation, I took the base-10 logarithm of both sides of equation 2 above. This required that the absolute value of  $(CH-CH_0)/CH_0$  be used, because logarithms cannot be taken on negative numbers. This is the resulting equation:

$$(3) \quad \log_{10} (AGE - AGE_e) = \log_{10} (AGE_{tpl} - AGE_e) + m \log_{10} |(CH-CH_0)/CH_0|$$

This equation has the form of the standard equation of a line ( $y = mx + b$ ) where  $y = \log_{10} (AGE - AGE_e)$ ,  $x = \log_{10} |(CH-CH_0)/CH_0|$ , and the  $y$ -intercept  $b = \log_{10} (AGE_{tpl} -$

AGEe);  $m$  is the slope in both equations. Next, I calculated  $x$  ( $\log_{10} |(CH-CH_0)/CH_0|$ ) and  $y$  ( $\log_{10} (AGE - AGEe)$ ) for each tooth in my sample using that tooth's crown height and the AGEe and  $CH_0$  values listed in Table 4.4. I plotted the  $x$  and  $y$  values for  $M_1$ s and performed a standard least squares regression. The result was the following regression equation:

$$(4) \quad y = 2.18548 + 1.99177 x$$

Substituting back in for  $x$  and  $y$ , the resulting equation is:

$$(5) \quad \log_{10} (AGE - AGEe) = 2.18548 + 1.99177 \log_{10} |(CH-CH_0)/CH_0|$$

The slope of this equation is 1.99 ( $r = 0.90$ , 95% confidence interval of 1.84-2.14), which directly confirms the use of a quadratic equation (exponent equaling 2) for estimating age from  $M_1$ . When this procedure was applied to the other teeth, the resulting slope for  $P_4$  was 0.84 ( $r = 0.85$ , 95% confidence interval of 0.72-0.96),  $M_2$  was 1.33 ( $r = 0.91$ , 95% confidence interval of 1.17-1.49),  $M_3$  was 1.56 ( $r = 0.93$ , 95% confidence interval of 1.33-1.79), and  $dP_4$  was 1.56 ( $r = 0.90$ , 95% confidence interval of 0.76-0.95). These results suggest that a quadratic equation is appropriate for  $M_1$ , but it may not best describe the relationship between crown height and age for the other tooth types. The values for  $P_4$  and  $dP_4$  suggest that wear is initially slow in comparison to the other teeth. These results should be considered preliminary. There are gaps in the  $P_4$  and  $M_2$  data where crown heights of some young individuals were not measurable, because the crown-root junctions were masked by bone. With larger known-age samples, adjusting the exponents by calculating the slopes as described above could improve age estimation using these teeth.

In Pike-Tay *et al.*'s (2000) study of known-age caribou, they determined that the exponent ( $m$ ) of the curves describing the relationship between  $M_1$ ,  $M_2$ , and  $M_3$  crown

height and age was 1.6, which is similar to my value for  $M_3$ , but different from my values for  $M_1$  and  $M_2$ . It is probable that elk and caribou teeth wear at different rates, because caribou teeth are less hypsodont (have lower crowns) than elk teeth. As concluded by Pike-Tay *et al.* (2000), these relationships should be empirically determined for the species under study whenever possible.

Equation 5 also provides a value for  $AGE_{tpl}$ , which can be calculated from the y-intercept  $b$  in the equation. This provides an additional method for estimating the age at which crown height reaches '0'. For  $M_1$ , the y-intercept was  $b = 2.18548$ .

The variable  $\log_{10}(AGE_{tpl} - AGE_e)$  was resubstituted for  $b$  to obtain:

$$(6) \quad \log_{10}(AGE_{tpl} - AGE_e) = 2.18548$$

To solve for  $AGE_{tpl}$ , the logarithms were removed by raising both sides of the equation to the 10<sup>th</sup> power, obtaining:

$$(7) \quad AGE_{tpl} - AGE_e = 153.2780618$$

The empirical value for  $AGE_e$  (6 months for  $M_1$ ) was then substituted back into equation 7 to solve for  $AGE_{tpl}$ . The resulting  $AGE_{tpl}$  for  $M_1$  was 159.3 months, and the value of 163.6 months obtained from the quadratic regression equation of known-age on crown height for  $M_1$  was within the 95% confidence limits (142.5-178.1). The  $AGE_{tpl}$  for  $P_4$  was 158.7 months (95% confidence limits 133.9-189.3), which was inconsistent with the known-age data and the age of 269.0 months obtained from the quadratic regression. The relationship between  $P_4$  crown height and age needs further investigation, and inconsistent wear in this tooth may be affecting these results (Brown & Chapman, 1991b). Using the transformations described above, the age at which  $M_2$  crown height reaches '0' was 186.6 months (95% confidence interval of 164.3-212.1), and the age 218.5 months from the quadratic regression was just outside the confidence limits. The

AGE<sub>tpl</sub> for M<sub>3</sub> was 231.9 months (95% confidence interval of 199.0-271.2), which was consistent with the age of 224.2 months from the quadratic regression. Finally the age when dP<sub>4</sub> crown height reaches '0', when the tooth is shed, was calculated as 27.9 months (95% confidence interval of 25.1-31.0). This result was consistent with the age of 26 months from published data (Table 4.4) and younger than the age of 33.9 months obtained from the quadratic regression. Clearly larger known-age samples are needed, but the method described above presents a way to empirically test the assumptions of the QCHM.

### Summary and conclusions

This study demonstrates that adjustments to the formula for M<sub>1</sub> can be viewed with confidence. Research with larger sample sizes is necessary for P<sub>4</sub>, M<sub>2</sub>, and M<sub>3</sub>. The traditional QCHM formula for dP<sub>4</sub> is sufficiently accurate, although adjustments to this equation would provide better age estimates. The focus of the remainder of this study will be dP<sub>4</sub> and M<sub>1</sub>, because they are the only two teeth that provide a complete age profile when combined; M<sub>2</sub> and M<sub>3</sub> crown heights are not measurable until after dP<sub>4</sub> is shed. The following formulas will be used throughout this study and referred to as the QCHM formulas:

$$dP_4: \quad AGE = AGE_s [(CH-CH_0)/CH_0]^2$$

$$M_1: \quad AGE = (AGE_{tpl} - AGE_e) [(CH-CH_0)/CH_0]^2 + AGE_e$$

Where AGE<sub>s</sub> is the age dP<sub>4</sub> is shed (26 months). AGE<sub>e</sub> for M<sub>1</sub> is still 6 months, but AGE<sub>pel</sub> is changed to AGE<sub>tpl</sub> or age of tooth potential longevity, here taken as 163.6 based on the quadratic regression. CH<sub>0</sub> is determined for each sample.

In general, crown height provided a good estimation of age as shown by quadratic regressions of age on tooth crown height. Using these regressions, ages were reliably estimated to within one adjacent 10% of life span age class ( $\pm 19.2$  months for *C. elaphus*) for individuals from the same population as the known-age elk. Using the QCHM, adjustments need to be made to the age of potential ecological longevity and possibly to the rate of wear assumed by the model. The age of potential ecological longevity needs to be the *tooth's* potential longevity – the age at which the tooth's crown height reaches '0' and will be different for each tooth type. In this study, I determined tooth longevity from the quadratic regression formulas, but more studies of known-age animals are needed to determine these ages empirically. The adjustments made here are only applicable to *C. elaphus* and should not be generalized to other species. Unfortunately, for poorly studied or extinct species, these adjustment values may never be known. For many species, the only alternative will be the QCHM or direct comparisons of tooth crown heights, as described in Chapter 5.

## **Chapter 5: Methods of mortality profile construction**

Age-at-death distributions, or mortality profiles, provide a powerful tool for reconstructing the causes of death of fossil animals (Klein, 1978; Klein, 1982a; Klein, 1982b; Kurtén, 1953; Stiner, 1990; Voorhies, 1969). Three methods have emerged as common ways researchers analyze the age distributions of a species in a fossil assemblage: 1) histograms, often constructed with 10 age classes, the length of which is species specific; 2) boxplots, usually of medians of crown heights or crown height indices; and 3) triangular graphs of the proportions of young, prime, and old animals. The goal of this chapter is to evaluate the strengths and weaknesses of these mortality profile construction methods using two model profiles and two samples with known age structures. In testing each method, the known age profiles are compared along with profiles based on age estimation techniques appropriate for an archaeological assemblage. I will use the methods presented here to analyze my fossil data in Chapter 7.

### **Using mortality profiles to interpret ancient behavior**

#### ***Model age structures***

All analyses of age-at-death data are theoretically grounded in life tables. As described by Deevey (1947:284) in his review of age structures across taxa, a life table follows a cohort of individuals from birth to death and provides the numbers of individuals that survived until the next age class, died between age classes, and the rate of mortality (Table 5.1). When a population is not changing in size and births are seasonally restricted, the number of individuals in the “living” column of the life table is equal to the

“typical” age structure of the population on the landscape at the end of the birthing season (Caughley, 1966; Deevey, 1947). The frequencies of individuals in this “living” column can be used to construct a histogram to visualize the population’s age structure, as shown by the darkly shaded bars in the histogram in Figure 5.1.A, (Klein, 1982b; Voorhies, 1969). Because this histogram shows how many individuals are alive in a stable population at a given point in time, it is often referred to as the “living-structure” (Stiner, 1990). This age structure is also called a “catastrophic” profile, because it is the age distribution that would be found in a fossil assemblage where the entire herd died at once (Klein, 1982b; Klein & Cruz-Uribe, 1984; Voorhies, 1969).

The crosshatched area in Figure 5.1.A shows the number of “dead” individuals from the hypothetical life table (Klein, 1982b; Voorhies, 1969). This is the number of individuals that must die between each age class to produce the living structure, and, therefore, it is entirely dependent on the shape of the living structure. These deaths, caused by disease, malnutrition, and predation by non-human carnivores, are the natural attrition on the population and are highest in the youngest and oldest individuals of the population, as is described by the high mortality rates in the first and last age classes of Table 5.1. For this reason, this age distribution is known as the “attritional” structure (Klein, 1982b; Klein & Cruz-Uribe, 1984; Voorhies, 1969). When the attritional mortality profile is graphed alone, it is possible to see the two peaks representing higher numbers of juveniles and old individuals, so this age distribution is also called a “U-shaped” profile (Figure 5.1.B; Caughley, 1966; Klein, 1982b; Levine, 1983; Stiner, 1990).

### ***Interpreting age structures***

A fossil age profile that resembles a living herd can indicate one of four situations. In a synchronic sample where all the bones are deposited at once, the assemblage might be the result of 1) a natural catastrophe such as a flood, volcano or blizzard or 2) hunters driving an entire herd either into a trap or surround or over a cliff. In both situations, all age classes and sexes of the herd must be together. In a diachronic assemblage where bones are accumulated a few at a time, a similar structure might be created by people 3) hunting individual animals where prey of different ages are obtained in equal proportion to their presence in the herd or 4) setting individual traps that are equally successful in trapping animals of all ages.

An attritional mortality profile represents natural attrition on the herd: death by endemic disease, starvation, senility, and predation by non-human carnivores. A fossil age profile that resembles an attritional one could represent hunting of the most vulnerable individuals of the herd through chasing (the weakest would be easier to exhaust) by human or non-human hunters or in the case of just humans, encounter stalking with short-range or inefficient weaponry, such as thrusting spears (Enloe, 1993:107; Levine, 1983). Another possibility is that the assemblage was accumulated through scavenging, because the scavenger would be consuming carcasses produced by attritional deaths.

### ***Differences between human and non-human hunting***

An example of how two different predators hunt the same prey species will demonstrate how mortality profiles can illuminate hunting strategies and how human hunting differs from that of wolves. The prey species is Rocky Mountain elk from

Wyoming and Montana just north of Yellowstone National Park. The hunters are wolves reintroduced into Yellowstone in 1995 and 1996 and contemporary humans hunting with rifles. The mortality profiles created by the two hunters are shown in Figure 5.2. Visual inspection clearly shows that the humans and wolves were targeting animals of very different ages, and the wolf kills more closely resemble the attritional profile while the human kills more closely approximate the living structure. Research on other populations of wolves shows that they target the youngest and the oldest animals, the most vulnerable individuals, in a population (Boyd *et al.*, 1994; Carbyn, 1983; Kunkel *et al.*, 1999; Mech, 1970; Mech *et al.*, 1998; Mech *et al.*, 2001; Smith *et al.*, 2000), and the Yellowstone wolves also are hunting this way. The Yellowstone wolves killed many more individuals over ten years of age, the old adults, while the humans hunted many more two- to six-year-olds, the young adults. It appears that both groups took equal numbers of juvenile individuals, those younger than two-years-old, but the wolves actually hunted a higher percentage of this most vulnerable age group. The wolf-kill sample actually is biased against juveniles, because many of the youngest individuals in the wolf sample were consumed before the park biologists could collect the mandibles (D. Smith, personal communication); therefore I could not collection data on them.

The humans hunted certain age classes, two- to six-year-olds, and were not taking individuals in proportion to the model age structures. Three possible hypotheses are that 1) hunters preferred the younger adults because of their larger size relative to juveniles, but the subadults' inexperience compared to full adults made them easier to take; 2) due to heavy hunting for antlers, there could be a limited number of older males available in the prime age classes, and, therefore, humans were hunting the next best antler carriers,

younger adult males, along with females of any age class; or 3) seasonal hunting regulations imposed by Montana Fish, Wildlife, and Parks dictated the ages of the hunted animals, and not the preference of the human hunters.

The wolf versus human example shows that recent humans and wolves hunt elk in very different ways. Human hunters are more likely to kill adult prey while non-human hunters are more likely to take the most vulnerable members of the herd. Klein (1982b) found a similar pattern when comparing lion (*Panthera leo*) killed Burchell's zebra (*Equus burchelli*) and Cape Buffalo (*Syncerus caffer*) from the Serengeti Plain to chamois (*Rupicapra rupicapra*) killed by modern hunters in the Alps and pronghorn (*Antilocapra americana*) killed by prehistoric Native Americans in Wyoming. Comparative data assembled by Stiner (1990) suggested that in some situations non-human predators do take prime individuals, but most researchers agree that the ability to consistently taking prime adults distinguished humans from other predators. This is not to say that humans always target prime individuals, but that they are able to be more selective than other carnivores in what age animals they hunt. This selectivity could create many different types of hunting strategies that result in different mortality profiles. Tracking the emergence of this selective behavior will help paleoanthropologists understand the evolution of humans.

### ***Assumptions that are fundamental to morality profile analysis***

In order to study mortality profiles in fossil assemblages in this way, researchers must assume that the rates of births and deaths described by a particular life table are similar to those found in fossil animals. Ideally, the age structure of a species from a faunal assemblage would be compared to a life table of a modern population of same

species. Unfortunately, few reliable life tables exist for the prey species of Late Pleistocene hominids. Although life tables are available for modern populations of *C. elaphus*, I have chosen to compare my fossil samples to a model table, because the tables from studies of modern *C. elaphus* are usually reconstructed from populations that are heavily exploited by hunters with firearms or are changing in size (Houston, 1982; Lowe, 1969; Taber *et al.*, 1982). The model life table that I use is Klein's (1982b:51) hypothetical population of large mammals that has a stable size and synchronized birth of one offspring per year. Researchers have found that life tables, and particularly patterns of age-specific mortality, are remarkably consistent across taxa with similar life histories (Caughley, 1966; Caughley, 1977). The large ungulate prey species common in the Late Pleistocene of Europe have similar life histories of seasonal births of one offspring per year, which indicates that Klein's (1982) life table is a suitable description of the proportion of individuals in each age class in a stable prey population.

My second assumption when comparing fossil age distributions to the model life table is that the ancient prey population has a constant size, because population growth or decline will change its age structure. Unbiased fluctuations in population age structure over decades or centuries will be "time-averaged" in the archaeological record, allowing researchers to identify "typical" hunting strategies rather than individual hunting strategies. In more recent sites, shifts in age structures have been detected from faunal remains (Koike & Ohtaishi, 1985). The age structure and size of a population also changes with the season, so a season specific population age structure should also be used when possible. This level of detail is rare in the Late Pleistocene fossil record, although Lubinski (2000) examined recent archaeological faunal assemblages with consideration

of seasonal variations in age structure. In the Middle and Upper Paleolithic record, seasonal fluctuations in age structure of the prey species will be averaged out over the course of the year if a site is occupied throughout the year. If there is clear evidence of seasonal hunting, the age structure of the herds during that time should be considered, as some researchers have done (Farizy *et al.*, 1994).

The degree of exploitation also will change the stable age structure of a prey population. The model life table presented here assumes attritional death, where the most vulnerable individuals are removed from the population. Human hunters are able to hunt prime adult animals, which could change the age structure of the prey herd. Taber (1982) simulated the effects of different exploitation strategies on a hypothetical herd of elk. They modeled differing degrees of predation on the adults and found that predation reduces the total size and the average age of the population. Populations can remain stable while sustaining a 40% harvest rate of adult males (1982:297). Hunting pressure higher than this rate reduces the number of breeding individuals below the sustainable threshold. In order for stability to be achieved in this situation, calf mortality must be reduced. In Lyman's (1987) study of elk that were killed by the Mount St. Helen's volcanic explosion in Washington, there were very few old individuals in the population, despite normal levels of pregnancies. By studying the mortality profile of the sample, Lyman showed that the reduced average age of the population was due to hunting, but that the population was stable. Koike and Ohtaishi (1985) used the zooarchaeological record to show a similar reduction of the average age of a population due to human exploitation. These studies show that although prey populations can sustain some amount of harvesting of the adult members, it can reduce the average size of the population. If

predation pressure is too great, the population is compromised and a local extinction may occur.

The model living and attritional age distributions are not the only possible mortality profiles, but they are useful guidelines for interpreting profiles produced from faunal assemblages. Much variation exists in the archaeological and paleontological records, and more work is necessary to determine how accumulation strategies produce different fossil mortality profiles. Levine (1983) offers multiple hypothetical age distributions that might be found in archaeological equid assemblages, including an animal husbandry model, various social group models, and a stalking model. Her stalking model has many adult individuals and is based on “an attritional hunting technique, which may produce a non-random, non-representative distribution” (Levine, 1983:28). Stiner (1990:310) offers a “prime-dominated” model that is the same as Levine’s stalking model. Other researchers have suggested that this “prime-dominated” profile is really a living structure where the juveniles have been removed from the fossil record by pre- and post-depositional destruction (Marean, 1995; Marean, 1997; Munson, 1991). Although mortality profiles may take these many forms, in order to be sustainable, the hunting intensity must be low, a likely situation when human population densities were low.

### ***Pre- and post-depositional processes***

The archaeological record rarely exactly reflects the animals hunted by an ancient group. Faunal assemblages may be biased in the number of individuals and the percentages of each age class represented. Ethnoarchaeological studies of Hadza and Kua hunter-gatherers show that carcasses of different sized prey will be processed differently (e.g. Bartram, 1993; Bunn, 1993), and the same likely is true of differences in carcass

size resulting from different aged animals of the same species. Although a hunter might be taking all ages of prey, animals of different ages may be treated differently, which will affect resulting mortality profiles. Marean (1997:214) describes the multiple transitions of a mortality profile before a researcher describes it. First is the death profile: the distribution of the animals that the predator actually hunts. Next is the transport profile: the parts that are transported back to the campsite or den. This is inversely related to the profile left behind at the kill site. As an example, all heads of small species and only the heads of juveniles from large species may be transported to a campsite while the heads of large animals may be left at the kill site. Thus the mortality profiles for the two species at the two sites will look different, although they were hunted similarly. At the processing site, large and small mandibles may be processed differently and, therefore, preserve differently. Large mandibles may be processed for marrow by being broken while the small mandibles are left whole. In this situation, the large mandibles may actually not preserve as well as small mandibles. Mandibles of juveniles are more likely to be fully consumed by non-human predators or subsequent scavengers because of their small size and softer bones and teeth and, therefore, are often underrepresented in faunal assemblages (Binford & Bertram, 1977; Blumenshine, 1987; Munson, 1991; Munson, 2000).

Less dense juvenile teeth and bones also are less likely to survive the post-depositional processes of archaeological or paleontological sites than their adult counterparts (Klein & Cruz-Urbe, 1984; Levine, 1983; Lyman, 1994:288). Fortunately, the decreased durability of juvenile remains is not a problem when comparing to living and attritional age structures, because both profiles contain high proportions of

individuals in the first age class. This means that the informative difference is between the prime and old age classes. When studying mortality profiles, two types should be constructed: one that compare all ages and another that compares only adults. I take this multifaceted approach in this study, although other researchers have proposed correction factors to account for biases against juvenile teeth (Ducos, 2000; Levine, 1983; Marean, 1997; Munson, 1991).

To account for pre- and post-depositional processes, multiple tooth types should be compared using multiple methods of age structure calculation. If the results are concordant, then the faunal analyst can be more confident in the age structure. When possible, comparing multiple types of sites (camp-site versus kill-site) within the same settlement system will also be informative. Comparing samples with similar post-depositional histories will help control for some biases. Paleontological assemblages also provide data on age distributions in death assemblages where humans were not involved so that the human component of archaeological assemblages can be better isolated. The context of an assemblage must always be considered, and results should be regarded with caution until a consistent pattern appears.

### **Samples with known age structures**

To test the three methods for constructing mortality profiles of archaeological assemblages, I use two samples with known age structures: the human and wolf-kill samples described in Chapter 3. The human-hunted sample consists of 226 mandibles of known age collected from hunter checkpoints north of Yellowstone (Hamlin *et al.*, 2000; Quimby & Gaab, 1957), and the wolf-kill sample includes 98 mandibles collected in 1999 by Yellowstone Park biologists from recent wolf kills, primarily from January to

May and October to November (see also Mech *et al.*, 2001). D. Smith provided the cementum annuli ages on the animals' incisors, which I take to be actual ages (see Hamlin *et al.*, 2000).

To simulate fossil assemblages, I measured tooth crown height on these specimens as I would on a fossil sample. When constructing an age distribution for a sample, the tooth eruption and replacement schedule for the species under study must be considered; deciduous teeth must be combined with adult teeth to obtain a complete profile. In elk, the second and third molar crown heights are not measurable (the crown-root junction is not visible) until long after the deciduous fourth premolar is shed, so that a gap would be created in the middle of the age distribution if these teeth were used (see Table 4.4 for the complete eruption and replacement schedule for *C. elaphus*). In elk, M<sub>2</sub>, and in many cases M<sub>3</sub>, comes into occlusion before dP<sub>4</sub> is shed (Brown & Chapman, 1991b). However, the base of the crown, necessary for measuring crown height, is not visible until after dP<sub>4</sub> is shed. It is possible that M<sub>2</sub> and M<sub>3</sub> could be analyzed if wear stages that do not require the crown base to be exposed were used to determine age, or if no fossil specimens in a sample were still in the mandible, or if X-rays were used to obtain crown heights. In this study I consider only dP<sub>4</sub>, M<sub>1</sub>, and P<sub>4</sub>.

## **Histograms**

The most common way of illustrating the age structure of a fossil sample is to create a histogram where each bar represents the number of individuals in each age class. The model life table is readily illustrated using histograms (Figure 5.3.A). Histograms are created from fossil assemblages by assigning each tooth to an age class and creating a histogram of the frequencies. When investigating large mammals, as is typical in

zooarchaeology, age classes are usually defined as either one year or 10% of potential life span, but any consistent, easily definable and replicable age class (such as one day, one week, or one month depending on life history traits) can be used. Age can be assigned from known ages, cementum annuli, wear coding, regression equations or the QCHM. Deciduous teeth should be combined with adult teeth so that all ages are counted. When doing this, the histogram created by the deciduous tooth must be graphed over the histogram created by the adult tooth to prevent individuals retaining both teeth from being counted twice. It is possible to make a histogram of the raw crown heights in a sample, but data on the relationship between crown height and age are still needed to interpret the graph. This method also assumes a linear rate of wear, but Chapter 4 showed that this is unlikely.

The Kolmogorov-Smirnov test compares the cumulative distributions of two histograms. This test can be applied to mortality profiles, because age classes have a consistent and logical order to them, from youngest to oldest (see full descriptions in Klein & Cruz-Urbe, 1984:59-60; Sokal & Rohlf, 1995:434-439). The Kolmogorov-Smirnov test can be used for pair-wise comparisons of fossil assemblages to the model profiles and to each other. Unfortunately, despite the ease of applying the Kolmogorov-Smirnov test, many researchers do not employ it in their analyses, and they still rely on visual comparisons. This can lead to contradictory results (see example in Lubinski, 2000:123). Biases in visually assessing profiles might be reduced by plotting the proportion or percentage of individuals found in each age class instead of the frequency, but the profiles should still be statistically compared.

### *The human and wolf-killed samples*

For the human and wolf-kill samples, I estimated ages for dP<sub>4s</sub> and M<sub>1s</sub> using the equation from the QCHM that I presented in the summary and conclusions of Chapter 4 and the values from Table 4.4. Table 5.2 lists the frequencies of individuals in each 10% of life span age class for the model profiles, the known ages, and the estimated ages. These values are reproduced as histograms in Figure 5.3, along with the results of Kolmogorov-Smirnov tests comparing the cumulative distributions of the histograms.

For the human-hunted sample, the estimated-age distribution is not significantly different from the known-age distribution ( $K = 0.64$ ,  $p = 0.88$ ). For the wolf-kill sample, the estimated-age distribution is different from the known-age distribution at  $p = 0.097$  ( $K = 1.23$ ). The discrepancy between the two wolf-kill profiles is because the cementum annuli Age Classes 9 and 10 are compressed into Age Class 9 with no individuals in Age Class 10 in the estimated-age distribution, which is a by-product of the adjusted QCHM. The predicted profile of the human-hunted sample could not be distinguished from the known age profile, because there was only a small number of individuals in the oldest age classes from the human-hunted sample. The profiles from the human kills based on the known and estimated ages are both significantly different from the living age structure ( $K = 2.93$ ,  $p < 0.0001$ ;  $K = 3.21$ ,  $p < 0.0001$  respectively). When the Kolmogorov-Smirnov test is done by hand (following Klein & Cruz-Urbe, 1984:57-60), it is possible to compare the significance of differences between each paired age class in the two distributions. This shows that the major difference between the human kills and the living structure is in Age Classes 2-5. The living structure contains a lower proportion of individuals in Age Class 2 and 3 compared to 1, whereas the human kills do not show a

large drop in individuals between Age Class 1 and Age Classes 2 and 3. The large drop in the human kills is between Age Classes 3 and 4. The human kills show a greater bias towards young adults than is found in the model living structure. The wolf age structure based on the cementum annuli ages is significantly different from the model attritional age structure ( $K = 1.72$ ,  $p = 0.005$ ), while the age structure based on estimated ages is close ( $K = 1.35$ ,  $p = 0.052$ ). The wolf kill profiles differ from the model attritional structure because they show a large proportion of individuals in Age Class 9 or 10. There are many individuals in these oldest age classes because the wolf-kill sample contains many individuals older than what is commonly considered the age of potential ecological longevity (192 months) for individuals of this species.

### ***Advantages of histograms***

A primary advantage of studying fossil age structures with histograms is that histograms provide fine resolution for the mortality distribution across many age classes. This advantage is demonstrated by the human-kill sample where it is possible to determine in which age classes the human kills differ from the living structure model. This greatly assists with the interpretation of the mortality profile. An additional advantage to histograms is that if 10% of life span age classes are used, then histograms can be compared easily across species. Finally, the ability to compare histograms statistically adds power and replicability to analyses, because the subjectivity is minimized.

### *Disadvantages of histograms*

One potential disadvantage of histograms is that species must be sufficiently well studied so that methods are available for assigning relatively precise age classes. Unfortunately, the relevant data are not available for many species. Also, there is some error around any age class estimation no matter how well studied the species, but there is no easy way to construct a confidence interval accounting for this error in the final histogram. Binning problems resulting from breaking a continuous variable into discrete age classes also introduces error that can obscure or create differences. Because of the high resolution, individuals may be wrongly assigned into an adjacent age class due to age estimation errors, but because the Kolmogorov-Smirnov test only examines the maximum difference between pairs of columns, it can produce statistical difference when no biological difference exists. For example, in the wolf sample, individuals with their  $M_1$ s worn completely away can be placed in either Age Class 9 or 10 depending on which age determine technique is used. Visually, the graphs will look similar and have the same biological meaning, but Kolmogorov-Smirnov test might show that they were significantly different from each other. This sensitivity may make it difficult to compare studies by different researchers who may use different age determination methods.

Unfortunately, the biggest obstacle confronting the wide spread use of histograms for analyzing the age structure of fossil assemblages is sample size. Shipman (1981:157) recommends a minimum of thirty individuals, while Klein (1984:59, 213) suggests that at least forty are necessary. Needless to say, paleontologists rarely have the luxury of sample sizes this large, which places limitations on the utility of this method. The critical values for the test are adjustable when sample sizes are smaller than 26 individuals (Sokal

& Rohlf, 1995:434 and accompanying Statistical Table W), but the researcher must consider the biological meaning of a mortality profile based on small sample sizes.

### **Boxplots**

The second method for analyzing age distributions is the boxplot method where boxplots are used to compare median crown heights of multiple samples, although actual ages or age classes could be used (Klein & Cruz-Urbe, 1996a). Boxplots show the sample medians as a line in the middle of the box, and the open box surrounds the middle 50% of the data (Figure 5.4.A). The solid line depicts the extent of the continuous data, and the extreme values are plotted as circles with very extreme points as starbursts (Velleman, 1997). The shaded area represents 95% confidence intervals around the median. If two samples' shaded intervals do not overlap, the two sample medians can be considered significantly different from each other (Velleman & Hoaglin, 1981:79).

Boxplots are best used with crown height data so that median crown heights can be compared across samples. The same criteria are necessary for choosing tooth type as with histograms. In order to construct a complete profile, the adult tooth must be measurable before the deciduous tooth is shed. The two model age structures are plotted as both histograms and boxplots in Figure 5.4.A (after Klein & Cruz-Urbe, 1996a:323). When boxplots are based on crown height measurements, each tooth type must be considered separately, and, therefore, I have constructed boxplots of only the adults in the model structures representing the specimens likely available as  $M_1$ s. The percentages of Age Class 1, here likely available as  $dP_4$ s, are represented by the open column and listed separately. The attritional boxplot on the right is more biased toward older individuals and has a higher percentage of juveniles than the living structure on the left.

### ***The human and wolf-killed samples***

Figure 5.4.B depicts the human and wolf kill data as boxplots showing the median  $M_1$  crown height and the distribution of crown heights in each sample. Heavily worn teeth representing older individuals fall to the right in the plot. The percentage of dP<sub>4s</sub> in each sample is shown to the right of the boxplots. The shaded regions in the two boxplots do not overlap, showing that the age distributions for the two samples are significantly different. The wolf-kill sample is biased toward old individuals, suggesting that the wolf-kill sample is more similar to the attritional model and the human-kill sample is more similar to the living model. The higher percentage of dP<sub>4s</sub> sample in the wolf-kill sample than in the human-kill also supports this.

### ***Advantages of boxplots***

The primary advantage of boxplots is that they employ raw measurements that are not translated into age classes, which is important because it allows for the analysis of unstudied or extinct species where no method for estimating age from teeth exists. Using raw crown heights also eliminates the introduction of estimation error that is inherent to any age estimate technique. It is almost always better to compare raw data whenever possible than to extrapolate from this data to derived variables that have error around them (see discussion in Smith, 1996).

Another advantage to using boxplots is that they can be statistically compared using smaller samples than is necessary for histograms, because the confidence intervals around the median reflect sample size. It is important to remember that although two samples composed of three specimens each may be statistically different, they may have little biological significance and provide only limited information about the sample's

mortality profile and prehistoric hunting behaviors because of potential sampling errors. Boxplots also make it easier to compare multiple samples at once than when using histograms.

A final advantage to using boxplots is that they compare only adults in a sample. Young mandibles are particularly susceptible to pre- and post-depositional destruction (e.g. Hulbert, 1982; Klein & Cruz-Uribe, 1983; Klein & Cruz-Uribe, 1984; Kurtén, 1953:75; Lyman, 1994; Munson, 1991; Munson, 2000), and, therefore, their decreased numbers may distort a profile. Because of this, juveniles must be discounted when examining a complete profile or should be removed from some analyses (see Munson, 2000 for a recent discussion). Boxplots using only permanent molar crown heights address this problem.

### ***Disadvantages of boxplots***

Boxplots can be difficult to interpret in isolation and are best used for comparing age structures for two or more samples. It also can be difficult to compare and interpret complete age profiles, because juveniles are considered separately from adults. This may not be critical, however, because the main difference between the living and attritional structures is in the relative proportions of prime to old individuals. Caution also should be taken when considering boxplots of permanent teeth plus boxplots or percentages of deciduous teeth, because the same individual may be counted twice, once as a deciduous tooth and again as a permanent tooth. This is seen in the human-kill sample where the total number of dP<sub>4s</sub> plus M<sub>1s</sub> is higher than the number of mandibles in the sample (see Table 5.1). Although this increased the percentages of dP<sub>4s</sub> in the sample, it did not affect my interpretation of the results.

In some species such as *C. elaphus*, body and tooth size varies in time and space. One assumption when estimating age from tooth wear, either by coding wear stages or measuring crown heights, is that teeth of different sizes from individuals of the same species wear at the same rate. Diet being comparable, 5 mm of wear on a tooth that had an unworn crown height of 22 mm is likely from a different aged animal than a tooth that had an unworn crown height of 27 mm and is now has 5 mm of wear. For example, two  $M_1s$  from *C. elaphus* can have unworn crown heights of 22 mm and 27 mm. This assumption of equal wear rates needs to be tested with known-age samples from populations of the same species that have different body sizes.

In taxa whose body size varies, it is necessary to standardize the crown height measurement to account for differences in tooth size. One possibility is to use the maximum crown height of the sample (Klein *et al.*, 1981:15) or the mean of all the unworn crown heights in the sample (Klein *et al.*, 1983:75). While this is the best solution, unworn crown heights often are not available, as is the case with the both the human and wolf-kill samples, or must be estimated from only one tooth. It is possible to extrapolate from other samples, published values, or from a regression equation of known age specimens, but each of these methods introduces uncertainty and error.

An alternative is to standardize by another measure of tooth size. Tooth length measured at the crown-root junction is one possibility, but this measure can be affected by wear. A better option is tooth breadth, because it is less affected by wear. This measure is most suitable for standardization between populations with different body sizes and not standardization of individual tooth size, because the relationship between tooth breadth and unworn crown height in individual specimens from my fossil samples

is relatively weak ( $n = 81$ ,  $r = 0.54$ ). In addition, standardization by dividing each individual crown height by that tooth's breadth would change the statistical procedure substantially from both the unstandardized method and unworn crown height standardization. If crown height is standardized by individual tooth breadth, the sample median no longer reflects only crown height, because it is now a median of the ratio of individual crown height divided by individual breadth and is thus affected by both variation in crown height and breadth. In addition, ratios have unpredictable statistical properties. Of particular importance here, the best estimate of a ratio is not usually the mid-point between its possible ranges (Sokal & Rohlf, 1995:17-18). The alternative is to standardize by the average tooth breadth of the sample to control for variation in tooth size between populations. Using this method, the statistical procedure is essentially the same as standardizing with unworn crown height, except that breadth replaces unworn crown height. Standardization by individual tooth breadth accounts for individual variation in tooth size, while standardization by mean breadth negates the influence of population differences in tooth size.

This problem of differences in initial tooth size becomes even more significant when comparing the mortality profiles of different species. Because of difference in tooth size, different species cannot be directly compared. One solution is to standardize the samples by unworn crown height when it is available.

### **Triangular graphs**

Stiner (1990) proposed using triangular, or ternary, graphs for analyzing age structures in fossil assemblages. In this method, teeth are assigned to one of only three age classes: young, prime, and old, and the percentage of individuals in each class is

plotted on a triangular graph. Essentially, this method is a simple way to present a three-bar histogram of age classes. All deciduous teeth are automatically assigned to the young class, and either wear stage or crown height can be used to assign prime and old. Stiner (1990) recommends using  $dP_4$  and  $P_4$ . To avoid counting the same individual twice, only  $P_4$ s that exhibit wear should be counted, because both  $dP_4$  and  $P_4$  are present in the same individual while  $P_4$  is erupting and before  $dP_4$  is shed. Stiner (1990:311-312) defined the transition from prime to old as occurring at roughly 61-65% of the maximum potential life span and identified this point on  $P_4$ s as when more than half of the tooth crown is worn away.

The percentages of the three ages classes are plotted on a triangular graph where the bottom axis is the percentage of young, the right axis is the percentage of prime, and the left axis is the percentage old (Figure 5.5). The extremes of the plot correspond to dominance by the indicated age class. The areas that represent either the living structure or the attritional age structure are labeled on the graph. If a sample plots within one of these areas, it is interpreted as having that age structure. If two points plot close to each other based on visual inspection, they probably have similar age patterns.

### ***The human and wolf-killed samples***

I calculated young, prime, and old for the human and wolf-kill samples and the model age structure from the age class frequencies used in the above histogram analysis. I marked all individuals in Age Class 1 as juveniles (Table 5.2). As mentioned above, Stiner (1990:311-312) defined the transition from prime to old as occurring at roughly 61-65% of maximum potential life span. Klein and Cruz-Urbe (1984:56) defined old as being beyond 50% of potential life span, while Lyman (1994:130) followed Stiner's

(Stiner, 1990) definition and considered old to begin at about 70% of natural ecological longevity. In studies of elk, Houston (1982) considered old female elk as those beyond 10-12 years old, or 62.5-75% of life span, although he noted females living to 20 years old. Male red deer 11 years and older are no longer able to hold harems, and their condition begins to decline (Clutton-Brock *et al.*, 1982:117). Based on these figures, I classified individuals in Age Classes 2-5 as prime and those in Age Classes 6-10 (beginning at 50% of life span) as old. I also plotted the wolf-kill sample using Stiner's (1990:312) age determination method where I considered all dP<sub>4</sub>s as juveniles and used crown heights to determine when the P<sub>4</sub> was worn beyond 50%. The P<sub>4</sub> sample in the human kills is not complete, and thus I did include it in this analysis.

When plotted on the triangular graph, the samples all plot where expected: the model structures plot within the correct zones, the two human-kill samples plot near each other and in the living age structure zone, and the three wolf-kill samples plot almost in the same spot and within the attritional zone, although close to the old-dominated zone (Figure 5.5.A). These results mirror the profiles created by the histograms and the boxplots, although the lack of resolution compared to the histograms makes further interpretations difficult. It does appear that the human-kill sample contains fewer old individuals than the living structure, but it is unclear if the difference is meaningful.

### ***Advantages of triangular graphs***

Triangular graphs are frequently used because they are easy to create and simple to analyze. They also facilitate comparisons of multiple samples and multiple species. Zooarchaeologists frequently draw on wildlife biology and hunting literature; these data often are presented as only rough age class designations, so they are translated most

easily into the three age classes represented in the triangular graph. Finally, because percentages are plotted, there is no apparent minimal sample size necessary when comparing samples, although Stiner (1998:315) recommended having at least 12 individuals.

### ***Disadvantages of triangular graphs***

The triangular graph method has three important disadvantages. First, the triangular graph has the same disadvantage as the histograms where juveniles cannot be considered separately from adults. The problem actually is worse with the triangular graphs, because there is no way to omit the juveniles; in the histograms, Age Class 1 can be eliminated. Second, percentages of each age class are plotted, and, therefore, sample sizes are not taken into account when comparing assemblages. This increases the tendency to consider small samples as informative even though sampling processes can heavily influence them. Third, samples cannot be compared statistically. Graphs are visually inspected, and patterns may be erroneously identified where none actually exist. If these last two limitations can be addressed, the triangular graph method will be more informative.

### **Modified triangular graphs**

T. D. Weaver and I devised a method to address the limitations of the triangular graph method, and what follows is part of our resulting publication (Steele & Weaver, 2002). We found that bootstrapping the age class data offered a way to account for sample size and approximate confidence intervals around age structure data points on the triangular graph. The bootstrap is a simulation method for making statistical inferences

based solely on the observed data, and it typically is used when standard parametric inference techniques are difficult or inappropriate (Efron & Tibshirani, 1993; Mooney & Duval, 1993).

As used here, the method works as follows (for further discussion, see Efron & Tibshirani, 1993; Mooney & Duval, 1993; Sokal & Rohlf, 1995). A fictional sample is created by randomly re-sampling with replacement from the observed age class data. This process is repeated 10,000 times. For each of these 10,000 re-samples, the percentages of the three age classes are recalculated and plotted on the triangular graph. This produces a scatter of points around the original sample location, since each re-sample potentially can have duplicates or be missing individuals from the original sample. A 95% density contour is then calculated and drawn around the bootstrapped re-samples. This density contour can be considered a 95% confidence interval around the observed age class percentages. When multiple samples are compared, and two density contours do not overlap, then the two age structures differ at approximately the 0.05 level. If two contours overlap or touch, then the two samples are not significantly different at approximately the 0.05 level. Figure 5.6.A shows the re-sampled points and the resulting 95% density contour for a hypothetical sample (Hypothetical sample 1 listed in Table 5.3). Note that not all 10,000 points are visible, because multiple re-samples often have the same proportions of age classes and plot at the same spot.

This procedure works because, as the original sample size increases, the bootstrapped scatter of points approaches the distribution which would have been obtained by repeated sampling from the true age structure or population in a statistical sense (Efron & Tibshirani, 1993; Mooney & Duval, 1993). The procedure is not as exact

with smaller sample sizes, but it is still usually very good (Mooney & Duval, 1993). Once the distribution is approximated by the 10,000 re-samples, 95% confidence limits are obtained by excluding the outlying five percent in a way analogous to using the normal distribution to obtain confidence limits around a sample mean.

In the modified triangular graph, 95% confidence limits are approximated using density contours. These contours are similar in function to the density ellipses calculated by many statistical software packages; however, ellipses should be used only with normally distributed data, because they are drawn using parametric statistical techniques. The bootstrap points on the triangular graph are not normally distributed, and the axes are not standard. Therefore, the 95% density contour must be calculated non-parametrically, similar to drawing a topographic contour, except that point density is being contoured instead of elevation. A contour is picked such that 95% of the point density is enclosed. The scatter of points is first smoothed using a Gaussian kernel smoother (Silverman, 1982; Silverman, 1986) to make the contour less ragged and more accurately reflect the true 95% confidence interval.

Figure 5.6.B illustrates the modified triangular graph method using three hypothetical samples each with a sample size of 35 and different percentages of the three age classes (listed in Table 5.3). The three samples were bootstrapped, and the 95% density contours were calculated. The density contours for Samples 1 and 2 overlap, as do those for Samples 1 and 3, while those for Samples 2 and 3 do not. This suggests that Sample 1 cannot be differentiated from 2 or 3, while Samples 2 and 3 probably do represent different age structures. These results can be tested with the Kolmogorov-Smirnov test, because the triangular graph is really a simple alternative to representing a

3-bar histogram of age class frequencies. Samples 1 and 2 and Samples 1 and 3 cannot be differentiated (Kolmogorov-Smirnov  $K = 0.84$  and  $0.96$ ,  $p = .49$  and  $.32$  respectively), while Samples 2 and 3 are significantly different (Kolmogorov-Smirnov  $K = 1.67$ ,  $p = 0.008$ ). These results suggest that age distributions in samples cannot be differentiated simply because they fall within one of the five designated zones on the triangular graph. The confidence interval around each point must also be considered.

### ***The human and wolf-killed samples***

The human and wolf-kill samples are plotted on the modified triangular graph shown in Figure 5.5.B using the same percentages of each age class as in Figure 5.5.A. The living and attritional models are plotted using a sample size of 170, which is the average of the two. All data are presented in Table 5.2. The confidence interval for the attritional model is contained within the intervals for all the wolf kill calculations, so as expected, these profiles cannot be considered significantly different from the attritional model. The confidence intervals around the known-age human kills overlap with the living model, in contrast to the histogram analysis, but the interval using the ages derived from the regression formula does not, indicating that this calculation is different from the model living structure, similar to the histogram analysis.

### ***Advantages of modified triangular graphs***

All of the advantages of the triangular graph method mentioned above also apply to the modified triangular graph. An additional advantage to bootstrapping the three age class data is that the resulting density contours are sensitive to sample size. Figure 5.7 depicts three assemblages where their age class frequencies remain the same, but sample

sizes are 100, 40, and 12 (data are listed in Table 5.3). The density contours around the data points become larger with decreased sample size. Bootstrapping allows smaller samples to be compared more informatively. The confidence interval around the sample of 12 is quite large, but it need not overlap with another sample if the other sample is large and in a distinctly different section of the graph. The density contour around the sample of 100 is still sizable. This indicates that if data are compared without confidence intervals, misinterpretations are possible.

### ***Disadvantages of modified triangular graphs***

The modified triangular graph still only compares three ages classes, so that fine-grained analyses using many age classes are still not possible (although see Lubinski, 1997; 2000 for an adjustment to the method that allows further investigation into the younger age classes). This limitation is illustrated by the human-kill sample. The histogram analysis with ten age classes provided enough resolution to show that human hunters were taking animal in proportions that were different from the model living structure. The histogram results encouraged further consideration to determine if they are the result of selective hunting or if the original herd age structure differs from the model living structure. The modified triangular graph, which uses only three age classes, does not provide enough resolution for this always to be apparent or to test further hypotheses.

### **Summary and conclusions**

The advantages and limitations of each method are summarized in Table 5.4. It is encouraging that all methods produced consistent results and were not biased by the age determination methods or the specific tooth used. All methods now can statistically

compare samples, and these statistics should always be part of the method. Histograms are best used when a species is well studied and more than thirty individuals are present in the assemblage, but they are limited by not accounting for the error inherent in age estimation techniques. Boxplots are good because they employ raw crown heights which removes error introduced in assigning specimens to age classes and allows the analysis of poorly studied species. Triangular graphs are easy to use and allow comparisons between multiple samples and species, but without being able to statistically compare samples, they have limited utility. The modified triangular graph solves this problem by bootstrapping the observed three-age-class data to create 95% confidence contours around samples. These ellipses also reflect sample size, which allows samples to be more confidently compared. The modified triangular graph allows easy comparisons of multiple samples and species. Even though all methods work, any age structure analysis should employ multiple methods in order to secure confidence in the results.

Both the histograms and triangular graphs compare complete age structures, while the boxplots compare adults separately from juveniles. Because juvenile mandibles are more susceptible to pre- and post-depositional destruction than adult mandibles, it is often desirable to compare only adult specimens. In histograms, the deciduous teeth can easily be omitted, and boxplots always compare deciduous and permanent teeth separately. It is more difficult investigating only adults using the modified triangular graphs. Juveniles should not be ignored in every circumstance, however, and multiple methods should be used.

More consideration needs to be given to biologically meaningful minimum sample sizes. Statistically, the Kolmogorov-Smirnov test should be used with a sample of

at least 26 individuals, and the confidence intervals in the boxplots and modified triangular graphs increase with decreasing sample size so that theoretically there is no minimum sample size. Should analyses be limited to sample of more than 30-40 individuals even if samples of five or ten provide significant differences? Even if ten specimens might be enough to characterize the age structure of a particular fossil assemblage, is it enough to make inferences about modes of accumulation?

In my fossil analysis, I will limit my primary analyses to samples totaling 26 or more dP<sub>4</sub>s plus M<sub>1</sub>s. In some boxplot analyses, I will include samples with ten or more measurable M<sub>1</sub>s; other methods will not be applied to these small samples. I will use all three methods in my analyses where applicable. In histogram analyses, age class will be assigned using the modified quadratic crown height formula presented in Chapter 4. In boxplot analyses, crown height will be standardized with the mean unworn crown height, when available, and the mean breadth for each assemblage. In modified triangular graph analyses, I will investigate M<sub>1</sub> and P<sub>4</sub>, and the division between prime and old will be based on crown height measurements.

## **Chapter 6: Size variation in modern and fossil *Cervus elaphus***

Modern *C. elaphus* shows considerable body size variation across its geographic range, and adult male lean weight ranges from 110-478.6 kg (Geist, 1998:349-350). The elk of North America in particular are considerably larger than the red deer of western Europe. This size fluctuation is also visible in the fossil record of European red deer, where body size occasionally was in the same range as modern North American animals (this study). If the factors influencing modern *C. elaphus* size variation can be determined, it may be possible to use body size in fossil red deer as an indicator of environmental variation.

### **Previous research on size variation in *C. elaphus***

The influence of the environment on animal body size has stimulated much research since at least 1847 when Bergmann studied the relationship between mammalian body size and climate. Mayr (1956) provided the modern interpretation of what has become known as “Bergmann’s Rule,” which states that “races of warm-blooded animals from cooler climates tend to be larger than races of the same species from warmer climates.” Bergmann’s original proposal related body size to thermoregulation and hypothesized that larger body size is adaptive for heat conservation in colder climates. Ashton *et al.* (2000) recently reviewed the data supporting Bergmann’s rule, and although the empirical pattern that body size increases as latitude increases or temperature decreases has been supported by many researchers, the causal mechanism of the pattern remains uncertain.

Walvius (1961) reviewed much of the early literature on variation in the body size of red deer from Europe. While he mainly was interested in correlating decreases in red deer body size from the Neolithic to the present with human-induced habitat changes, his insights are also relevant for variation in space. Many early researchers recognized the phenotypic plasticity of red deer. Walvius cited Beninde (1937) and Botezat (1935) as both noting that in as little as one generation, the offspring of red deer that were relocated to a different environment looked like the red deer native to that area (see also Clutton-Brock *et al.*, 1982 for more recent examples). Dierich (1910 as in Walvius 1961) noted that modern red deer could attain the same size as prehistoric deer when their food supplies were adequate and their ranges were large, and Bieger (1931 as in Walvius 1961) found that red deer body weight varied with soil composition. This early research suggested that factors other than thermoregulation might influence red deer size, although Hesse (1921 as in Walvius 1961) did note that body size varied across Europe in relation to minimum temperature.

Although this research is valuable for preliminary data, more systematic studies of red deer size variation in space and time were not published until the 1980's. Clutton-Brock and Albon (1983) examined the relationship through time between environmental variables and body weight in one population of red deer from the Scottish Isle of Rhum. Although non-lactating hind weight did not vary significantly with any of their climatic parameters, stag weight in August and September was significantly lower after more severe winters (characterized by lower mean daily temperatures). Because the severity of the previous winter decreases stag weight by decreasing their fat stores, smaller animals potentially could be more vulnerable to severe winters because of their possible lower fat

stores. If body size is a heritable trait and if small animals are more vulnerable, winter severity could provide a selection mechanism where larger body size helps an animal survive through winter, which would create an empirical pattern of variation in size that follows Bergmann's rule. However, this needs to be further tested by examining differential survivorship of small versus large animals after severe winters, because it could be that smaller animals are more likely to survive a severe winter because they do not require as much forage as a larger animal.

Langvatn and Albon (1986) found that Norwegian red deer were larger in higher latitudes and further inland from the coast. Body weight increased with decreasing temperature and decreasing precipitation. Their data supported Bergmann's empirical pattern, but they offered an alternative mechanism to thermoregulation. They found that temperature and precipitation affected primary plant physiology and that plant productivity and quality increased in the cooler and drier climates of Norway. They concluded that the higher quality forage in these cool and dry environments provided a mechanism for the larger size of the red deer. Langvatn and Albon were unable to distinguish the effects of temperature from precipitation in their data, however. Clutton-Brock and Albon (1989) also found that within Scottish highland red deer, those living on open hills were substantially smaller than those living in more forested areas, because the open hills had lower quality forage.

Although latitude, temperature, and precipitation appear to be related to animal size, the mechanism creating Bergmann's pattern remains unclear, at least in *C. elaphus*. A common explanation involves large body size increasing resistance to cold, including larger animals' ability to survive longer without food (Ashton *et al.*, 2000). For

carnivores, in addition to thermoregulation, Dayan *et al.* (1991) have proposed character displacement as the cause, where morphological change (here size) increases the ecological distance between closely related species or competitors. Finally, primary production of the landscape may increase with latitude. For herbivores, this means that either higher quality or more abundant food will support larger body sizes. Carnivores may respond to changes in the primary production of the area, because they are larger in order to hunt larger herbivore prey or because prey are more abundant in areas with higher primary productivity (Ashton *et al.*, 2000). Identifying herbivores that adhere to Bergmann's rule may be difficult, because they often depend on specific plant foods, which limit their geographic distribution. Carnivores are often more widespread and therefore cross more climatic zones, so the patterns will with climate will be easier to detect (Klein, 1986), although differences relating to climate may not best explain their body size variation (Dayan *et al.*, 1991).

### **Modern samples and climatic parameters**

To investigate the utility of *C. elaphus* size as an indicator of past climates I first needed to investigate the relationship between body size and climate in modern populations. To do this, I collected M<sub>1</sub> basal breadth, M<sub>1</sub> basal length, and distal metacarpal and metatarsal breadth on modern individuals from seven subspecies of *C. elaphus* from North America and western Europe (Table 6.1, measurements are described in Chapter 2).

To estimate climatic data for each modern specimen, I recorded locality as accurately as possible from museum records and used maps to assign a latitude and longitude to each locality. I then used Willmott and Matsuura's Terrestrial Air

Temperature and Precipitation: Monthly and Annual Climatologies (2001) to obtain the mean annual temperature, mean January and mean July temperature, and the mean annual precipitation for each latitude by longitude. I also subtracted the mean January temperature from the mean July temperature as an indicator of seasonality, as recommended by Ashton *et al.* (2000). Willmott and Matsuura's database uses data collected from 1950 through 1999 at 20,000 weather stations located throughout the world to interpolate station averages of monthly air temperature and precipitation to a 0.5 degree by 0.5 degree of latitude/longitude grid. The average number of stations that influence a grid-node is 20. By using this interpolated database, I was able to estimate climatic variables for each sample without directly locating the nearest weather station. All data for each sampled area are listed in Table 6.2.

### **Fossil samples and climatic parameters**

In addition to examining the variation in *C. elaphus* body size across space in modern animals, I examined variation through time and space in the Pleistocene fossil record from western Europe. After examining variation in tooth breadth in western European red deer during the Late Pleistocene, I divided my samples into three regions to more closely study size variation in each region. The northern Spanish samples came from the Cantabrian shoreline of Spain, the Mediterranean region included samples from the southwestern Pyrenees, the French Mediterranean coast, and Italy, and the northern European samples are from England, Germany, and northern France (see Figure 3.2). Combe-Grenal did not fit into any of these categories, so I excluded it from the regional analyses. Finally, I examined variation in red deer tooth size across Western Europe during each OIS that provided sufficiently large samples (OIS 1,3, 7 and 9; OIS 9 = 279-

334). Finally, I considered the variation in distal metacarpal breadth for all my larger samples.

In these analyses, I used OIS as a proxy for climate, and I considered the odd stages as interglacials (warmer) and the even as glacial periods (colder). This is a gross oversimplification of the complex environments and climatic changes that occurred in western Europe during the late Pleistocene, but more fine-grained climatic data were unavailable for most samples. More ideal climatic data would include pollen records, micromammal assemblages, or sedimentary evidence. While this information is certainly available for the larger and more recently excavated samples, relying only on these data would have greatly limited the assemblages that I could include. I also considered OIS as a proxy for time, which also allowed me to include poorly dated samples. Given the previous discussion of Bergmann's rule, I expected that red deer would be larger during the glacials and smaller during the interglacials.

### **Modern *C. elaphus* tooth breadth and climate**

I began my investigation into the relationship between *C. elaphus* body size and climate by examining patterns of variation in tooth size. Teeth are abundant in the fossil record, making them desirable as an environmental indicator. Also, they are more easily identified to species than most post-cranial elements, so that size differences within species will not be confused with size differences between species. Tooth size likely reflects the average size of a population not individual body mass, because they are not weight bearing like limbs and because they are not sexually dimorphic (Figure 6.1.A). Between different species of cervids, mandibular tooth breadth and length are good predictors of species body size ( $M_1$  breadth:  $r^2 = .91$ ,  $M_1$  length:  $r^2 = .93$ , Janis, 1990). No

known studies investigate the relationship between individual body size and tooth size in *Cervus*, and the relevant data currently are not available. I obtained average male and female body weights from published sources for the subspecies considered here, but the small sample size ( $n = 5$ ) precluded statistical analyses, although it is apparent that as body mass for the subspecies increases, so does tooth breadth (Table 6.1). In the following study I used tooth breadth instead of tooth length, because it is not affected by wear until much later in life. I excluded all heavily worn teeth from the analysis.

Figure 6.2 shows the relationship between  $M_1$  breadth and the various climatic parameters for a combined sample of North American and European specimens, and Table 6.3 lists the statistical results. In the combined sample, tooth breadth actually decreases as latitude increases, contradicting Bergmann's rule, albeit the relationship is weak ( $r = -0.37$ ). The stronger relationships are with mean annual temperature ( $r = -0.45$ ), mean January temperature ( $r = -0.60$ ), and July minus January ( $r = 0.60$ ). These all follow the pattern suggested by Bergmann. I investigated the possibility of curvilinear relationships between tooth breadth and the climatic variables (Klein & Cruz-Uribe, 1996b), but this did not describe the relationship better; the coefficients of determination are broadly similar between the linear and curvilinear regressions (Table 6.3).

North American elk are so much larger than western European red deer that the tooth breadths of the two samples are almost mutually exclusive in Figure 6.2, suggesting that a bilinear relationship may best describe the patterning in the data. To explore this, I also ran my analyses of the relationship between  $M_1$  breadth and various climatic parameters separately for elk and red deer.

For M<sub>1</sub> tooth breadth in North American elk, latitude and mean annual precipitation are positively, although weakly, correlated with tooth breadth ( $r = 0.27$  and  $0.20$  respectively; Figure 6.3 and Table 6.3). Annual temperature and mean January and July temperatures are similarly weakly negatively correlated with tooth breadth ( $r = -0.21$ ,  $-0.16$  and  $-0.25$  respectively). The measure of seasonality is not related to tooth breadth ( $r = -0.03$ ). Coefficients of determination for linear regressions are weak in all cases ( $r^2$  always  $< 0.08$ ), and curvilinear regressions do not better describe the patterning of the data ( $r^2$  always  $\leq 0.08$ ). Thus, I conclude that although there is a relationship between tooth breadth and various climatic parameters that seems to follow Bergmann's rule, the relationships are weak.

In the western European red deer, relationships between tooth breadth and latitude, mean annual temperature, and mean January temperatures are extremely weak ( $r < 0.09$  for all) and are often non-significant (Table 6.3 and Figure 6.4). The relationship with annual precipitation is slightly stronger ( $r = -0.19$ ), but this relationship is in the opposite direction from the pattern found in North American elk. The relationship with mean July temperature is similar ( $r = 0.12$ ) and also is opposite the relationship in elk. The strongest correlation with tooth breadth in red deer is July minus January temperature ( $r = 0.31$ ), which was the weakest relationship in elk.

### **Fossil *C. elaphus* tooth breadth and climate**

#### ***All of western Europe through time***

In my first analysis of the fossil data, I calculated the mean M<sub>1</sub> breath for all fossil samples containing five or more first molars (Table 6.4). I then plotted only these means

by OIS. By treating the mean of each site as an individual observation, Figure 6.5.A shows the mean of the means as filled circles, the standard deviations as solid lines, and small hatched lines show the standard error. The line through the middle of the graph depicts the grand mean. Relative to each sample's nearest neighbor, tooth breadth is larger during the glacials and smaller during the interglacials. There is no consistent trend through time.

In my next analysis, and all subsequent analyses, I included my entire sample of measured  $M_1$  breaths ( $n = 852$ ) as individual teeth. Figure 6.5.B shows the means and 95% confidence intervals for the tooth breadths in each OIS; means are calculated from all individual teeth found in that OIS stage, but individual points are not plotted. I used the Tukey-Kramer Honestly Significant Difference statistic in the JMP software package to perform unplanned comparisons of my many means (Sall & Lehman, 1996:161), and I present these results in Table 6.5.A. In sum, animals in OIS 1, 2, and 3 are smaller than those in stages 4 and 6. According to Bergmann's rule, we would expect that red deer during OIS 4 and 6 would be larger, as OIS 6 is identified as the penultimate glacial, the time of the most severe glacial conditions in the Late Pleistocene, and OIS 4 is part of the last glaciation. Given that OIS 2 and parts of 3 were also part of this glacial event, I would expect these samples to be more similar to 4, but this is not the case. OIS 5 has the smallest individuals except for stages 8 and 9. This follows expectations, because this is the time of optimal conditions during the Late Pleistocene, particularly OIS 5e. OIS 9 has smaller individuals than OIS 4 or 6, again following interglacial versus glacial expectations. The OIS 8 (244-279 kya) sample contains too few individuals for evaluation.

The abundance of different taxa is often considered when reconstructing paleoenvironments. I investigated the relationship between mean tooth breadth of an assemblage and the abundance of red deer in that assemblage to see if red deer are larger or smaller when they are the dominant species (data listed in Table 6.4). There is no relationship present in a pooled analysis of all western European assemblages ( $n = 38$  sample means,  $r = -0.01$ ). If size was investigated in relation to specific taxa, such as reindeer, horse, or bison, then perhaps a relationship would become apparent.

### ***The Mediterranean coast, northern Spain and northern Europe through time***

My next step was to investigate size variation through time in relation to glacial cycles in three regions of western Europe: the Mediterranean coast, northern Spain, and northern Europe, as defined above. My analyses followed those described above for all of western Europe.

Figure 6.6.A shows the relationship between  $M_1$  breadth and OIS for the Mediterranean coast, and Table 6.5.B lists the statistical results. The mean sizes of the specimens from stages 1 and 3 are smaller than the specimens from 6 and 7. This is the expected result for comparing 1, 3, and 6, but I also would expect specimens from interglacial stage 7 to be smaller and more comparable to 3. Even then 3 might be larger because the conditions during this stage were not as warm as during either 5 or 7. The samples from 6, 2, and 8 have the largest means, which are consistent with being glacial stages, but the samples for OIS 2 and 8, along with 4, are too small to really differentiate between the other stages. OIS 9 has a larger sample size, but it cannot be differentiated either.

The specimens from northern Spain are considered in Figure 6.6.B and Table 6.5.C. Individuals from only OIS 1, 2, and 3 are represented. Red deer in OIS 3 are significantly larger than those from OIS 1 or 2, and those from OIS 1 and 2 cannot be differentiated. This is opposite of the expected result, in which OIS 3 would have smaller specimens because, although this was part of the last glaciation, it was warmer than OIS 2. I would have expected that OIS 2 would have larger specimens than OIS 3 because, as the Last Glacial Maximum, the glacial conditions were very extreme. These results are also different from those for the Mediterranean region, where specimens from OIS 1 and 3 were similar in size. The results for northern Spain should be taken as preliminary, because of the inconsistent sampling in this region; the vast majority of specimens are from OIS 2.

Finally, the relationship between OIS and  $M_1$  breadths in northern Europe is illustrated in Figure 6.6.C, and the statistical results are shown in Table 6.5.D. Samples are small in this analysis, and none of the samples can be differentiated using the Tukey-Kramer Honestly Significant Difference test. Using the less conservative student's t-test, the mean for OIS 9 is significantly smaller than those for OIS 1 and 7, but OIS 1 and 7 cannot be separated. These results are different from those obtained for the Mediterranean coast, where OIS 7 had a larger mean than OIS 1.

### ***During each Oxygen Isotope Stage***

Oxygen Isotope Stages 1, 3, 7, and 9 provided large enough samples so that it was possible to compare between regions during each stage (Figure 6.7). During OIS 1, northern European specimens were significantly different from red deer in the Mediterranean and northern Spain, while there was no significant difference between

these latter two regions, following the expectations of Bergmann's rule. During OIS 3 no specimens from northern Europe were available, but the red deer from northern Spain were significantly larger than those from the Mediterranean coast (1.3 mm,  $p < 0.0001$ ). Given that the two regions had red deer of similar size during OIS 1, are at similar latitudes, and have similar mountainous coastal environments, it is unclear what may have caused this significant difference. Further investigations using more specific environmental indicators may provide some possible explanations. During OIS 7 and 9, only the Mediterranean coast and northern Europe can be compared. The means between the regions cannot be statistically differentiated during either time period ( $p = 0.89$  and  $p = 0.39$  respectively). These results suggest that during these interglacial periods, the red deer living in northern Europe and along the Mediterranean might be considered as belonging to one population; today they are all considered part of the subspecies *C. e. hippelaphus*. The results from OIS 3 could support this, with the red deer from northern Spain being considered a separate population isolated by the Pyrennes, as today they are considered the separate subspecies *C. e. hispanicus*. The data from OIS 1 do not support this, meaning that further variables need to be considered.

### **Modern *C. elaphus* metatarsal breadth and climate**

While tooth breadth does show a relationship with climate in modern North American elk and fossil European red deer, the pattern is weak. This may be because tooth size is a more heritable trait while body size is more plastic. Because of the highly functional nature of teeth, teeth have undergone morphological selection pressure that is not directly related to body size (Janis, 1990). Because skeletal body size is more plastic, it has the potential to respond more rapidly to environmental changes. Previous

researchers have noted that tooth size and skeletal measures of body size change at different rates and respond differently to environmental factors. Lister (1989) studied the decrease in body size of red deer isolated on Jersey, Channel Islands, and he found that post-cranial remains were 55.9% of the ancestral population's size, while teeth were 76.5% of the ancestral population's size. This reduction occurred in less than 6,000 years, showing that these changes can happen in a geologically short amount of time. Hadly (1997) found that in pocket gophers (*Thomomys talpoides*), tooth row length remained stable through climatic fluctuations during the last 3,000 years, but diastema length of the mandible changed, reflecting a change in pocket gopher body size as a response to climatic change. These studies suggest that skeletal elements are plastic and readily influenced by nutrition and the environment during growth and development (including *in utero*), while tooth size is more genetically controlled. Skeletons will respond more rapidly to changing environmental conditions, while changes in tooth size will occur more slowly, but the variation present in tooth size shows that tooth size is still not a static trait.

Due to the plastic nature of postcranial elements and their greater potential to reflect the influences of the environment on body size, I also studied the relationship between distal metatarsal and metacarpal breadth and climate, because these elements are well represented in the fossil record. Scott suggested that there are biomechanical reasons why the weight bearing bones of an animal's body (the limbs) will have the best relationship with body mass (Scott, 1990). She found that in general, non-length dimensions of proximal and distal elements show the best relationship with body mass between species of cervids (Scott, 1987). Between different species of cervids, distal

metacarpal breadth and distal metatarsal breadth are good predictors of species average body mass (metacarpal:  $r^2 = .87$ , metatarsal:  $r^2 = .94$ , Scott, 1990:375-376). As with tooth breadth, it is currently not possible to directly investigate the relationship between body mass and skeletal dimensions between the subspecies of *C. elaphus* or between individual animals. It is probable that distal metapodials provide a good indicator of body mass, because they are sexually dimorphic, reflecting differences in body mass between males and females (Figure 6.1.B).

I first investigated geographic patterning in modern North American elk size using distal metatarsal breadth. Sample sizes for modern European red deer were too small to include in this analysis. Because elk are sexually dimorphic, I analyzed males and females separately. In both males and females, there is a strong relationship between distal metatarsal breadth and latitude, mean annual precipitation and temperature, and mean annual January and July temperature (Figure 6.8). All correlation coefficients are above 0.52, and all regression lines are significantly different from zero, indicating a significant relationship between these measures of climate and size (Table 6.6). The relationship between distal metatarsal breadth and July minus January temperature is not as strong. In males,  $r = 0.18$  only and the line is not significantly different from zero; the relationship is stronger in females where  $r = 0.49$  and the line is significantly different from zero. With the exception of the measure of seasonality, the male and female regression lines have comparable slopes and correlation coefficients, indicating that males and females respond to variation in climate in similar ways (contra Clutton-Brock & Albon, 1989 for Scottish highland red deer and Weinstock, 1997 for reindeer).

These significant patterns should be taken with caution, however. They mainly reflect differences in size between the larger *C. e. nelsoni* that live in colder, wetter Rocky Mountain environments and the smaller *C. e. nannodes* that live in hotter, drier valleys of southern California, and regressions between two discrete clusters of points can provide strong relationships where none actually exists. Unfortunately only two male specimens of *C. e. roosevelti*, the largest of the remaining North American subspecies, were available for study. This subspecies lives in similar latitudes to *C. e. nelsoni*, but in an area that is much less seasonal in temperature and much wetter. The divergence of these two individuals, along with one male *C. e. nannodes* from Monterey County, CA, is the reason for a lack of relationship between distal metatarsal breadth and July minus January temperatures. Female representatives of these populations were not available, so the relationship in females appears much better. In sum, the metatarsal data are suggestive of the pattern described by Bergmann.

### **Fossil *C. elaphus* metacarpal breadth and climate**

Metacarpals are better represented in my fossil samples than metatarsals, so I investigated the relationship between distal metacarpal breadth and paleoclimate. Nonetheless, the Late Pleistocene red deer metacarpal sample sizes are still small, so I was only able to compare the samples from the Mediterranean and northern Spain. Figure 6.9 illustrates the relationship between OIS and distal metacarpal breadths, and Table 6.7 lists summary statistics for my samples. Only the samples from OIS 2, 3, and 6 are large enough for discussion, and the sample from OIS 2 is far larger than for any other time period. Comparisons using the Tukey-Kramer HSD test shows that individuals during OIS 3 are significantly larger than those found during stages 2 or 6. This is opposite to

what would be expected based on Bergmann's rule, although this is consistent with the results from  $M_1$  breadths from northern Spain (Figure 6.7.B). It is not surprising that these results would be consistent with those found in the teeth, because the overwhelming majority of metacarpal breadths are measured on Spanish populations (Spain:  $n = 133$ , Mediterranean:  $n = 28$ ). Due to inconsistent sampling, all of the specimens from OIS 1 and 6 derive from Mediterranean samples, while all those from Spain are from OIS 2, 3, and 4 (Figure 6.9). The metacarpal and tooth breadths converge to show that the red deer were smaller during OIS 2 than OIS 3, which contradicts Bergmann's rule. In the Mediterranean, the metacarpals and teeth agree in showing that individuals in OIS 1 were smaller than during OIS 6, despite the small sample size for OIS 1, supporting Bergmann's rule. The results from small samples of metacarpals should be considered with caution, because of the sexual dimorphism found in distal metacarpal breadths.

## **Discussion**

In North American elk, both distal metatarsal breadth and tooth breadth follow the empirical pattern described by Bergmann, but the relationship between tooth size and climate is much weaker than the relationship with distal metatarsal breadth and climate. European red deer do not show the same pattern as elk, and in fact their relationships with climate are weaker and often opposite. Researchers have noted that Europe is under a more East-West environmental cline than North-South (Hesse 1921 as in Walvius, 1961; Weinstock, 1997), so it not surprising that the relationship between latitude and tooth breadth was poor. However, there should still be a relationship with temperature and precipitation. The relationships with temperature are not significant (Jan:  $p = 0.54$ ; July:  $p = 0.26$ ), but the relationship with precipitation is moderate and negative ( $r = -$

0.19), which supports Langvatn and Albon's (1986) results for Norwegian red deer. In North America, body size increases with increased precipitation almost to the same degree ( $r = 0.20$ ). In addition to precipitation, nutrient availability determines vegetation quality and abundance (Olf *et al.*, 2002), so that precipitation may affect the productivity of some ecosystems differently than others. The composition of the vegetation in North America and Europe may respond differently to changes in climate, and therefore a more direct indicator of vegetation may have a better relationship with body size in both groups.

Another reason for the weak patterning may be that none of the climatic variables chosen for this study are the key factors influencing size. Snow depth or persistence, length of growing season, or wind speed may actually have a stronger relationship with body size. Qualities of vegetation other than nutritional value, such as their ability to provide thermal cover, may be more important. Finally, variation in body size in *C. elaphus* may not be related to climate in any way. Abiotic variables may be important, such as elevation, topography or soil fertility. Possible other factors include predator pressure, population density, and competition with other ungulates. Competition with other ungulates could result in a shift in body size, a character displacement or release, that would segregate the niches of two similarly adapted species living in the same place (Dayan *et al.*, 1991). The data available here do not permit me to test any of these possibilities.

The current data are limited by the extinction in the recent past of many subspecies of *C. elaphus*. These gaps in the data may obscure previous patterns. In particular, the extinct Merriam elk (*C. e. merriami*) inhabited Arizona, New Mexico, and

the mountains of Mexico (Bryant & Maser, 1982), making it the southern-most subspecies of *C. elaphus*. Contrary to Bergmann's rule Murie (1951) describes this subspecies as being larger than either *C. e. nelsoni* or *roosevelti*. An even bigger problem may be that the remaining populations in both North America and Europe have been overexploited and are often not in their native environments; many individuals have been relocated to start new populations and revive existing population. The postcrania of the offspring of relocated individuals should acclimate rapidly to reflect the new environment, but tooth size will lag behind, which would obscure relationships with the climate. These recent population movements may prevent characterization of the relationship between climate and modern *C. elaphus* tooth size, but by using the time depth of the fossil record, it may be possible to establish a relationship between tooth size and climate. If a pattern is consistently detected, then it may be possible to use red deer tooth size a paleoclimatic indicator in subsequent analyses. More detailed studies using larger samples of metapodial breadth from diverse populations should clarify the relationship between postcranial size and the environment, allowing fossil red deer body size to inform on past environmental conditions. Because of the sexual dimorphism of this species, care will be needed to not mistake sex biases samples for differences in average population body sizes.

### **Summary and conclusions**

Modern North American elk size correlates with climatic parameters to support Bergmann's rule. This relationship is stronger in sex divided analyses of distal metacarpal breadths than it is in analyses of  $M_1$  breadths. This supports evidence that skeletal elements are more plastic than teeth and more closely reflect body mass, as

indicated by the sexual dimorphism present in distal metapodial breadth but not detected in  $M_1$  breadth. Western European red deer do not exhibit relationships with the climatic parameters that would suggest that red deer follow Bergmann's rule. Seasonality has the strongest relationship with size in red deer, yet this is the only relationship that is not present in elk. There are multiple explanations that require further investigation: red deer and elk may respond to climatic or environmental pressures in different ways, neither is responding to these pressures and the relationship in elk is spurious, or there is a relationship present in elk, but recent habitat loss and over exploitation in Europe masks the pattern in red deer. Also unresolved is if there is a real relationship with the climatic variables presented here, are the animals responding to thermoregulatory constraints or are the climatic variables a good proxy for another environmental variable, such as vegetation quality. A final possibility is that there is no relationship with climate, but other aspects of the community are important, such as predator pressure or competition with other ungulates.

The Late Pleistocene red deer generally appear to follow Bergmann's rule. They are mostly larger during glacial cycles and smaller during the interglacial cycles. Unfortunately, environmental variables that could provide more detailed data than Oxygen Isotope Stages are not available for many sites or are not consistent across many sites. As it stands, without full knowledge of relationships between modern *C. elaphus* body size and climatic parameters and without more detailed analyses of environmental variables of fossil sites, *C. elaphus* body size cannot be used as a paleoclimatic indicator. Within a well-documented region, however, red deer body size could still be useful as a biostratigraphic indicator to place assemblages within a relative sequence or as

supporting evidence for other paleoenvironmental indicators, such as abundance of other species or pollen records.

## **Chapter 7: Mortality profiles in paleolithic western Europe**

I chose to study mortality profiles of Late Pleistocene red deer from West European archaeological sites by analyzing the data using multiple methods and ways of defining my samples, and I based my final interpretations on the consistent patterns that emerged from my data. In my first analysis, I used excavator-defined stratigraphic layers to define my samples, and I included samples with combined a dP<sub>4</sub> and M<sub>1</sub> total of more than twenty-five measured crown heights. I ran histogram, boxplot, and modified triangular graph analyses on all samples. In my second analysis, I grouped multiple layers from one archaeological site whenever they had the same tool industry. I did this because levels in older excavations often were defined by stone tool industries and not on finer stratigraphy within different cultural periods. In this analysis, I included all assemblages with combined dP<sub>4</sub> and M<sub>1</sub> samples of more than twenty-five measured crown heights. Grouping samples increased the number of samples that I could include in my analyses. I also ran histogram, boxplot, and modified triangular graph analyses on all these samples. In my third analysis, I used excavator-defined stratigraphic layers to define my samples, but I included samples with ten or more measured M<sub>1</sub> crown heights to maximize the samples that I could include. I excluded dP<sub>4</sub>, because they may be inconsistently biased. Because sample sizes were smaller, I constructed only boxplots and bivariate plots. This allowed me to best investigate patterning in my data. To maximize the amount of information available in one place, I graphed the medians of these smaller samples on a bivariate plot with time, and I used these smaller samples to investigate the relationship

between the age of the animals in the assemblages and the environment. I based my final interpretations on patterns that consistently emerged in all three analyses.

### **First analysis: Samples with more than twenty-five individuals**

#### ***Sample definition***

I limited my first analysis of the fossil data to assemblages with combined dP<sub>4</sub> and M<sub>1</sub> samples of more than twenty-five measurable teeth. I also included the wolf and human hunted elk samples described in Chapters 2 and 5 for comparison. I chose twenty-six individuals as my cut-off point because this is the minimum number of specimens necessary to easily perform the Kolmogorov-Smirnov test when analyzing histograms (Sokal & Rohlf, 1995). I used dP<sub>4</sub> and M<sub>1</sub> because they provide a complete age profile and because the relationship between age and crown height is best understood for these teeth. I included P<sub>4</sub> in the triangular graph analysis, because the method was originally described using this tooth (Stiner, 1990; Stiner, 1994).

Summary statistics for each assemblage are provided in Table 7.1, and more details are given in Appendix D. I use stratigraphic layers as defined by the excavators to delineate my assemblages, and this can create some inconsistencies. For example, more recent excavators may define many stratigraphic layers within one cultural unit, but in older excavations, the layers are defined by the cultural units and probably lump many stratigraphic layers (compare La Riera or Combe-Grenal to Urutiaga, for example in Appendix D). Because this analysis depends on samples from potentially fine layers, the sample sizes are small and limit the included assemblages. I address these problems by

performing a second analysis, below, were I lump samples within a site by tool industry so that levels defined by stratigraphy are comparable to those defined by tool industry.

### ***Histograms***

Mortality profiles were created as histograms using the modified QCHM formulas provided at the end of Chapter 4. The relevant equations are below:

$$dP_4: \quad AGE = AGE_s [(CH-CH_0)/CH_0]^2$$

$$M_1: \quad AGE = (AGETpl - AGE_e) [(CH-CH_0)/CH_0]^2 + AGE_e$$

Where AGE<sub>s</sub> is the age when dP<sub>4</sub> is shed (26 months), AGE<sub>e</sub> is the age when M<sub>1</sub> erupts (6 months), and AGETpl is the age of tooth potential longevity (here 163.6 months based on the quadratic regression of known age on tooth crown height as discussed in Chapter 4). CH<sub>0</sub> is the unworn tooth crown height and was determined for each sample (values are listed in Table 7.1). These equations estimate age in months, and to construct the histograms, I divide these months into 10% of life span age classes. For red deer, age of potential ecological longevity is approximately 16 years or 192 months, and therefore, each age class is 19.2 months long. By using the AGETpl as 163.6, no specimen is placed in the 10<sup>th</sup> age class, because this age class begins at 172.8 months. Because this bias is consistent across all samples, it will not affect the application of the Kolmogorov-Smirnov test.

The histograms for the fossil samples are shown in Figure 7.1, and the Kolmogorov-Smirnov test results are listed in Table 7.2. Visually, the histograms fall into two categories. In the first, there is a large number of individuals in the first age class relative to the adult age classes. El Castillo, El Juyo 4, 6, and 8, Gabasa e and f, Urtiaga D, and the wolves follow this pattern. The pattern is characteristic of both the living and

the attritional model age structures (see Figure 5.1.A) and indicates an ability to obtain these vulnerable juvenile individuals. The alternate pattern visible in the histograms is little differentiation between the number of individuals in the first age class and the subsequent age classes. Combe-Grenal 52, Lazaret E, Urtiaga C and D, and the recent human hunters follow this pattern. Both Middle and Upper Paleolithic assemblages create the pattern, indicating that if this pattern is reflecting hunting strategies, then these strategies are shared by both Middle and Upper Paleolithic people. An alternate explanation is that the deciduous teeth represented in Age Class 1 are more susceptible to pre- and post-depositional destruction, as discussed in Chapter 5, and the variation is due to preservation biases. If such is the case, Age Class 1 should not be used to indicate differences in hunting strategy unless possible biases are controlled for with specific knowledge about depositional histories. The alternative is to discount the juveniles and focus on the adult specimens. In these fossil samples, adult patterns vary in the number of age classes represented. Most assemblages contain relatively few specimens beyond Age Class 5; El Juyo 4 and Gabasa f do not contain any. Lazaret E, Urtiaga D, and the wolves contain the highest number older specimens, and to a lesser extent, Gabasa e, El Juyo 8, and the recent humans do, too. However, only Lazaret E and the wolf kills show more individuals in the oldest age class represented than in previous ones, resembling what is commonly seen in the attritional profile.

Table 7.2 provides the Kolmogorov-Smirnov results for the complete age distribution. The Upper Paleolithic samples do not significantly differ from each other. Gabasa e is also not significantly different from the Upper Paleolithic assemblages. The other Middle Paleolithic assemblages do differ statistically from some Upper Paleolithic

assemblages, most notably Gabasa f from Urtiaga F and Lazaret E from both Urtiaga D and El Juyo 4. Gabasa e and particularly Gabasa f are significantly different from the other Middle Paleolithic assemblages but not from each other. Combe-Grenal 50 and 52 and Lazaret E are not significantly different from each other. The wolf kills are significantly different from every sample but Lazaret E, but Lazaret E is also not significantly different from the recent human hunters and some Upper Paleolithic samples. The majority of the fossil assemblages are significantly different from both the living and attritional model age structures. The exceptions are Lazaret E and Combe-Grenal 52, which are not significantly different from either, and Combe-Grenal 50, which is not significantly different from the living structure.

Due to the taphonomic issues previously discussed, ideally I would run a Kolmogorov-Smirnov test with Age Class 1 excluded. Unfortunately, this decreases most sample sizes to less than twenty individuals, and the Kolmogorov-Smirnov test in the Smirnov program would always show non-significant differences (R. G. Klein, personal communication). Only El Castillo, El Juyo 6, and Combe-Grenal 50 remain large enough to compare. When Age Class 1 is excluded, none of these samples are significantly different from each other or the recent human hunters sample (in all cases  $p > 0.1$ ). All three assemblages are significantly different from the wolf-kill sample (in all cases  $p < 0.001$ ). When the complete age distributions for these three fossil assemblages were compared above, they were not significantly different either. El Castillo and El Juyo 6 were significantly different from the recent human hunters. These samples were all also significantly different from the wolf kills. Eliminating the juvenile individuals did not change the results for these three fossil samples.

The histogram analysis shows variation between all samples, and no consistent trends distinguish Middle and Upper Paleolithic assemblages. With the exception of Lazaret E, wolf kills have a different age distribution from all the fossil assemblages. Major differences between the assemblages appear to be in the number of juveniles present, but sample sizes are too small to test this hypothesis.

### ***Boxplots***

I created boxplots for each of the samples with more than twenty-five measurable dP<sub>4</sub> and M<sub>1</sub> specimens combined. Mortality distributions can be compared using boxplots that show the median tooth crown height and the spread around that median. Because boxplots are created from raw measurements, only one tooth type can be plotted at a time. For red deer, M<sub>1</sub> is best, because M<sub>2</sub> and M<sub>3</sub> are not consistently measurable until 2.5 and 4.5 years of age, respectively. Because juveniles are considered separately, boxplots help address the pre- and post-depositional destruction bias mentioned above. Red deer body and tooth size fluctuates through time and space, so I standardized each crown height measurement by the mean unworn crown height for that sample (Klein & Cruz-Uribe, 1983) and also by the mean M<sub>1</sub> breadth for that sample (both listed in Table 7.1). I standardized both ways because there are often only 2-5 unworn crown height measurements available for a sample, if any are available at all. Breadth usually can be measured on any tooth where crown height can be measured, so the means are based on larger sample sizes (although heavily worn teeth are excluded). I used both methods in my first two analyses to show that they produce consistent results, because in my third analysis I could only standardize by mean breadth as many of the samples did not have unworn M<sub>1</sub>s.

Figure 7.2 shows the  $M_1$  boxplots for the larger Late Pleistocene red deer samples. The median value is in the center of the box, and the darkly shaded areas approximate the 95% confidence intervals around these medians. If the shaded areas for two samples do not overlap, then they can be considered significantly different. The approximate zone for prime animals, estimated from the known-age sample, is lightly shaded throughout the chart. With the exception of the wolf-kill samples, all medians are either within the prime zone or indicate even younger animals. This bias towards young individuals is consistent with the histogram results. In many instances in the histograms, both  $dP_4$  and  $M_1$  had large numbers of individuals in Age Class 1, and I chose the larger of the two numbers. I expected that these young  $M_1$ s would appear in the boxplot analysis, too. In general, Combe-Grenal 50 and 52 and Lazaret E contain more prime adult individuals than the other samples. Lazaret E is distinct from all the Upper Paleolithic assemblages except El Castillo. Gabasa e and f cannot be distinguished from any Upper Paleolithic assemblage. All samples are significantly different from the wolf-kill sample.

Figure 7.3 shows the larger samples with their crown heights standardized by the mean breadth of the sample. The overall pattern is the same as when the samples are standardized by unworn crown height, but a few differences do occur. Lazaret E is now significantly different from all of the Upper Paleolithic samples and Gabasa e and f. Combe-Grenal 50 and 52 are significantly different from Gabasa f, El Juyo 4, 6, and 8, and Urutiaga C. Gabasa e and f overlap with all of the Upper Paleolithic samples. All of the samples are still significantly different from the wolf kills.

The boxplot analysis demonstrates that all of the Upper Paleolithic samples except El Castillo are biased towards young individuals. Gabasa e and f are also biased towards young specimens and are indistinguishable from the Upper Paleolithic samples. The older Mousterian assemblages of Combe-Grenal 50 and 52 and Lazaret E contain less juvenile and more prime individuals than the other samples.

### ***Modified triangular graphs***

The final analysis of the larger samples employed the modified triangular graph described in Chapter 5. In my first analysis using this method, I divided the ten age classes used in the histogram analysis into three age classes: young, prime, and old. I placed all individuals in Age Class 1 into the “young” age class and those in Age Classes 2-5 into the “prime” category. I defined the beginning of “old” as older than 50% of life span following Klein and Cruz-Urbe (Klein & Cruz-Urbe, 1984:56), and, therefore, I placed individuals from Age Classes 6-10 in the “old” age class. In *C. elaphus*, Age Class 6 begins at 115.2 months (9.6 years), which is consistent with wildlife research considering *C. elaphus* individuals as “old” beginning at around 8 to 12 years old (Clutton-Brock *et al.*, 1982; Flook, 1970; Houston, 1982; Taber *et al.*, 1982).

Figure 7.4.A shows the first modified triangular graph for the larger samples. The circles approximate 95% confidence intervals around each sample’s point. If two circles do not touch or overlap, then the two samples can be considered significantly different. When looking at Figure 7.4.A, two things are immediately apparent. First, none of the archaeological assemblages resemble the wolf-killed sample, and second, none of the archaeological assemblages contain many old individuals. A few samples are biased toward prime or young individuals. The intervals around Gabasa e and f and Urutiaga D

are within the left side of the graph, representing mostly juvenile individuals, and are distinct from Combe-Grenal 50 and 52, Lazaret E and the recent human hunters. All of these samples are in the right side of the graph, representing prime individuals. This pattern is consistent with the boxplot results.

I performed a second triangular graph analysis following the directions of the method's original formulator (Stiner, 1990; Stiner, 1994). In this analysis I assigned all dP<sub>4</sub>s in the assemblage, including those that were not measurable and therefore were excluded from the histogram analysis, to the "juvenile" category. For the adults, Stiner uses P<sub>4</sub> and classifies all those that are less than 50% worn as "prime" and those over 50% worn as "old" using her outlined wear stages. I assigned degree of wear by calculating the mean unworn crown height of P<sub>4</sub> for each assemblage (values listed in Table 7.3) and defined 50% worn using this measurement; I assigned "prime" or "old" as appropriate. Also following Stiner, I excluded any completely unworn P<sub>4</sub>s from the analysis to prevent double counting with dP<sub>4</sub>. Unlike Stiner, I plotted my samples with the modified triangular graph program, which produced confidence intervals around my points. Some samples were excluded from this analysis because P<sub>4</sub> measurements were unavailable. Summary statistics for the included samples are in Table 7.3.

The results for the modified triangular graph analysis using dP<sub>4</sub> and P<sub>4</sub> are shown in Figure 7.4.B. More variation is apparent in the samples, because they are not as clustered in the bottom of the graph as in 7.4.A. Combe-Grenal 50 and 52 still cluster in the lower right of the graph, along with Urutiaga F, in the area for high percentages of prime individuals. Gabasa e and f and Urutiaga D are clustered in the lower left. Lazaret E

has the highest percentage of old individuals, but this point is encompassed by a large density contour that is significantly different only from Gabasa e and f and Urtiaga D.

Both modified triangular graph analyses show that there is considerable overlap of age distributions in the Middle and Upper Paleolithic assemblages. Most samples do not contain very many old individuals and primarily differ in the number of juveniles that they contain.

### ***Summary***

In all of the analyses, some Middle Paleolithic samples cannot be distinguished from Upper Paleolithic samples, suggesting that at least some Neandertals hunted in similar ways to modern humans. Most of the variation between samples is in the number of juvenile individuals, whether indicated by  $dP_4$  or slightly worn  $M_1$ s. This variation might be due to differences in hunting, transportation of mandibles of different ages back to the cave sites, the degree of carnivore ravaging, or post-depositional histories. Urtiaga F and particularly El Castillo have fewer juveniles than the other Magdalenian assemblages. Multiple results show that Lazaret E has a greater abundance of older individuals than the other samples, although this is not always statistically significant. Lazaret E is the oldest assemblage included in these analyses, and its stone tool industry is from around the time of the transition from Acheulean to Mousterian in southern France. If later Middle Paleolithic people were hunting in ways indistinguishable from Upper Paleolithic peoples, as indicated by Gabasa e and f, then Lazaret E could be showing changes in hunting practices that might have co-occurred with changes in stone tools. More samples and better understanding of the depositional history of these samples will help test this idea.

## **Second analysis: Grouped samples**

### ***Sample definition***

For my second analysis of the red deer fossil specimens, I wanted to include more assemblages to see if they confirmed the patterns that I detected in my first analysis. For this analysis I also wanted to increase my sample sizes, and the only way I could do this was to group multiple samples together. Granted, lumping can obscure fine patterns seen between stratigraphic layers, but my approach to this project was to attempt many different ways of looking at the data and base my conclusions on patterns that repeatedly emerge. I began by grouping layers within one site by their tool assemblages. By doing this, a La Riera Solutrean sample was added; no Solutrean assemblages were included in the first analysis. The Magdalenian layers from Urutiaga and El Juyo included in the first analysis are each grouped into a sample. All of the layers from Gabasa and Lazaret are now included; hopefully larger samples from these unique sites will help illuminate their histories. I grouped all Combe-Grenal samples into layers 1-35 and 36-54. Although these assemblages are defined as different Mousterian facies, I chose to group them in this way because other aspects of the deposits show a break at this time (Delpech, 1996). Grouping these layers allows much more of this rich site to be studied. Finally, I grouped all of the Azilian samples from northern Spain so that this most recent time period could be included; Urutiaga C is included in this sample. Summary statistics for the samples considered in these analyses are listed in Table 7.4, and full descriptions are provided in Appendix D. My methods for analyzing the age distributions are exactly the same as for my first fossil analysis and are described in Chapter 5, so I will not repeat them here.

## *Histograms*

Consistent with the first histogram analyses, the grouped samples differ primarily in the number of juveniles relative to the subsequent age classes. El Castillo, El Juyo, Gabasa, La Riera, and the wolf kills all have higher numbers of individuals in Age Class 1 than in the subsequent age classes. In contrast, Combe-Grenal 1-35 and 36-54, Lazaret, and the recent hunters all have similar numbers of individuals in Age Class 1 and the immediately subsequent ages classes. Combe-Grenal 1-35 is unique in that it is the only sample where the number of individuals in each age class increases as the age classes get older. Lazaret E in the first analysis is the only sample that is comparable, because this sample has the same number of individuals in Age Classes 1, 2, and 3.

The Kolmogorov-Smirnov results show that none of the Upper Paleolithic assemblages are significantly different from each other (Table 7.5.A). All of the Middle Paleolithic assemblages are significantly different from the Upper Paleolithic assemblages with the exceptions of Gabasa with the north Spanish Azilian sample and Combe-Grenal 36-54 with La Riera. Gabasa is also significantly different from the other three Mousterian samples, suggesting that this site is unique. The two Combe-Grenal samples are significantly different from each other, but neither sample is significantly different from Lazaret. All fossil samples are significantly different from the wolf-kill sample and the model attritional structure, although most samples are also significantly different from the recent human hunters and the model living age structure. Lazaret is not significantly different from the model living age structure.

Grouping the samples created large enough sample sizes so that I was able to compare only the adult distributions, excluding Age Class 1, using the Kolmogorov-

Smirnov test (Table 7.5.B). The northern Spanish Azilian and Gabasa samples were too small to include in the analysis. The Upper Paleolithic samples are not significantly different from each other, and many of the differences between the Upper and Middle Paleolithic samples are no longer significant. Combe-Grenal 1-35 is still significantly different from El Juyo and Urtiaga, and Lazaret is still significantly different from El Juyo. Combe-Grenal 1-35 and 36-54 are no longer statistically different from either other and are still not significantly different from Lazaret. All of the samples remain significantly different from the wolf-kill sample and the model attritional profile. Many of the significant differences between the fossil samples, the human hunters, and the model living age structure are no longer present. These results confirm that many of the differences between samples are due to the proportion of juveniles present relative to the adults in the sample.

The proportion of juveniles present thus accounts for most of the variation between samples and causes most of the distinctions between the Middle and Upper Paleolithic. Most of the Middle Paleolithic samples have few juvenile individuals compared to adults. The Gabasa sample is unique, because it has a very high proportion of juveniles and is more similar to the Upper Paleolithic samples than are the other Middle Paleolithic samples. When juveniles are eliminated, the most of the samples are statistically indistinguishable. The question remains about whether or not the variation in  $dP_{4s}$  reflects hominid behavior or pre- or post-depositional destruction of deciduous teeth.

### ***Boxplots***

Figure 7.6 shows boxplots of the median  $M_1$  crown heights from the grouped samples standardized by the mean unworn crown height calculated from that sample, and

Figure 7.7 shows the same samples but crown heights are standardized by the mean  $M_1$  breadth of the sample (Table 7.4 provides the values). Both analyses show similar results, indicating that both adequately standardize the samples. In both analyses, Combe-Grenal 1-35 and 36-54 and Lazaret have median crown heights that are significantly lower than Gabasa and all of the Upper Paleolithic samples except El Castillo. Gabasa resembles the Upper Paleolithic samples, and this assemblage, northern Spanish Azilian, El Juyo, and La Riera contain large numbers of young individuals. El Castillo contains the fewest of the Upper Paleolithic sites.

### ***Modified triangular graphs***

In the last analysis, I plotted the grouped samples on the modified triangular graphs using the age classes from the histogram analysis derived from  $dP_4$  and  $M_1$  (Figure 7.8.A) and using  $dP_4$  and  $P_4$  (Figure 7.8.B; samples summarized in Table 7.6), as I described above. In the analysis of  $dP_4$  and  $M_1$ , all of the samples are distinct from the wolf-kill sample. Most of the variation is in the percentage of juveniles present, but Combe-Grenal 1-35 and Lazaret do contain more old individuals. Combe-Grenal 1-35 is distinct from all of the samples except for Lazaret. Lazaret and Combe-Grenal 36-54 overlap with each other and La Riera, Urutiaga, and the recent human hunters; these samples plot on the right of the graph showing an abundance of prime individuals, and they are distinct from all other Upper Paleolithic assemblages and Gabasa. Gabasa plots in the far left of the graph and has the highest abundance of juveniles. It overlaps primarily with El Castillo and to a much lesser extent with the northern Spanish Azilian.

The  $dP_4$  and  $P_4$  analysis shows more separation between the samples (Figure 7.8.B). El Castillo and the recent human hunters were excluded from the analysis because

measurements on P<sub>4</sub> were unavailable. The 95% confidence interval of the wolf-kill sample just barely overlaps with the 95% confidence interval of Lazaret. Lazaret has the highest proportion of old individuals and overlaps only with Combe-Grenal 1-35. Combe-Grenal 1-35 overlaps with El Juyo, too, but not Combe-Grenal 36-54. At the 95% confidence level, the Upper Paleolithic samples are not significantly different from each other, except for El Juyo and Urtiaga. The Gabasa sample is isolated in the far left of the graph showing a high abundance of juveniles.

The modified triangular graph analyses show that Combe-Grenal 1-35 and Lazaret have higher proportions of old individuals than the other samples and are for the most part distinct from the Upper Paleolithic samples; Combe-Grenal 36-54 is more similar to the Upper Paleolithic samples. Gabasa is distinct with its high percentage of juveniles. The Upper Paleolithic samples vary among themselves mainly in the percentages of juveniles compared to adults; all have low proportions of old individuals.

### ***Summary***

The results of the analyses using grouped samples are consistent with those for the samples defined by stratigraphic layers. Lazaret and Combe-Grenal 1-35 are similar to each other and distinct from the Upper Paleolithic assemblages. Combe-Grenal 36-54 is not as distinct, which is intriguing because it is the more ancient of the two Combe-Grenal samples. Gabasa is unique among the Middle Paleolithic assemblages and is often indistinguishable from the Upper Paleolithic samples, interesting because it is the youngest of the Middle Paleolithic samples. The Azilian, Magdalenian, and Solutrean samples are all similar, with the exception of El Castillo. This sample has a larger

percentage of dP<sub>4s</sub>, but a lower median M<sub>1</sub> crown height. None of the archaeological assemblages resemble the wolf-killed elk sample.

### **Third analysis: Many samples**

#### *Boxplots*

#### *Sample definition*

In order to maximize the number of samples that could be included, my final analysis incorporated all samples with ten or more measurable M<sub>1</sub>s. These samples were grouped samples, sometimes encompassing many layers from a site or layers from multiple closely grouped sites, as described for the second analysis. All of the samples from the second analysis above are included. I added an additional sample composed of multiple Epipaleolithic (= final Paleolithic) Federmesser assemblages from the Neuwied Basin region of Germany and a Mesolithic sample from Star Carr, England. I also included the Magdalenian layers from Altamira and La Riera and the Solutrean material from Altamira. The Châtelperronian assemblage from Labeko Koba in northeastern Spain, the early Mousterian assemblage from Piegu in northern France, and the Acheulo-Yabrudian material from Tabun in Israel are all large enough to be included. Figure 3.2 provides a map of the sites, and Table 7.7 lists summary statistics, including the percentage of dP<sub>4s</sub> in each sample. Appendix D provides more detailed information about each assemblage. In this analysis, I standardized M<sub>1</sub> crown height medians by mean breadth only; sample sizes of unworn M<sub>1</sub> crown heights were very small or absent, and previous analyses showed that both standardization techniques provide consistent results.

## *Results*

Figure 7.9 shows boxplots of these many samples in approximately chronological order and grouped by tool industry. The most recent Paleolithic samples and the German Federmesser and Azilian samples from northern Spain have an abundance of young individuals. Of the Magdalenian assemblages, El Juyo and La Riera are comparable to the more recent assemblages, while the other Magdalenian samples and the Mesolithic Star Carr sample have medians that are solidly within the prime-age zone. The Solutrean assemblages are indistinguishable from the Magdalenian and more recent samples. The Châtelperronian assemblage from Labeko Koba is interesting not only because its median is comparable to the Upper Paleolithic medians and Gabasa, but also because the crown heights are tightly clustered. This is unusual in a sample of only 12 individuals. Among the Mousterian samples, the median of the Gabasa sample shows a high abundance of juvenile individuals and is indistinguishable from all of the Upper Paleolithic samples. The median of the Combe-Grenal 1-35 sample is significantly lower than the Upper Paleolithic samples' medians, but Combe-Grenal 36-54 is not significantly different from five of the nine Upper Paleolithic samples. Of the Early Mousterian assemblages, Lazaret has more old specimens than each of the Upper Paleolithic samples, including Labeko Koba, and Gabasa. However, the contemporaneous or slightly older sample of Piegu from northern France overlaps with most of the Upper Paleolithic assemblages, except the Azilian sample and El Juyo, and it is distinct from Labeko Koba and Gabasa. The Tabun sample has more old individuals than the Azilian sample, El Juyo, the Solutrean sample from Altamira, Labeko Koba, and Gabasa. All samples are significantly different from the wolf-kill sample.

In sum, Mousterian and Acheulean samples overlap with some of the Upper Paleolithic samples. The Gabasa sample, the youngest of the Middle Paleolithic samples, is indistinguishable from the Upper Paleolithic assemblages in all analyses. Although there is variation present, in general the older Mousterian assemblages are more biased towards older red deer individuals than the Upper Paleolithic assemblages. The one Châtelperronian sample included in this analysis follows the Upper Paleolithic pattern.

### ***Bivariate plots***

#### *Sample definition*

For my final set of analyses, I included all samples with ten or more measurable first molars. I defined the samples as in my first analyses where each layer of each site was considered separately. There were two exceptions: the grouped Federmesser sample used in the second analysis and a grouped sample of the Acheulo-Yabrudian layers (E) from Tabun in Israel. By considering smaller samples, I was able to include many additional assemblages. Table 7.8 lists the samples and provides the summary information, and Appendices C and D provide more details, including references. Table 7.8 also provides the relevant contextual information included in the following analyses.

#### *Median crown height by date*

Figure 7.10 plots the median  $M_1$  crown height for each sample standardized with the mean  $M_1$  breadth for that sample by the sample's approximate age in thousands of years ago. The dates derive from multiple dating techniques, including radiometric dating and biostratigraphy, and are shown without confidence intervals. They are mainly used to place samples in relative sequence on the graph. Inspection of the graph produces striking

results. All samples from 60 kya or older all have median crown heights that indicate higher numbers of older prey than samples from 50 kya younger. I tested the strength of this relationship using Spearman's rho ( $r = -0.74$ ,  $p < 0.0001$ ) and Kendall's Tau ( $r = -0.51$ ,  $p = 0.0001$ ), because neither data set is expected to be normally distributed. Both tests showed a strong negative relationship between time and median crown height. The data are clustered into two groups, which may be artificially inflating the strength of the relationship, but the pattern is still clear.

The Mousterian tool industry spans the shift at 50 kya, and the most recent Mousterian samples are similar to the Upper Paleolithic samples, including the Châtelperronian, while the older Mousterian samples are similar to the even more ancient assemblages. The two recent Mousterian assemblages that cluster with the Upper Paleolithic are both from Gabasa Cave and have clustered with the Upper Paleolithic assemblages in all the above analyses. All of the medians of the more ancient samples fall below the grand mean of all the samples, although they are still the range for prime adult red deer.

#### *Median crown height by red deer abundance*

I next wanted to investigate if there was a relationship between the proportion of red deer hunted by prehistoric people and the ages of the animals hunted. Because red deer abundance changes with environmental variables, the percentage of red deer can provide an indicator of the local environmental conditions, if we assume that human hunters were taking prey in equal abundance to their proportions on the landscape. Also, by knowing the percentage of red deer in an assemblage, it may be possible to determine if red deer were hunted differently depending on whether or not they were the primary

prey item or taken only occasionally. I measured the abundance of red deer as the percentage of red deer by NISP in the total ungulate assemblage.

There is no visible patterning in the relationship between red deer abundance and prey age at death; points plot in all corners of the graph (Figure 7.11.A). Spearman's rho ( $r = 0.01$ ,  $p = 0.96$ ) and Kendall's Tau ( $r = 0.01$ ,  $p = 0.94$ ) also show that there are no correlations in the data. Not surprisingly, many samples plot in the abundant end of the graph, because these were the European assemblages that provided the largest sample sizes. The patterning in the graph seems to be by industry, and samples representing all tool industries plot in the abundant red deer portion of the graph. The early Mousterian samples have the lowest medians (0.5-0.9) while the Magdalenian samples have the highest (1.0-1.3). The percentage of red deer in Mousterian samples ranges from 23-87%; samples with low percentages have both high (1.2 and 1.3) and low (0.6 and 0.7) medians. Magdalenian samples with approximately the same median (1.0-1.1) plot in the high, medium, and low abundance portions of the graph (40-95%).

#### *Median crown height by temperature*

As listed in Table 7.8, some assemblages have environmental conditions associated with them. These are from the published descriptions of the site and are based on various sources of data, including pollen, sedimentology, and large and small mammals. The temperatures listed in site descriptions were rarely more specific than cold, cool, or temperate. Figure 7.11.B plots the median  $M_1$  crown heights standardized with mean  $M_1$  breadth for the sample by temperature. Visually inspecting the graph, it is possible to see that the sample distributions overlap. Because I would not expect the samples to be normally distributed, I ran the Wilcoxon rank sum test ( $p = 0.65$ ) and the

median test ( $p = 0.60$ ), and neither showed a significant difference between the cold and temperate samples. The distributions of the median crown heights actually did not deviate from normal, so I also ran the student's t-test ( $p = 0.51$ ). This test is more likely to find differences than the non-parametric tests. No significant difference can be detected in the median ages of the red deer hunted during cold and temperate periods of both the Middle and Upper Paleolithic.

## **Discussion**

### ***Variation in the number of juveniles***

There is a large amount of variation in the percentages of juveniles, represented by dP<sub>4s</sub>, in the samples, but this variation does not appear to be systematic. There is no significant difference in the proportion of dP<sub>4s</sub> present between the assemblages accumulated by Neandertals and those accumulated by modern humans (Table 7.8, Wilcoxon test:  $p > 0.47$ , Median test:  $p > 0.14$ ). Differences in the percentages of juveniles may be due to differences in hunting practices or pre- and post-depositional histories. Juvenile bones and deciduous teeth are not fully ossified and, therefore, are more susceptible to carnivore ravaging, compaction, fragmentation, and soil leaching than adult specimens, which will eliminate them from the fossil record (Hulbert, 1982; Klein *et al.*, 1983; Klein & Cruz-Uribe, 1984; Kurtén, 1953; Lyman, 1994; Munson, 2000).

It may be possible to control for biases caused by pre- and post-depositional destruction to better estimate the composition of the original assemblage. One way is to discount deciduous teeth and use boxplots to compare wear on only permanent teeth.

Lightly worn  $M_1$ s do indicate the presence of younger individuals in an assemblage, although the very youngest will not be included. Pre-depositional destruction can be assessed by looking for evidence of carnivore damage, such as skeletal part representation, gnaw marks, and gastric acid marks (Cruz-Urbe, 1991; Lyman, 1994; Marean & Spencer, 1991). The degree of post-depositional loss can be considered by examining the surface condition of the bones, the degree of fragmentation, and skeletal part representation (Lyman, 1994). If skeletal part representation is highly correlated with the density of those parts where the most abundant elements are the densest elements, then juvenile specimens were likely lost (Lyman, 1984; Lyman, 1985). Samples with similar kinds of biases should be compared only to each other or only using boxplots. Only once differences in the representation of  $dP_4$ s has been considered in light of pre- and post-depositional destruction can investigators firmly conclude differences in the hunting of juveniles. Because the goal of this study was to compare as many assemblages as possible, I was unable to conduct detailed analyses of all the bone assemblages. In many cases previous researchers had already conducted these analyses, but their data were not always comparable. Therefore, for this study, boxplots are the best method for investigating mortality profiles when destructive processes cannot be controlled for adequately.

### ***Hunting during the Upper Paleolithic***

The Upper Paleolithic assemblages have an abundance of young adult animals. The histogram analyses show a high number of individuals in Age Class 1, and the median crown heights for these samples are very near the line distinguishing prime from young individuals. By the time  $M_1$  erupts enough for the crown height to be measurable,

the animal is about 1.5 years old. Because boxplots only consider  $M_1$ s and the  $M_1$ s have been measured, the individuals are likely to be at least 1.5 years old. However, in many archaeological assemblages, teeth are commonly isolated from their mandibles, so  $M_1$ s of individuals younger than 1.5 years are often measured.

The Magdalenian sample from El Castillo is an exception to the trend of an abundance of young animals in Upper Paleolithic assemblages. El Castillo and El Juyo 4 can be compared, because they are roughly contemporaneous and from the same geographic region. They both contain about 47% juveniles, as indicated by the number of  $dP_4$ s, yet El Castillo's median  $M_1$  crown height is significantly lower than the median  $M_1$  crown height of El Juyo in most of the analyses. It is possible that these two groups had different hunting strategies for red deer. El Juyo is closer to the present coastline, while El Castillo is further inland, and perhaps the Magdalenian people hunted red deer during different seasons in the two locations. Cementum annuli studies of seasonality could address this. It is also possible the red deer from El Juyo and El Castillo had different diets, and therefore their teeth wore at different rates. In this case, the hunters from El Juyo and El Castillo could have been hunting the same age prey, but the environment around El Castillo made their teeth wear faster. A final possibility is that the two assemblages experienced different amounts of post-depositional destruction. More of the El Juyo  $M_1$  sample is composed of isolated teeth (28%) than the El Castillo sample (2%), and so  $M_1$ s from younger individuals may have been more readily measured in the El Juyo sample.

My results agree with Pike-Tay's (1991) study of mortality profiles in red deer from Upper Paleolithic assemblages in southwestern France. Pike-Tay (1991) found that

the age distributions of prey from Magdalenian and Azilian assemblages had many more juvenile than adult specimens in comparison to the model living age structure, while the early Upper Paleolithic samples more closely resembled the model living age structure. She hypothesized that the pattern was the result of the later people hunting with spear throwers, while the early Upper Paleolithic people lacked projectile technology. My Solutrean, Magdalenian, and Azilian samples also show an abundance of young adults. These people could have been hunting with spear-throwers, so this is one explanation for the patterning in the data. Unfortunately, none of my early Upper Paleolithic samples contained enough individuals to include in the analyses.

An alternative explanation is that the Upper Paleolithic red deer were being heavily exploited, possibly as a result of increasing human population densities. As discussed in the introductory chapter, there is evidence that Upper Paleolithic people were living at higher population densities and intensifying their use of the environment by acquiring more fish and birds than their Middle Paleolithic predecessors. It is possible that these larger human populations were exerting more pressure on red deer populations than the animals experienced during most of the Middle Paleolithic, resulting in a skewing of the living herd structure towards younger individuals. This type of overexploitation pressure is visible in simulations of life tables (Taber *et al.* 1982). It also is apparent in the histogram of the known-age elk that were killed by contemporary hunters in Montana (Figure 5.2). Males over six years of age either are in low abundance in the population (K. Hamlin, personal communication) or are inaccessible to hunters given the terrain and regulations, so the modern-human-hunting mortality profile shows

an abundance of individuals in the younger adult age classes and fewer in the prime and old classes compared to a typical herd.

### ***Comparison of the Middle to the Upper Paleolithic***

The Mousterian and more ancient assemblages have more prime individuals than the Upper Paleolithic assemblages, including the Châtelperronian; the medians of the two groups are mutually exclusive (Figure 7.10). But there is one exception, the assemblages from Gabasa Cave, the most recent Mousterian site included in the study. These Mousterian assemblages cluster with the Upper Paleolithic samples in having more young specimens. This possible change in hunting during the Middle Paleolithic supports Stiner's (1990) conclusion that a shift in hunting strategies occurred approximately 45-55 kya. While my data support Stiner's hypothesis, these conclusions are only tentative because of the limited sampling involved. Gabasa is only one site with two larger assemblages.

It is important to note that Stiner (1990) suggested that the more ancient Neandertals were acquiring more prey by scavenging, while after 45-55 kya, they hunted in ways that resemble modern humans. My data do not provide evidence of scavenging, because the medians for all samples fall squarely within the prime zone or younger on the boxplots. My data show a shift from hunting prime animals to young adults. The Upper Paleolithic people and the inhabitants of Gabasa were hunting an abundance of either juvenile or young adult animals. My results confirm previous research showing that Neandertals were capable hunters of adult ungulates.

My results can be compared to Pike-Tay's (1991) study of hunting during the Upper Paleolithic. Her early Upper Paleolithic samples had "catastrophic" mortality

profiles, while her more recent samples contained more young individuals. The early Upper Paleolithic assemblages can be compared to Neandertal accumulated samples, because both groups lacked projectile technology. Both Pike-Tay's (1991) early Upper Paleolithic hunters and my Mousterian hunters were taking adult prey in similar proportions to their abundance on the landscape. Pike-Tay (1991:108) hypothesized for the early Upper Paleolithic that this would require organized, cooperative interception and detention; traps, pits or snares; or stalking and ambushing prey. Similar hunting strategies may be postulated for the Neandertals.

My more ancient samples indicated hunting, while Stiner's more ancient samples indicated scavenging. The difference is in the proportion of old prey represented in the samples, which may be due to our different methods for estimating age-at-death and constructing mortality profiles. Stiner (1990) investigated mortality profiles using  $dP_4$  and  $P_4$  to determine the percentages of juvenile, prime, and old in each sample. By visually assessing wear, she assigns all  $dP_4$ s as "juvenile," all  $P_4$ s with crown heights less than 50% worn as "prime," and all  $P_4$ s with crown heights more than 50% worn as "old." In my analyses, I defined my age classes for  $dP_4$  and  $P_4$  the same as Stiner did, but I measured  $P_4$  crown height to determine the percentage of wear. I also performed additional analyses with  $dP_4$  and  $M_1$  where I assigned the three ages classes based on the ten age-class values of the histogram method. I classified all of Age Class 1 as "juvenile," specimens in Age Classes 2-5 (less than 115.2 months or 9.6 years) as "prime," and those in Age Classes 6-10 as "old." Assigning age classes using  $P_4$ s instead of  $M_1$ s created more separation along the "old" axis, and some samples have even more old individuals than the wolf-kill sample (Figures 7.4 and 7.8). It appears that  $P_4$  and  $M_1$  assign different

ages to the same individuals. The known-age sample shows that P<sub>4</sub> becomes more than half worn between 10-12 years of age, while M<sub>1</sub>s are considered “old” at 9.6 years of age. This suggests that the modified QCHM may be slightly underestimating the ages of the animals, and this problem needs further research. Primarily, I conclude that Neandertals were regularly hunting prime individuals from the boxplots analyses, where I calculated the “prime” zone for the boxplots using the known-age sample. All of the medians for the more ancient samples clearly fall into this area indicating prime hunting. The discrepancy between these results needs to be further investigated.

All of the fossil mortality profiles are different from the attritional profile that resulted from wolf hunting. These results fully support previous studies in concluding that Neandertals were capable hunters and did not obtain the majority of their meat by scavenging. The sample that most closely resembles the wolf kills in some analyses is Lazaret E. This sample was deposited approximately 170 kya and is one of the earliest Mousterian assemblages; researchers have debated if the tools should actually be classified as Acheulean, the preceding industry (P. Valensi, personal communication). At first this may suggest that the ability to hunt adult animals occurred with the change from the Acheulean to Mousterian industry, but two even more ancient assemblages, Piegu and Tabun, were included in the final analysis, and they have younger animals. Although they are not significantly different from Lazaret, they are also not significantly different from many Upper Paleolithic samples. This older time period deserves more research.

Finally, there is no relationship between prey age-at-death and environment. Tool industry and time, which strongly covary, have the strongest relationship with the mortality distributions. Unfortunately, only coarse environmental variables were

available for this study, and more detailed data are needed for further investigation into this issue.

### **Summary and conclusions**

In summary, the age-at-death data show a clear relationship with time where more ancient samples contain more prime individuals while more recent samples have many young adults. This change does not occur with the Middle to Upper Paleolithic transition, as expected, but actually occurs within the Mousterian perhaps 50 kya, similar to previous research by Stiner (1990) in west-central Italy. These results are preliminary, however, because they are based on limited samples and the break is seen between two assemblages, Gabasa and the upper layers of Combe-Grenal, neither of which is securely dated. Once data from additional samples are collected, this hypothesis of a change in hunting during the Middle Paleolithic can be further tested.

There are two possible explanations for this shift in the red deer mortality profiles. First, there could have been a change in hunting strategy, which could have been the result of changes in social or spatial organization or in still undetected changes in tool technology. Second, increasing human population densities may have placed hunting pressure on local red deer populations. In either case, my results indicate that both modern humans and Neandertals were able to regularly take fit, adult animals and did not have to rely on the youngest, oldest, and infirm members of the red deer herd, although they hunted these individuals, too. These results confirm that the ability to regularly hunt prime adult animals is a human characteristic that distinguishes us from other carnivores, but they also show that Neandertals were clearly very similar to us in that they also could regularly hunt prime-aged prey.

## **Chapter 8: Summary and conclusions**

### **Significance of this research**

Fossil hominid morphology, archaeology, and genetics all indicate that the Neandertals were replaced by modern humans in Europe 30-40 kya. The early modern humans' stone tool industries were more refined than the Neandertals' Mousterian industry, and they also contained bone, antler, and ivory fashioned into tools. The aim of this research was to investigate if the changes in tool industries correlated with a difference in the ability to hunt large ungulates. A difference in resource extraction ability is one potential explanation for why modern humans were able to replace Neandertals, because it could have enabled modern humans to have larger population sizes or densities. I investigated this problem by focusing on the hunting of only one species, red deer, so that I could better control for prey behavior. I used prey age-at-death as my indicator of hunting strategies, because humans are unique in their ability to regularly hunt prime adult individuals. In contrast, non-human carnivores usually take the young, old, and infirm from a population.

My results show that Neandertals and modern humans did not differ significantly in their ability to hunt prime-aged ungulates, and they both did so regularly. None of the mortality distributions of the assemblages studied here resemble the distribution constructed from wolf kills, suggesting that by at least 200 kya, hominids were hunting differently than a top carnivore. There is a trend in the Paleolithic data for more recent assemblages, those younger than 50 kya, to have more young adult animals, while the

more ancient sites, those older than 50 kya, have more prime red deer. This change happened during the Middle Paleolithic and not with the change from Middle to Upper Paleolithic as I would have expected. Stiner's (1990) study of assemblages spanning the Middle to Upper Paleolithic transition in west-central Italy also showed a shift in large game use within the Middle Paleolithic about 40-50 kya, but she attributed this to a shift from more scavenging to more hunting. These results should be taken cautiously and a shift in hunting during the Middle Paleolithic should be considered a hypothesis for future research, because only limited samples are available. In my samples, the assemblages from only one Middle Paleolithic site show a mortality distribution that is indistinguishable from the Upper Paleolithic samples, so this pattern needs to be confirmed with more data.

The technological difference that most clearly distinguishes modern humans from Neandertals is the working of bone, antler, and ivory into the formal tools and art objects found in Upper Paleolithic industries. These new tools may have allowed modern humans to more fully exploit new niches, including birds and aquatic resources. In addition, bone and ivory needles and awls that are part of this new industry provide the earliest evidence for tailored clothing, which may have played a role in allowing modern humans to live at latitudes far north from where Neandertals have ever been found (Hoffecker, 1999).

This study also investigated the methods used to estimate the age-at-death of fossil specimens and to construct mortality profiles from fossil assemblages. I conclude that boxplots showing median tooth crown heights are the best method for assessing age distributions. Boxplots are based on raw crown height measurements, so no detailed knowledge about the relationship between tooth crown height and age are needed. Only

two assumptions are necessary, and they are true of all wear-based age determination techniques. First, a more worn tooth indicates an older individual than a less worn tooth. Second, tooth wear rates are comparable between populations. Unfortunately, boxplots prevent detailed analyses of nuances in the age distribution such as is available with histograms, but enough differences in age structure can be identified for meaningful comparisons and interpretations. The boxplot method is more difficult to apply to species whose average tooth size changes through time and space, such as *C. elaphus*, but unworn crown height and average tooth breadth both appear to be adequate for standardization. Ideally, histograms would be used to investigate mortality distributions, but their widespread applicability is inhibited by the errors involved in translating tooth crown heights into chronological ages and idiosyncratic differences due to small sample sizes. I am confident that once more known-age samples are studied, the problem of estimating chronological age can be addressed, but small sample size will always be an issue when studying fossil assemblages.

Finally, I investigated the relationship between *C. elaphus* body size and climate. Modern North American elk size correlates with climatic parameters to support Bergmann's rule. This relationship is stronger in sex divided analyses of distal metacarpal breadths than it is in analyses of grouped male and female  $M_1$  breadths. This is likely because skeletal elements are more plastic than teeth and more closely reflect body mass and, therefore, will respond more readily to environmental changes. Western European red deer metatarsals and teeth do not exhibit relationships with the climatic parameters that would suggest that red deer follow Bergmann's rule. Analyses are confined by the fact that many of *C. elaphus* subspecies are extinct, which limits the

range of variation available for study. This is particularly evident in North America where the southern-most and eastern-most subspecies no longer exist. The problem is further complicated in both North America and western Europe by recent re-introductions of individuals from different subspecies into areas where local populations have gone extinct. Because skeletal size is so plastic and has been anecdotally noted to change within one generation of introduction into a new area, these recent re-introductions may not significantly affect patterning in distal metapodial breadth. The teeth are more conservative, so they will maintain the size of the parent population for a longer period of time, obscuring any relationship that tooth breadth may have once had with climate.

The Late Pleistocene red deer generally appear to follow Bergmann's rule. They are mostly larger during glacial cycles and smaller during the interglacial cycles. Until the relationship between body size and climate is understood using data on modern specimens, *C. elaphus* body size should not be used as a paleoclimatic indicator. Within a well-documented region, however, red deer body size is useful as a biostratigraphic indicator to place assemblages within a relative sequence or as supporting evidence for other paleoenvironmental indicators.

### **Future research directions**

The results of this study provide many indications of where future research should be focused, and it is clear that there is still much to be done to understand how and why modern humans replaced the Neandertals and ultimately the origins of fully modern humans.

First, red deer mortality profiles from archaeological assemblages from all time periods need to be more comprehensively studied. To further test some of the trends

found in this study, sampling needs focus on the late Middle Paleolithic and the Aurignacian. Early Upper Paleolithic assemblages need to be studied in detail whenever they are available. Epipaleolithic assemblages could be used to form an archaeological baseline of modern human subsistence strategies for comparisons with the more ancient assemblages. Studying more recent sites, as well as paleontological sites, will further our understanding of how pre- and post-depositional biases impact mortality profiles. Sampling should focus on areas where red deer were always abundant, such as Spain and Italy, so large samples can be obtained for all time periods. This will allow many variables to be controlled, and thus allow hunting strategies to be better investigated.

Second, the earliest Upper Paleolithic deserves more attention. In order to understand fully how and why modern humans replaced the Neandertals, studies need to directly compare the latest Mousterian with the earliest Upper Paleolithic. One criticism of the archaeological evidence for the Out of Africa model is that “modern” characters do not actually appear until later in the Upper Paleolithic, particularly with the Solutrean and Magdalenian (Lindly & Clark, 1990; Straus, 1977; Straus, 1992). This bias towards discussing later periods is because later Upper Paleolithic sites are more numerous in western Europe, as evidenced by a population explosion during the Magdalenian following the last glacial maximum (Bocquet-Appel & Demars, 2000b). However, early Upper Paleolithic sites in Eastern Europe do show characteristics of “modern” behavior very early. Much more detailed information on the early Aurignacian and its conspecifics is needed, not only in western Europe, but also in eastern Europe and western Asia. As the early Aurignacian becomes better known, it will be easier to make meaningful

comparisons with the late Mousterian. In addition, more data are needed on the Upper Paleolithic assemblages created by Neandertals, such as the Châtelperronian.

Third, studies similar to the current one need to be conducted on other prey species; reindeer, bison, aurochs, horse, and ibex would all be good subject species. The best way to choose the next species for detailed comparisons is to determine which species is most common in the earliest Upper Paleolithic assemblages. Because the Mousterian extends back further in time, it may be easier to find suitable samples for comparison in this more ancient period. Species of small animals should certainly be included in future comparisons of Middle and Upper Paleolithic resource gathering strategies. Current evidence indicates that the frequent exploitation of small game, particularly fish and birds, is characteristic of the Upper Paleolithic. This is particularly important because the exploitation of these species probably indicates more sophisticated tool technology involving bone and ivory working. Comparisons of tortoise and shellfish gathering across the Middle to Upper Paleolithic transition can also provide data on population densities and resource intensification. Studying these small animals will require the re-evaluation of many previously excavated assemblages and careful excavation of new assemblages. Fortunately, saving the remains of these small animals is now standard practice, and so much more data on small game exploitation should become available in the near future.

Fourth, more detailed climatic data than were available for this study are needed. Fortunately, many researchers are currently directly addressing this knowledge gap and data sets are accumulating which will help with future research (Davies *et al.*, 2000). These data will help illuminate hunting strategies and also will be beneficial for knowing

what areas were inhabitable at certain times, which then could be linked to the migration of modern humans into Europe. Around the time of the Middle to Upper Paleolithic transition in Europe, climate was rapidly fluctuating (van Andel, 1998; van Andel & Tzedakis, 1996). More research is needed on these paleoclimates before it is possible to know what role these periods of change and stability played in modern human origins and the replacement of the Neandertals.

Finally, all of these studies should be extended back in time to comparisons of the early to the late Middle Paleolithic. The idea of a shift in behavior during this time is intriguing. Knowing how Neandertals, our closest relatives, responded to changing resources, climate, and possibly population pressure will help us better understand our own adaptations. As for determining when people acquired the ability to regularly hunt large game animals, more research is needed on more ancient times. I think that comparisons between the Acheulean and the Middle Paleolithic will help illuminate this issue.

## **Conclusions**

This research shows that Neandertals were capable of regularly hunting prime-aged red deer. The ability to regularly hunt prime-aged large prey distinguishes modern humans from all other carnivores, and the data presented here demonstrate that hominids had entered this niche by the time of the Neandertals at least 200 kya. However, the samples included in this study show a shift in prey age-at-death during the Middle Paleolithic approximately 50 kya. Young adult prey are more abundant in recent assemblages than in more ancient assemblages. Over 25 archaeological samples from throughout western Europe contributed to this conclusion, making this the most

comprehensive study to date. Because Neandertals and modern humans were both capable of hunting the most desirable prey and could do so regularly, researchers must explore other reasons than differences in big game hunting to explain the demise of the Neandertals.

## **Appendix A Tables**

**Table 3.1 Interobserver measurement error for tooth crown height and breadth**

Comparison of measurements taken on the same specimens by the author and other researchers. R.G. Klein and the author measured the British Natural History Museum's *C. elaphus* comparative collection, and C. Wolf and the author measured the known-age elk sample. The samples are pooled samples of dP<sub>4</sub>, P<sub>4</sub>, M<sub>1</sub>, M<sub>2</sub> and M<sub>3</sub>. All values are in millimeters.

| measurement  | n   | mean        | standard deviation | minimum | maximum |
|--------------|-----|-------------|--------------------|---------|---------|
| crown height | 110 | 0.24 (2.9%) | 0.35 (4.4%)        | 0       | 2.8     |
| breadth      | 81  | 0.29 (2.5%) | 0.29 (3.1%)        | 0.01    | 1.4     |

**Table 3.2. Eruption and wear stages recorded in this study**

E1 through E4 describe stages of tooth eruption, and the others describe wear. Erupting teeth were not included in any of the analyses discussed here. In complete mandibles, teeth come into occlusion before the crown-root junction is visible, so their full crown heights remain unmeasurable at young ages. Unworn crown heights can only be recorded in *C. elaphus* on isolated teeth, by taking X-rays of the mandible, or by cutting the bone away from the crown-root junction of the tooth.

| wear stage code | description of wear stage   |
|-----------------|---|
| E1              | tooth still in crypt  |
| E2              | tooth unworn and less than halfway to occlusion   |
| E3              | tooth unworn and over halfway to occlusion  |
| E4              | tooth in occlusion, but crown-root junction is not visible, therefore crown height is not measurable  |
| UW              | unworn tooth (not yet in occlusion). The crown-root junction is visible and full crown height is measurable   |
| VEW             | very early wear. There is some wear on the anterior or posterior edge of the cusp, but the crown height can still be used as an unworn crown height |
| LW              | light wear. Cusps are still high peaks and dentine bands are narrow   |
| MW              | medium wear. Occlusal surface of the cusps are rounded to completely flat. The crown is approximately 30-50% worn. Dentine bands are wide           |
| HW              | heavy wear. Occlusal surface is flat and the crown is more than 50% worn. Some infundibulum remains   |
| VHW             | very heavy wear. Infundibulums are absent. Enamel of the crown nearly or completely worn away   |

**Table 4.1 Summary of elk specimens with known ages**

The number of known-age elk specimens in the original Klein *et al.* studies (1981, 1983a, 1983b; data collected by C. Wolf) plus the number of new specimens added in this study provides the total individuals in the known-age sample. The number of crown heights that were measured in each age cohort is provided.

| age cohorts<br>years (months) | original   | new       | total      | males     | females    | dP <sub>4</sub> | P <sub>4</sub> | M <sub>1</sub> | M <sub>2</sub> | M <sub>3</sub> |
|-------------------------------|------------|-----------|------------|-----------|------------|-----------------|----------------|----------------|----------------|----------------|
| 0.5 (5-10)                    | 41         | 1         | 42         | 27        | 15         | 42              |                |                |                |                |
| 1.5 (17-20)                   | 39         | 2         | 41         | 19        | 20         | 41              |                | 21             | 2              |                |
| 2.5 (27-33)                   | 25         | 11        | 36         | 15        | 15         | 3               | 3              | 36             | 1              |                |
| 3.5 (40-44)                   | 24         | 9         | 33         | 7         | 23         |                 | 22             | 33             | 5              |                |
| 4.5 (53-57)                   | 14         | 11        | 25         | 6         | 17         |                 | 11             | 25             | 10             | 2              |
| 5.5 (65-68)                   | 10         | 5         | 15         | 4         | 9          |                 | 15             | 15             | 13             | 4              |
| 6.5 (77-79)                   |            | 6         | 6          |           | 5          |                 | 6              | 6              | 3              | 3              |
| 7.5 (89-92)                   | 1          | 7         | 8          |           | 7          |                 | 8              | 8              | 7              | 4              |
| 8.5 (101-104)                 | 9          | 1         | 10         |           | 8          |                 | 9              | 10             | 10             | 9              |
| 9.5 (113-114)                 | 3          |           | 3          |           | 3          |                 | 3              | 3              | 3              | 3              |
| 10.5                          |            |           |            |           |            |                 |                |                |                |                |
| 11.5 (138)                    | 1          |           | 1          |           | 1          |                 | 1              | 1              | 1              | 1              |
| 12.5 (150-156)                |            | 2         | 2          |           | 2          |                 | 2              | 2              | 2              | 2              |
| 13.5                          |            |           |            |           |            |                 |                |                |                |                |
| 14.5 (173)                    |            | 1         | 1          |           | 1          |                 | 1              | 1              | 1              | 1              |
| 15.5 (185)                    | 2          |           | 2          | 1         | 1          |                 | 2              | 2              | 2              | 2              |
| 16.5                          |            |           |            |           |            |                 |                |                |                |                |
| 17.5                          |            |           |            |           |            |                 |                |                |                |                |
| 18.5                          |            |           |            |           |            |                 |                |                |                |                |
| 19.5                          |            |           |            |           |            |                 |                |                |                |                |
| 20.5                          |            |           |            |           |            |                 |                |                |                |                |
| 21.5 (260) *                  | 1          |           | 1          |           | 1          |                 | 1              | 1              | 1              | 1              |
| <b>total</b>                  | <b>170</b> | <b>56</b> | <b>226</b> | <b>79</b> | <b>128</b> | <b>86</b>       | <b>84</b>      | <b>163</b>     | <b>61</b>      | <b>32</b>      |

\* Excluded from all analyses

**Table 4.2 Summary of regressions of age on crown height in the known-age elk sample**

The sample sizes, mean age and crown height, standard deviations of age and crown height, coefficients of determination, and standard errors of estimate associated with the linear and quadratic regressions of age on crown height for the known-age sample of elk.

| <i>sample information</i>               | $dP_4$ | $P_4$ | $M_1$ | $M_2$ | $M_3$ |
|---|--------|-------|-------|-------|-------|
| sample size (n)                         | 86     | 83    | 163   | 60    | 31    |
| mean age (months)                       | 13.4   | 72.5  | 53.5  | 81.4  | 103.6 |
| standard deviation of age (months)      | 6.4    | 34.7  | 33.1  | 36.8  | 35.5  |
| mean crown height (mm)                  | 8.2    | 17.0  | 12.9  | 15.5  | 15.23 |
| standard deviation of crown height (mm) | 2.6    | 3.8   | 4.3   | 5.0   | 4.6   |
| <i>linear regression</i>                |        |       |       |       |       |
| coefficient of determination ( $r^2$ )  | 0.83   | 0.85  | 0.84  | 0.87  | 0.84  |
| standard error of estimate (months)     | 2.62   | 13.28 | 13.26 | 13.21 | 13.81 |
| <i>quadratic regression</i>             |        |       |       |       |       |
| coefficient of determination ( $r^2$ )  | 0.83   | 0.87  | 0.87  | 0.90  | 0.85  |
| standard error of estimate (months)     | 2.61   | 12.44 | 12.09 | 11.35 | 13.69 |

**Table 4.3 Summary of regressions of age on crown height in the known-age white-tailed deer sample**

The sample sizes, mean age and crown height, standard deviations of age and crown height, coefficients of determination, and standard errors of estimate associated with the linear and quadratic regressions of age on crown height for the known-age sample of white-tailed deer.

| <i>sample information</i>               | $dP_4$ | $M_1$ | $M_2$ | $M_3$ |
|---|--------|-------|-------|-------|
| sample size (n)                         | 55     | 109   | 91    | 42    |
| mean age (months)                       | 11.5   | 22.1  | 24.76 | 30.4  |
| standard deviation of age (months)      | 6.0    | 16.4  | 16.6  | 21.2  |
| mean crown height (mm)                  | 4.4    | 8.5   | 10.6  | 11.0  |
| standard deviation of crown height (mm) | 1.4    | 1.6   | 1.6   | 2.1   |
| <i>linear regression</i>                |        |       |       |       |
| coefficient of determination ( $r^2$ )  | 0.79   | 0.60  | 0.70  | 0.84  |
| standard error of estimate (months)     | 2.69   | 10.33 | 9.01  | 8.30  |
| <i>quadratic regression</i>             |        |       |       |       |
| coefficient of determination ( $r^2$ )  | 0.80   | 0.72  | 0.82  | 0.88  |
| standard error of estimate (months)     | 2.67   | 8.59  | 6.93  | 7.13  |

**Table 4.4 Values used in the Quadratic Crown Height Method**

The shedding and eruption ages and the unworn crown heights used in the QCHM for estimating age-at-death in Rocky Mountain elk from western Montana. Ages of eruption and shedding for each tooth are consistent across populations of *C. elaphus*, but unworn crown heights need to be determined for each sample. Values are from Klein *et al.* (1983:53) and Klein and Cruz-Urbe (1984:49-50) and are based on Quimby and Gaab (1957) and Lowe (1967). See also Brown and Chapman (1991:525).

| AGEpel (potential ecological longevity) = 192 months (16 years) |                   |                     |                                    |
|---|-------------------|---------------------|------------------------------------|
| tooth type  | age shed (months) | age erupts (months) | estimated unworn crown height (mm) |
| dP <sub>4</sub>   | 26                |                     | 14.0                               |
| P <sub>4</sub>  |                   | 26                  | 23.0*                              |
| M <sub>1</sub>  |                   | 6                   | 27.0                               |
| M <sub>2</sub>  |                   | 12                  | 29.6                               |
| M <sub>3</sub>  |                   | 30                  | 31.0                               |

\* From this study

**Table 4.5 Comparison of regression and theoretical equations**

Regression equations are based on the sample of known-age elk, and the theoretical equations were calculated for Rocky Mountain elk using the QCHM. Values used to derive the theoretical formulas are listed in Table 4.4.

| Regression equations                              | Theoretical equations                         |
|---|---|
| Age = 31.77 - 2.241 CH                            | dP <sub>4</sub>                               |
| Age = 33.925 - 2.826 CH + 0.036 CH <sup>2</sup>   | Age = 26 - 1.857 CH                           |
|   | Age = 26 - 3.714 CH + 0.133 CH <sup>2</sup>   |
|   | P <sub>4</sub>                                |
| Age = 214.301 - 8.360 CH                          | Age = 192 - 7.217 CH                          |
| Age = 269.018 - 16.028 CH + 0.249 CH <sup>2</sup> | Age = 192 - 14.435 CH + 0.314 CH <sup>2</sup> |
|   | M <sub>1</sub>                                |
| Age = 143.602 - 6.975 CH                          | Age = 192 - 6.889 CH                          |
| Age = 163.601 - 11.522 CH + 0.209 CH <sup>2</sup> | Age = 192 - 13.778 CH + 0.255 CH <sup>2</sup> |
|   | M <sub>2</sub>                                |
| Age = 186.819 - 6.810 CH                          | Age = 192 - 6.081 CH                          |
| Age = 218.53 - 11.595 CH + 0.160 CH <sup>2</sup>  | Age = 192 - 12.162 CH + 0.205 CH <sup>2</sup> |
|   | M <sub>3</sub>                                |
| Age = 211.286 - 7.069 CH                          | Age = 192 - 5.226 CH                          |
| Age = 224.182 - 9.159 CH + 0.075 CH <sup>2</sup>  | Age = 192 - 10.452 CH + 0.169 CH <sup>2</sup> |

**Table 5.1 Model life table**

A life table follows a cohort of individuals from birth to death and provides the numbers of individuals that survived until the next age class, died between age classes, and the rate of mortality. The table below shows "the age structure of a hypothetical population of large mammals in which females give birth once a year, total births are 500 per year, and potential individual longevity is 9 years " (Table reproduced from Klein, 1982:51).

| <i>age in years</i> | <i>number of live individuals</i> | <i>number of dead individuals</i> | <i>mortality rate</i> |
|---------------------|-----------------------------------|-----------------------------------|-----------------------|
| 0-1                 | 500                               | 250                               | 0.5                   |
| 1-2                 | 250                               | 25                                | 0.1                   |
| 2-3                 | 225                               | 22                                | 0.1                   |
| 3-4                 | 203                               | 20                                | 0.1                   |
| 4-5                 | 183                               | 37                                | 0.2                   |
| 5-6                 | 146                               | 44                                | 0.3                   |
| 6-7                 | 102                               | 41                                | 0.4                   |
| 7-8                 | 61                                | 37                                | 0.6                   |
| 8-9                 | 24                                | 24                                | 1                     |
| 9-10                | 0                                 | 0                                 |                       |

**Table 5.2 Data used to compare methods of reconstructing age distributions**

In the histogram analysis, 10% of life span age classes were assigned to each  $dP_4$  and  $M_1$  using the modified QCHM. For the boxplot analyses, “% juvenile” is the percentage of  $dP_4$ s in the combined  $dP_4/M_1$  sample. In the triangular graphs for  $dP_4/M_1$ , the three age classes were assigned based on the ten age classes of the histogram analysis so that age class 1 was juvenile, age classes 2-5 were prime and age classes 6-10 were old. For the  $dP_4/P_4$  triangular graph, all  $dP_4$ s were considered young,  $P_4$ s less than half worn were prime, and  $P_4$ s over half worn were old. The model living and attritional data are based on Klein (1982). ca = cementum annuli.

| histograms<br>age class  | living |           | attritional |           | human kills |        | wolf kills |            |
|--------------------------|--------|-----------|-------------|-----------|-------------|--------|------------|------------|
|                          | model  | known age | model       | known age | $dP_4/M_1$  | ca age | $dP_4/M_1$ | $dP_4/P_4$ |
| 1                        | 500    | 72        | 250         | 86        | 43          | 45     | 43         |            |
| 2                        | 250    | 47        | 25          | 57        | 4           | 3      | 4          |            |
| 3                        | 225    | 58        | 22          | 51        | 4           | 3      | 4          |            |
| 4                        | 203    | 15        | 20          | 23        | 7           | 2      | 7          |            |
| 5                        | 183    | 14        | 37          | 10        | 6           | 15     | 6          |            |
| 6                        | 146    | 13        | 44          | 9         | 5           | 2      | 5          |            |
| 7                        | 102    | 0         | 41          | 3         | 6           | 1      | 6          |            |
| 8                        | 61     | 2         | 37          | 0         | 2           | 2      | 2          |            |
| 9                        | 24     | 1         | 24          | 5         | 19          | 6      | 19         |            |
| 10                       | 0      | 4         | 0           | 0         | 0           | 17     | 0          |            |
| total                    | 1694   | 226       | 500         | 244       | 96          | 96     | 96         |            |
| <i>boxplots</i>          |        |           |             |           |             |        |            |            |
| n $dP_4$                 | 500    |           | 250         | 86        | 45          |        | 45         |            |
| % juvenile               | 29.5%  |           | 50.0%       | 35.2%     | 46.9%       |        | 46.9%      |            |
| n $M_1$                  | 1194   |           | 250         | 163       | 53          |        | 53         |            |
| % adult                  | 70.5%  |           | 50.0%       | 64.8%     | 53.1%       |        | 53.1%      |            |
| median $M_1$ CH          | N/A    |           | N/A         | 13.66     | 4.0         |        | 4.0        |            |
| total                    | 1694   |           | 500         | 249       | 98          |        | 98         |            |
| <i>triangular graphs</i> |        |           |             |           |             |        |            |            |
| n young                  | 50     | 72        | 85          | 86        | 43          | 45     | 45         |            |
| % young                  | 29.5%  | 31.9%     | 50.0%       | 35.2%     | 44.8%       | 46.9%  | 45.9%      |            |
| n prime                  | 86     | 134       | 35          | 141       | 21          | 23     | 24         |            |
| % prime                  | 50.8%  | 59.3%     | 20.8%       | 57.8%     | 21.9%       | 24.0%  | 24.5%      |            |
| n old                    | 33     | 20        | 50          | 17        | 32          | 28     | 29         |            |
| % old                    | 19.7%  | 8.8%      | 29.2%       | 7.0%      | 33.3%       | 29.2%  | 29.6%      |            |
| total                    | 170    | 226       | 170         | 244       | 96          | 96     | 98         |            |

**Table 5.3 Data used to describe the modified triangular graph**

The hypothetical samples have the same sample size, but different numbers of juvenile, prime, and old individuals so that each sample plots in a different part of the triangular graph. The sample size samples have the same percentages of juvenile, prime, and old individuals, but different sample sizes. These samples show how the density contours around the data points in the modified triangular graph reflect sample size. Percentages are shown in parentheses.

| <i>sample</i>     | <i>n</i> | <i>juvenile</i> | <i>prime</i> | <i>old</i> |
|-------------------|----------|-----------------|--------------|------------|
| Hypothetical 1    | 35       | 12 (34.3)       | 17 (48.6)    | 6 (17.1)   |
| Hypothetical 2    | 35       | 19 (54.3)       | 11 (31.4)    | 5 (14.3)   |
| Hypothetical 3    | 35       | 5 (14.3)        | 16 (45.7)    | 14 (40.0)  |
| Sample size = 100 | 100      | 33 (33.0)       | 50 (50.0)    | 17 (17.0)  |
| Sample size = 40  | 40       | 13 (32.5)       | 20 (50.0)    | 7 (17.5)   |
| Sample size = 12  | 12       | 4 (33.3)        | 6 (50.0)     | 2 (16.7)   |

**Table 5.4 Properties of the four methods for summarizing mortality profiles discussed in this study**

|  | Histograms   | Boxplots   | Triangular graphs   | Modified triangular graphs  |
|--|--|--|---|---|
| Number of age classes                    | Often 10, but can be any amount  | Juveniles separated out, otherwise not divided   | 3   | 3   |
| Minimum sample size                      | 30-40  | Theoretically = none<br>Biologically = ?   | 12 suggested  | Theoretically = none<br>Biologically = ?  |
| Best individual age determination method | Any well established method <sup>a</sup>   | Raw crown heights <sup>b</sup><br>Therefore, no error introduced by age estimation technique   | Either crown heights or eruption/wear <sup>d</sup>  | Either crown heights or eruption/wear <sup>d</sup>  |
| Statistics possible?                     | Yes. Kolmogorov-Smirnov  | Yes. Confidence intervals around medians   | No  | Yes. Confidence intervals based on bootstrapping  |
| What is being compared                   | Cumulative distributions   | Confidence intervals around medians <sup>c</sup>   | Percentages of each age class   | Confidence intervals based on sample size   |
| Deciduous teeth included?                | Yes  | No. Must be given as a separate boxplot or percentage of the assemblage  | Yes   | Yes   |
| Unworn crown heights needed?             | Yes  | No, although necessary for standardization   | No  | No  |
| Ease of comparing many samples           | Harder   | Medium, but difficult to interpret in isolation.   | Easiest (but cannot tell statistical differences)   | Easy  |
| Ease of comparing between species        | Medium. Must use 10% of life span age classes to do so   | Harder. Possibly can be done with indices  | Easy  | Easy  |
| Misc.                                    | <sup>a</sup> Species needs to be well studied<br>Cannot account for error around age estimates | <sup>b</sup> Therefore, can be used with unstudied species.<br><sup>c</sup> Similar medians can result from differently shaped distributions | <sup>d</sup> Need clear division between prime and old<br>Cannot account for error around age estimates | <sup>d</sup> Need clear division between prime and old<br>Cannot account for error around age estimates |

**Table 6.1 Modern specimens used in the study of size variation in *C. elaphus***

| subspecies<br>common name    | atlanticus<br>Norwegian<br>red deer<br>Norway | hippelaphus<br>European<br>red deer<br>France & Germany | hispanicus<br>Spanish<br>red deer<br>Spain | nannodes<br>Tule elk<br>CA | nelsoni<br>Rocky Mountain elk<br>WY & MT | roosevelti<br>Roosevelt<br>elk<br>WA | scoticus<br>Scottish<br>red deer<br>British Isles | total  |
|------------------------------|---|---|--|----------------------------|--|--------------------------------------|---|--------|
| male body mass (kg)          |   | 130 <sup>a</sup>  |  | 251 <sup>b</sup>           | 331 <sup>c</sup>                         | 478 <sup>c</sup>                     | 93.5 <sup>d</sup>                                 |        |
| <i>M<sub>1</sub></i> breadth |   |   |  |                            |  |                                      |   |        |
| sample size                  | 7   | 33  | 32   | 24                         | 95                                       | 12                                   | 18  | 221    |
| mean (mm)                    | 11.97   | 12.25   | 11.93                                      | 15.08                      | 15.48                                    | 15.69                                | 11.48   | 14.01  |
| standard deviation (mm)      | 0.18  | 0.72  | 0.59                                       | 0.51                       | 0.61                                     | 0.43                                 | 1.05  | 1.83   |
| coefficient of variation     | 1.50  | 5.88  | 4.95                                       | 3.38                       | 3.94                                     | 2.74                                 | 9.15  | 13.06  |
| Male/Female <sup>e</sup>     | 3/2   | 3/2   | 12/8                                       | 10/13                      | 38/57                                    | 4/7                                  | 5/10  | 74/100 |
| <i>M<sub>2</sub></i> length  |   |   |  |                            |  |                                      |   |        |
| sample size                  | 7   | 20  | 28   | 17                         | 52                                       | 8                                    | 17  | 149    |
| mean (mm)                    | 17.60   | 18.40   | 17.90                                      | 23.43                      | 21.87                                    | 22.72                                | 17.36   | 20.17  |
| standard deviation (mm)      | 0.70  | 1.18  | 1.29                                       | 1.81                       | 1.49                                     | 1.26                                 | 1.13  | 2.65   |
| coefficient of variation     | 3.98  | 6.41  | 7.21                                       | 7.73                       | 6.81                                     | 5.55                                 | 6.51  | 13.14  |
| Male/Female <sup>e</sup>     | 3/2   | 1/2   | 10/7                                       | 8/8                        | 20/32                                    | 3/4                                  | 5/10  | 50/65  |
| metacarpal breadth           |   |   |  |                            |  |                                      |   |        |
| sample size                  |   | 14  | 27   | 35                         | 18                                       | 3                                    | 3   | 100    |
| mean (mm)                    |   | 39.56   | 35.77                                      | 49.68                      | 53.48                                    | 52.86                                | 36.36   | 44.88  |
| standard deviation (mm)      |   | 4.31  | 2.79                                       | 2.78                       | 3.20                                     | 2.77                                 | 2.26  | 7.84   |
| coefficient of variation     |   | 10.89   | 7.80                                       | 5.60                       | 5.98                                     | 5.24                                 | 6.22  | 17.47  |
| Male/Female <sup>e</sup>     |   | 3/4   | 0/4  | 22/12                      | 9/4                                      | 2/1                                  | 1/0   | 37/25  |
| metatarsal breadth           |   |   |  |                            |  |                                      |   |        |
| sample size                  |   | 17  | 19   | 35                         | 75                                       | 2                                    | 6   | 154    |
| mean (mm)                    |   | 38.63   | 37.43                                      | 50.38                      | 52.40                                    | 56.43                                | 37.60   | 48.05  |
| standard deviation (mm)      |   | 2.20  | 2.95                                       | 2.41                       | 3.12                                     | 0.51                                 | 1.51  | 6.87   |
| coefficient of variation     |   | 5.70  | 7.88                                       | 4.78                       | 5.95                                     | 0.90                                 | 4.02  | 14.30  |
| Male/Female <sup>e</sup>     |   | 4/5   | 1/3  | 21/12                      | 30/24                                    | 2/0                                  | 2/0   | 60/44  |
| total                        |   |   |  |                            |  |                                      |   | 625    |

<sup>a</sup> Waechter (1976 as in Silva and Downing, 1995:23)

<sup>b</sup> McCullough (1969 as in Bryant and Maser, 1982:26)

<sup>c</sup> Troyer (1960 as in Bryant and Maser, 1982:26)

<sup>d</sup> As cited in Clutton-Brock and Albon (1983:197)

<sup>e</sup> Male/Female totals and sample sizes are not always equal because many specimens were labeled "sex unknown"

**Table 6.2 Climatic data for the locations of the modern comparative specimens used to investigate the relationship between *C. elaphus* size and climate**

Environmental data are from Willmott and Matsuura (2001). Mean precipitation (ppt) and temperature (temp) are annual means.

| locality                                   | longitude | latitude | mean ppt mm | mean temp °C | Jan temp °C | July temp °C | July-Jan temp °C |
|--|-----------|----------|-------------|--------------|-------------|--------------|------------------|
| <i>C. e. atlanticus</i>                    |           |          |             |              |             |              |                  |
| Batnfjord, Norway                          | 8.00      | 63.0     | 1365.6      | 2.1          | -4.3        | 9.7          | 14.0             |
| Hitteren (Hitra Island), Norway            | 9.00      | 63.5     | 1343.2      | 3.1          | -3.5        | 11.2         | 14.7             |
| Surendal (Surnadal), Nordmore, Norway      | 9.00      | 63.0     | 1343.2      | 3.1          | -3.5        | 11.2         | 14.7             |
| <i>C. e. hippelaphus</i>                   |           |          |             |              |             |              |                  |
| Bebenhausen, Germany                       | 9.05      | 48.6     | 691.0       | 9.3          | 0.1         | 18.5         | 18.4             |
| Catineau Frontier, France                  | 2.50      | 46.5     | 734.7       | 10.9         | 2.9         | 19.4         | 16.5             |
| Dominquin, France                          | 2.50      | 46.5     | 734.7       | 10.9         | 2.9         | 19.4         | 16.5             |
| Eningen, Germany                           | 9.50      | 48.5     | 840.5       | 7.8          | -1.0        | 17.2         | 18.2             |
| Hungary                                    | 19.00     | 47.0     | 563.0       | 10.8         | -0.9        | 21.9         | 22.8             |
| Ilselfeld, Germany                         | 9.25      | 49.3     | 736.7       | 9.5          | 0.8         | 18.8         | 18.0             |
| Monrepos, Germany                          | 7.45      | 50.4     | 692.8       | 8.2          | 0.3         | 16.7         | 16.4             |
| Schonbuch, Germany                         | 9.00      | 48.0     | 772.0       | 6.6          | -2.0        | 15.7         | 17.7             |
| Sigismond de Clermont, La Tenaille, France | -0.50     | 45.5     | 797.8       | 12.6         | 5.7         | 20.1         | 14.4             |
| Tubingen, Germany                          | 9.03      | 48.5     | 691.0       | 9.3          | 0.1         | 18.5         | 18.4             |
| <i>C. e. hispanicus</i>                    |           |          |             |              |             |              |                  |
| Andujar, Spain                             | -4.00     | 38.0     | 485.6       | 15.3         | 6.6         | 25.6         | 19.0             |
| Cazorla, Spain                             | -3.00     | 37.7     | 403.5       | 16.5         | 8.0         | 26.5         | 18.5             |
| Cordoba, Spain                             | -4.08     | 37.1     | 476.4       | 17.6         | 10.0        | 26.4         | 16.4             |
| Cuenca, Spain                              | -2.00     | 40.0     | 629.9       | 10.9         | 2.8         | 20.9         | 18.1             |
| Donana Nat'l Park, Spain                   | -6.50     | 37.0     | 533.8       | 17.6         | 11.5        | 24.1         | 12.6             |
| Huesca, Spain                              | -0.42     | 42.0     | 652.5       | 9.8          | 1.5         | 19.1         | 17.6             |
| Isla Cristina, Spain                       | -7.30     | 37.3     | 443.5       | 17.3         | 11.3        | 23.6         | 12.3             |
| Jaca, Spain                                | -0.55     | 42.1     | 639.7       | 12.6         | 4.5         | 21.8         | 17.3             |
| Quinto, Spain                              | -0.48     | 41.1     | 417.6       | 15.2         | 6.8         | 24.4         | 17.6             |
| Southern Spain                             | -4.00     | 38.0     | 485.6       | 15.3         | 6.6         | 25.6         | 19.0             |
| <i>C. e. nannodes</i>                      |           |          |             |              |             |              |                  |
| Big Pine, Inyo Co., CA                     | -118.30   | 37.2     | 180.4       | 12.5         | 2.9         | 23.5         | 20.6             |
| Buttontwillow, Kern Co., CA                | -119.50   | 35.4     | 179.3       | 13.3         | 3.9         | 23.3         | 19.4             |
| Mitchell Flat, Colusa Co., CA              | -122.50   | 39.0     | 899.1       | 11.1         | 3.1         | 20.1         | 17.0             |
| Mono Co., CA                               | -118.87   | 37.9     | 427.3       | 9.3          | 0.9         | 19.8         | 18.9             |
| Monterey Co., CA                           | -121.31   | 36.2     | 389.4       | 13.8         | 8.1         | 18.9         | 10.8             |
| Near Tinamaha Reservoir, Inyo Co., CA      | -118.00   | 37.0     | 180.4       | 12.5         | 2.9         | 23.5         | 20.6             |
| Owens Valley, Inyo Co., CA                 | -118.00   | 36.5     | 163.8       | 15.0         | 4.8         | 26.4         | 21.6             |
| Solano Co., CA                             | -122.00   | 38.0     | 658.9       | 14.4         | 8.2         | 19.5         | 11.3             |

**Table 6.2 con't**

| locality                               | longitude | latitude | mean ppt mm | mean temp °C | Jan temp °C | July temp °C | July-Jan temp °C |
|--|-----------|----------|-------------|--------------|-------------|--------------|------------------|
| <i>C. e. neelsoni</i>                  |           |          |             |              |             |              |                  |
| Bozeman, MT                            | -111.00   | 45.7     | 367.0       | 6.1          | -6.3        | 19.0         | 25.3             |
| Estes Park, Larimer Co., CO            | -105.50   | 40.4     | 367.6       | -2.0         | -12.4       | 9.3          | 21.7             |
| Gardiner, Park Co., MT                 | -110.00   | 45.0     | 212.5       | 2.3          | -9.0        | 14.2         | 23.2             |
| Idaho/Wyom                             | -111.00   | 43.0     | 486.1       | 3.5          | -8.8        | 16.2         | 25.0             |
| Jackson, WY                            | -111.00   | 43.5     | 447.8       | 4.3          | -8.3        | 17.1         | 25.4             |
| Missoula Co., MT                       | -114.00   | 46.5     | 353.9       | 5.0          | -5.7        | 16.1         | 21.8             |
| Rio Blanco Co., CO                     | -108.00   | 40.0     | 351.1       | 7.4          | -5.5        | 20.5         | 26.0             |
| Sanders Co., MT                        | -115.00   | 47.5     | 686.2       | 1.5          | -9.5        | 13.1         | 22.6             |
| Yellowstone Natl Park, WY              | -110.50   | 44.5     | 491.1       | 0.6          | -10.7       | 12.5         | 23.2             |
| <i>C. e. roosevelti</i>                |           |          |             |              |             |              |                  |
| Gray's Harbor Co., WA                  | -123.50   | 47.5     | 2689.2      | 1.8          | -4.4        | 8.4          | 12.8             |
| Hoh River, Jefferson Co., WA           | -124.00   | 48.0     | 2240.6      | 8.4          | 3.6         | 13.2         | 9.6              |
| Humbolt Co., CA                        | -124.00   | 41.0     | 1819.5      | 11.5         | 6.9         | 16.3         | 9.4              |
| Orrick, Humbolt Co., CA                | -124.00   | 41.3     | 1819.2      | 8.0          | 4.0         | 12.3         | 8.3              |
| Quatsino, Vancouver Island, B. C.      | -128.00   | 50.5     | 2440.5      | 8.7          | 4.0         | 13.9         | 9.9              |
| <i>C. e. scoticus</i>                  |           |          |             |              |             |              |                  |
| Balmacaan, Inverness, Scotland         | -4.25     | 57.5     | 882.4       | 4.9          | -0.3        | 10.8         | 11.1             |
| Balmoral, Aberdeenshire, Scotland      | -3.00     | 57.0     | 820.8       | 5.8          | 0.3         | 12.1         | 11.8             |
| Exmoor, Devon, England                 | -3.83     | 51.0     | 1142.0      | 9.9          | 5.0         | 15.8         | 10.8             |
| Ft. William, Scotland                  | -5.12     | 56.8     | 2041.6      | 9.0          | 3.8         | 14.1         | 10.3             |
| Glen Quoich, Inverness-shire, Scotland | -5.25     | 57.0     | 1720.2      | 4.9          | 0.1         | 10.4         | 10.3             |
| Rhum, Scotland                         | -6.30     | 57.0     | 1703.9      | 7.9          | 3.7         | 12.3         | 8.6              |
| Theford, Horfolk, England              | 0.75      | 52.4     | 591.2       | 9.8          | 3.5         | 16.7         | 13.2             |

**Table 6.3 The relationship between M<sub>1</sub> tooth breadth and climate**

The correlation coefficients, coefficients of determination, and the significance of the lines for the regression of M<sub>1</sub> breadths on climatic variables. Relationships that are significant at the 0.1 or below level are in italics, and those significant at the 0.05 or below level are in bold italics. Sexes are not separated.

|  | <i>latitude</i> | <i>mean annual ppt</i> | <i>mean annual temp</i> | <i>Jan temp</i> | <i>July temp</i> | <i>July-Jan temp</i> |
|--|-----------------|------------------------|-------------------------|-----------------|------------------|----------------------|
| <i>combined sample</i>                         |                 |                        |                         |                 |                  |                      |
| correlation coefficient (r)                    | -0.37           | -0.20                  | -0.45                   | -0.60           | -0.17            | 0.60                 |
| <i>linear regression</i>                       |                 |                        |                         |                 |                  |                      |
| coefficient of determination (r <sup>2</sup> ) | <b>0.14</b>     | <b>0.04</b>            | <b>0.20</b>             | <b>0.35</b>     | <b>0.03</b>      | <b>0.36</b>          |
| probability > F (p-value)                      | <0.0001         | 0.0034                 | <0.0001                 | <0.0001         | 0.0104           | <0.0001              |
| <i>quadratic regression</i>                    |                 |                        |                         |                 |                  |                      |
| coefficient of determination (r <sup>2</sup> ) | <b>0.19</b>     | <b>0.29</b>            | <b>0.20</b>             | <b>0.37</b>     | <b>0.08</b>      | <b>0.51</b>          |
| probability > F (p-value)                      | <0.0001         | <0.0001                | <0.0001                 | <0.0001         | 0.0001           | <0.0001              |
| <i>North America</i>                           |                 |                        |                         |                 |                  |                      |
| correlation coefficient (r)                    | 0.27            | 0.20                   | -0.21                   | -0.16           | -0.25            | -0.03                |
| <i>linear regression</i>                       |                 |                        |                         |                 |                  |                      |
| coefficient of determination (r <sup>2</sup> ) | <b>0.07</b>     | <b>0.04</b>            | <b>0.05</b>             | 0.03            | <b>0.06</b>      | 0.001                |
| probability > F (p-value)                      | 0.0021          | 0.0253                 | 0.0137                  | 0.0672          | 0.0034           | 0.725                |
| <i>quadratic regression</i>                    |                 |                        |                         |                 |                  |                      |
| coefficient of determination (r <sup>2</sup> ) | <b>0.07</b>     | 0.04                   | <b>0.06</b>             | 0.026           | <b>0.08</b>      | 0.03                 |
| probability > F (p-value)                      | 0.0083          | 0.0632                 | 0.0219                  | 0.1831          | 0.0048           | 0.1393               |
| <i>Western Europe</i>                          |                 |                        |                         |                 |                  |                      |
| correlation coefficient (r)                    | -0.09           | -0.19                  | 0.05                    | -0.07           | 0.12             | 0.31                 |
| <i>linear regression</i>                       |                 |                        |                         |                 |                  |                      |
| coefficient of determination (r <sup>2</sup> ) | 0.008           | 0.04                   | 0.002                   | 0.004           | 0.01             | <b>0.01</b>          |
| probability > F (p-value)                      | 0.4063          | 0.0737                 | 0.6552                  | 0.5435          | 0.2606           | 0.0035               |
| <i>quadratic regression</i>                    |                 |                        |                         |                 |                  |                      |
| coefficient of determination (r <sup>2</sup> ) | 0.04            | 0.06                   | 0.05                    | 0.01            | <b>0.08</b>      | <b>0.10</b>          |
| probability > F (p-value)                      | 0.1907          | 0.0668                 | 0.1146                  | 0.6174          | 0.0234           | 0.0137               |

**Table 6.4 Data on Late Pleistocene red deer M<sub>1</sub> breadths for studying size variation**

Analysis includes all samples with five or more measurable M<sub>1</sub> breadths. "Red deer" is the proportion red deer represented in the ungulate fauna by NISP, and "OIS" is the Oxygen Isotope Stage. Full descriptions of the samples can be found in Appendix D, and sites are labeled on the map in Figure 3. 1.

| sample          | n  | mean  | standard deviation | coefficient of variation | red deer | OIS |
|-----------------|----|-------|--------------------|--------------------------|----------|-----|
| Altamira (Mag.) | 9  | 13.30 | 0.85               | 6.41                     | 0.95     | 2   |
| Biache          | 7  | 13.35 | 0.88               | 6.62                     |          | 7   |
| Castillo (Mag.) | 60 | 13.27 | 0.64               | 4.86                     | 0.40     | 2   |
| Chaves 1        | 7  | 12.51 | 0.37               | 2.96                     |          | 1   |
| Combe-Grenal 25 | 10 | 14.38 | 0.72               | 5.00                     | 0.23     | 4   |
| Combe-Grenal 27 | 6  | 14.12 | 0.51               | 3.59                     | 0.31     | 4   |
| Combe-Grenal 28 | 7  | 13.58 | 1.31               | 9.62                     | 0.31     | 4   |
| Combe-Grenal 29 | 5  | 14.32 | 0.50               | 3.52                     | 0.34     | 4   |
| Combe-Grenal 33 | 5  | 13.05 | 0.57               | 4.34                     | 0.20     | 4   |
| Combe-Grenal 35 | 15 | 13.41 | 0.58               | 4.29                     | 0.50     | 4   |
| Combe-Grenal 50 | 33 | 12.51 | 0.60               | 4.83                     | 0.83     | 5   |
| Combe-Grenal 52 | 22 | 12.57 | 0.48               | 3.85                     | 0.77     | 5   |
| Combe-Grenal 54 | 11 | 12.78 | 0.79               | 6.17                     | 0.74     | 5   |
| El Juyo 4       | 32 | 13.01 | 0.69               | 5.33                     | 0.91     | 2   |
| El Juyo 6       | 95 | 13.22 | 0.72               | 5.44                     | 0.93     | 2   |
| El Juyo 8       | 23 | 13.21 | 0.76               | 5.72                     | 0.90     | 2   |
| Federmesser     | 13 | 13.92 | 0.64               | 4.59                     |          | 1   |
| Forcas 2        | 8  | 12.41 | 0.84               | 6.75                     | 0.79     | 1   |
| Gabasa e        | 13 | 12.34 | 0.57               | 4.62                     | 0.27     | 3   |
| Gabasa f        | 6  | 12.32 | 0.65               | 5.24                     | 0.33     | 3   |
| Gabasa g        | 11 | 12.51 | 0.87               | 6.98                     | 0.31     | 3   |
| Grays           | 9  | 12.95 | 0.65               | 4.99                     | 0.09     | 9   |
| I'Arago         | 45 | 13.57 | 0.64               | 4.71                     |          | 7   |
| La Riera 14     | 7  | 13.58 | 0.83               | 6.10                     | 0.77     | 2   |
| La Riera 15     | 5  | 13.35 | 0.92               | 6.90                     | 0.80     | 2   |
| La Riera 16     | 12 | 13.66 | 1.10               | 8.08                     | 0.79     | 2   |
| La Riera 21-23  | 17 | 13.30 | 0.46               | 3.48                     | 0.84     | 2   |
| La Riera 8      | 13 | 13.44 | 0.53               | 3.98                     | 0.70     | 2   |
| La Riera 9      | 9  | 13.38 | 0.67               | 5.04                     | 0.81     | 2   |

**Table 6.4 con't**

| sample         | n   | mean  | standard deviation | coefficient of variation | red deer | OIS |
|----------------|-----|-------|--------------------|--------------------------|----------|-----|
| Labeko Koba IX | 12  | 14.02 | 0.38               | 2.69                     | 0.68     | 3   |
| Lazaret A      | 18  | 13.62 | 0.56               | 4.13                     | 0.76     | 6   |
| Lazaret B      | 8   | 13.73 | 0.48               | 3.50                     | 0.86     | 6   |
| Lazaret C      | 10  | 14.13 | 0.67               | 4.76                     | 0.77     | 6   |
| Lazaret D      | 15  | 13.85 | 1.01               | 7.30                     | 0.81     | 6   |
| Lazaret E      | 17  | 13.59 | 0.62               | 4.58                     | 0.86     | 6   |
| Le Portel F2   | 5   | 13.38 | 0.84               | 6.31                     | 0.72     | 3   |
| Majolicas      | 9   | 12.34 | 0.68               | 5.50                     |          | 1   |
| Orgnac 4b      | 5   | 13.84 | 1.04               | 7.51                     | 0.31     | 8   |
| Orgnac 5b      | 5   | 13.41 | 1.15               | 8.56                     | 0.40     | 9   |
| Orgnac 6       | 14  | 13.26 | 1.17               | 8.81                     | 0.31     | 9   |
| Piegu          | 12  | 13.74 | 1.06               | 7.72                     |          | 6   |
| Romanelli      | 10  | 13.21 | 0.44               | 3.36                     |          | 1   |
| Urriaga C      | 24  | 13.56 | 0.80               | 5.87                     | 0.63     | 1   |
| Urriaga D      | 28  | 13.65 | 0.76               | 5.55                     | 0.47     | 2   |
| Urriaga F      | 26  | 13.56 | 0.70               | 5.15                     | 0.68     | 2   |
| <i>total</i>   | 733 | 13.30 | 0.83               | 6.25                     |          |     |

**Table 6.5 Comparisons of M<sub>1</sub> breadth by Oxygen Isotope Stage**

Results of Tukey-Kramer Honestly Significant Difference test to investigate differences in mean M<sub>1</sub> breadths between OIS. A significant difference is indicated by "\*\*\*", and no significant difference is indicated by "ns".

A. Complete sample of M<sub>1</sub> breadths from western Europe

| O/S | 1  | 2  | 3  | 4  | 5  | 6  | 7  | 8  | 9  |
|-----|----|----|----|----|----|----|----|----|----|
| 1   |    | ns | ns | ** | ** | ** | ns | ns | ns |
| 2   | ns |    | ns | ** | ** | ** | ns | ns | ns |
| 3   | ns | ns |    | ** | ** | ** | ns | ns | ns |
| 4   | ** | ** | ** |    | ** | ns | ns | ns | ** |
| 5   | ** | ** | ** | ** |    | ** | ** | ns | ns |
| 6   | ** | ** | ** | ns | ** |    | ns | ns | ** |
| 7   | ns | ns | ns | ns | ** | ns |    | ns | ns |
| 8   | ns |    | ns |
| 9   | ns | ns | ns | ** | ns | ** | ns | ns |    |

B. Fossil M<sub>1</sub> breadths from the Mediterranean coast

| O/S | 1  | 2  | 3  | 4  | 6  | 7  | 8  | 9  |
|-----|----|----|----|----|----|----|----|----|
| 1   |    | ns | ns | ns | ** | ** | ns | ns |
| 2   | ns |    | ns | ns | ns | ns | ns | ns |
| 3   | ns | ns |    | ns | ** | ** | ns | ns |
| 4   | ns | ns | ns |    | ns | ns | ns | ns |
| 6   | ** | ns | ** | ns |    | ns | ns | ns |
| 7   | ** | ns | ** | ns | ns |    | ns | ns |
| 8   | ns | ns | ns | ns | ns | ns |    | ns |
| 9   | ns |    |

C. Fossil M<sub>1</sub> breadths from northern Spain

| O/S | 1  | 2  | 3  |
|-----|----|----|----|
| 1   |    | ns | ** |
| 2   | ns |    | ** |
| 3   | ** | ** |    |

D. Fossil M<sub>1</sub> breadths from northern Europe

| O/S | 1  | 3  | 4  | 7  | 9  | 11 |
|-----|----|----|----|----|----|----|
| 1   |    | ns | ns | ns | ns | ns |
| 3   | ns |    | ns | ns | ns | ns |
| 4   | ns | ns |    | ns | ns | ns |
| 7   | ns | ns | ns |    | ns | ns |
| 9   | ns | ns | ns | ns |    | ns |
| 11  | ns | ns | ns | ns | ns |    |

**Table 6.6 The relationship between metatarsal breadth and climate**

The correlation coefficients, coefficients of determination, and the significance of the lines for the regression of metatarsal breadths on climatic variables. Data are for North American specimens only, and males and females were analyzed separately. Relationships that are significant at the 0.1 or below level are in italics, and those significant at the 0.05 or below level are in bold italics.

|  | <i>latitude</i> | <i>mean annual ppt</i> | <i>mean annual temp</i> | <i>Jan temp</i> | <i>July temp</i> | <i>July-Jan temp</i> |
|--|-----------------|------------------------|-------------------------|-----------------|------------------|----------------------|
| <i>males</i>   |                 |                        |                         |                 |                  |                      |
| correlation coefficient ( <i>r</i> )                   | 0.65            | 0.63                   | -0.57                   | -0.52           | -0.62            | 0.18                 |
| coefficient of determination ( <i>r</i> <sup>2</sup> ) | <b>0.42</b>     | <b>0.39</b>            | <b>0.32</b>             | <b>0.27</b>     | <b>0.38</b>      | 0.03                 |
| slope significantly different from 0 (p-value)         | <0.0001         | <0.0001                | <0.0001                 | <0.0001         | <0.0001          | 0.2166               |
| <i>females</i>   |                 |                        |                         |                 |                  |                      |
| correlation coefficient ( <i>r</i> )                   | 0.59            | 0.61                   | -0.63                   | -0.62           | -0.64            | 0.49                 |
| coefficient of determination ( <i>r</i> <sup>2</sup> ) | <b>0.34</b>     | <b>0.37</b>            | <b>0.40</b>             | <b>0.39</b>     | <b>0.40</b>      | <b>0.24</b>          |
| slope significantly different from 0 (p-value)         | 0.0002          | 0.0001                 | <0.0001                 | <0.0001         | <0.0001          | 0.0031               |

**Table 6.7 Data on Late Pleistocene red deer metacarpal breadths for studying the relationship between size and climate**  
 Analyses included samples with five or more measurable specimens. Full descriptions of the samples can be found in Appendix D, and sites are labeled on the map in Figure 3.1.

| sample                | n          | mean         | standard deviation | coefficient of variation | OIS |
|-----------------------|------------|--------------|--------------------|--------------------------|-----|
| Chaves I              | 7          | 39.46        | 2.46               | 6.25                     | 1   |
| Altamira (Mag)        | 20         | 44.54        | 2.39               | 5.37                     | 2   |
| Altamira (Solutrean)  | 14         | 44.31        | 1.43               | 3.22                     | 2   |
| Castillo (Mag)        | 18         | 43.15        | 3.24               | 7.50                     | 2   |
| Juyo 4                | 7          | 45.14        | 0.86               | 1.90                     | 2   |
| Juyo 6                | 24         | 43.46        | 2.40               | 5.51                     | 2   |
| La Riera 9-11         | 5          | 42.85        | 3.53               | 8.23                     | 2   |
| Urtiaga D             | 13         | 44.58        | 3.08               | 6.91                     | 2   |
| Labeko Koba IX        | 11         | 47.95        | 1.98               | 4.14                     | 3   |
| Urtiaga F             | 12         | 46.09        | 2.56               | 5.55                     | 3   |
| Castillo (Mousterian) | 9          | 44.48        | 2.46               | 5.54                     | 4   |
| Combe-Grenal 50-50a   | 5          | 41.22        | 1.66               | 4.03                     | 5   |
| Lazaret A             | 6          | 43.04        | 2.79               | 6.47                     | 6   |
| Lazaret D             | 9          | 43.36        | 1.23               | 2.83                     | 6   |
| Lazaret E             | 6          | 44.52        | 3.57               | 8.01                     | 6   |
| <i>total</i>          | <i>166</i> | <i>44.09</i> | <i>2.91</i>        | <i>6.61</i>              |     |

**Table 7.1 First analysis: Individual samples with more than twenty-five measurable dP<sub>4</sub>s and M<sub>1</sub>s**

The sample sizes are for the number of measurable teeth of each type. UW CH is the average unworn crown height of the sample, unless noted otherwise.

| sample                  | n dP <sub>4</sub> | n M <sub>1</sub> | dP <sub>4</sub> +M <sub>1</sub> | dP <sub>4</sub> UW CH | M <sub>1</sub> UW CH | M <sub>1</sub> CH median | M <sub>1</sub> breadth | median/breadth | % dP <sub>4</sub> |
|-------------------------|-------------------|------------------|---------------------------------|-----------------------|----------------------|--------------------------|------------------------|----------------|-------------------|
| <i>Azilian</i>          |                   |                  |                                 |                       |                      |                          |                        |                |                   |
| Urtiaga C               | 8                 | 24               | 32                              | 11.93                 | 24.18                | 16.99                    | 13.56                  | 1.25           | 25.0              |
| <i>Magdalenian</i>      |                   |                  |                                 |                       |                      |                          |                        |                |                   |
| El Castillo             | 54                | 61               | 115                             | 11.63                 | 23.50                | 14.00                    | 13.27                  | 1.06           | 47.0              |
| El Juyo 4               | 28                | 32               | 60                              | 11.63 <sup>a</sup>    | 22.87                | 16.95                    | 13.01                  | 1.30           | 46.7              |
| El Juyo 6               | 52                | 97               | 149                             | 11.63 <sup>a</sup>    | 22.82                | 16.50                    | 13.22                  | 1.25           | 34.9              |
| El Juyo 8               | 5                 | 26               | 31                              | 11.63 <sup>a</sup>    | 21.96                | 16.85                    | 13.21                  | 1.28           | 16.1              |
| Urtiaga D               | 33                | 33               | 66                              | 12.51                 | 21.30                | 15.86                    | 13.65                  | 1.16           | 50.0              |
| Urtiaga F               | 3                 | 28               | 31                              | 12.93                 | 21.57                | 14.46                    | 13.67                  | 1.06           | 9.7               |
| <i>Mousterian</i>       |                   |                  |                                 |                       |                      |                          |                        |                |                   |
| Combe-Grenal 50         | 5                 | 38               | 43                              | 11.72 <sup>b</sup>    | 20.37                | 11.76                    | 12.51                  | 0.94           | 11.6              |
| Combe-Grenal 52         | 0                 | 27               | 27                              | na                    | 20.37 <sup>e</sup>   | 12.16                    | 12.57                  | 0.97           | 0.0               |
| Gabasa e                | 22                | 17               | 39                              | 11.56                 | 22.43                | 15.39                    | 12.34                  | 1.25           | 56.4              |
| Gabasa f                | 21                | 7                | 28                              | 11.72                 | 21.12                | 16.73                    | 12.32                  | 1.36           | 75.0              |
| <i>Early Mousterian</i> |                   |                  |                                 |                       |                      |                          |                        |                |                   |
| Lazaret E               | 6                 | 22               | 28                              | 13.06 <sup>c</sup>    | 20.05                | 9.06                     | 13.59                  | 0.67           | 21.4              |
| <i>Modern</i>           |                   |                  |                                 |                       |                      |                          |                        |                |                   |
| Recent humans           | 86                | 164              | 250                             | 14.0 <sup>d</sup>     | 27.0 <sup>d</sup>    | 13.66                    | 15.37                  | 0.89           | 34.4              |
| Wolves                  | 45                | 53               | 98                              | 14.0 <sup>d</sup>     | 27.0 <sup>d</sup>    | 4.00                     | 15.49                  | 0.26           | 45.9              |

<sup>a</sup> estimated from Castillo (Mag)

<sup>b</sup> estimated from Gabasa f

<sup>c</sup> estimated from other Lazaret levels

<sup>d</sup> from Klein and Cruz-Urbe (1984:49)

<sup>e</sup> estimated from Combe-Grenal 50

**Table 7.2 First analysis: Results of the Kolmogorov-Smirnov test for individual samples with more than twenty-five measurable  $dP_4s$  and  $M_1s$**

Kolmogorov-Smirnov results for pair-wise comparisons of the histograms constructed from individual samples with more than twenty-five measurable  $dP_4s$  and  $M_1s$ . The box encloses the Middle Paleolithic assemblages to compare with the Upper Paleolithic samples listed above. The human and wolf kill samples and the model living and attritional age structures are included for comparison. C-G = Combe-Grenal.

| Sample      | Urtiaga C      | Urtiaga D       | Urtiaga F      | El Castillo     | El Juyo 4       | El Juyo 6       | El Juyo 8      | Gabasa e        | Gabasa f        | C-G 50        | C-G 52       | Lazaret E |
|-------------|----------------|-----------------|----------------|-----------------|-----------------|-----------------|----------------|-----------------|-----------------|---------------|--------------|-----------|
| Urtiaga D   | 0.917          |                 |                |                 |                 |                 |                |                 |                 |               |              |           |
| Urtiaga F   | 0.364          | <b>1.389*</b>   |                |                 |                 |                 |                |                 |                 |               |              |           |
| Castillo    | 0.431          | 0.741           | 0.93           |                 |                 |                 |                |                 |                 |               |              |           |
| El Juyo 4   | 0.757          | 0.595           | 1.211          | 0.646           |                 |                 |                |                 |                 |               |              |           |
| El Juyo 6   | 0.271          | 0.954           | 0.762          | 0.258           | 0.719           |                 |                |                 |                 |               |              |           |
| El Juyo 8   | 0.691          | 0.276           | 1.089          | 0.44            | 0.587           | 0.608           |                |                 |                 |               |              |           |
| Gabasa e    | 0.924          | 0.402           | 1.352          | 0.88            | 0.28            | 0.923           | 0.602          |                 |                 |               |              |           |
| Gabasa f    | <b>1.443*</b>  | 0.75            | <b>1.862**</b> | <b>1.396*</b>   | 0.878           | <b>1.562*</b>   | 0.781          | 0.608           |                 |               |              |           |
| C-G 50      | 1.018          | <b>1.591*</b>   | 1.042          | 1.121           | <b>1.396*</b>   | 1.121           | 1.225          | <b>1.557*</b>   |                 |               |              |           |
| C-G 52      | 0.842          | <b>1.626*</b>   | 0.853          | 1.197           | <b>1.445*</b>   | 1.031           | 1.301          | <b>1.57*</b>    | 0.623           |               |              |           |
| Lazaret E   | 1.166          | <b>1.876**</b>  | 1.19           | <b>1.476*</b>   | <b>1.692**</b>  | 1.314           | <b>1.525*</b>  | <b>1.801**</b>  | 0.437           | 0.446         |              |           |
| Human       | 0.972          | <b>2.132***</b> | 1.013          | <b>1.715**</b>  | <b>1.815**</b>  | <b>1.424*</b>   | <b>1.468*</b>  | <b>1.881**</b>  | <b>2.45***</b>  | 0.768         | 0.27         | 0.592     |
| Wolf        | <b>1.689**</b> | <b>1.945**</b>  | <b>1.684**</b> | <b>2.177***</b> | <b>2.301***</b> | <b>2.35***</b>  | <b>1.442*</b>  | <b>2.113***</b> | <b>2.054***</b> | <b>1.602*</b> | <b>1.36*</b> | 0.989     |
| Living      | <b>1.697**</b> | <b>2.681***</b> | <b>1.8**</b>   | <b>2.672***</b> | <b>2.554***</b> | <b>2.889***</b> | <b>1.815**</b> | <b>2.541***</b> | <b>2.821***</b> | 1.038         | 1.233        | 0.591     |
| Attritional | <b>1.552*</b>  | <b>1.875**</b>  | <b>1.701**</b> | <b>2.556***</b> | <b>2.303***</b> | <b>2.793***</b> | <b>1.437*</b>  | <b>2.019***</b> | <b>1.954***</b> | <b>1.579*</b> | 1.29         | 1.338     |

\*  $p < 0.05$

\*\*  $p < 0.01$

\*\*\*  $p < 0.001$

**Table 7.3 First analysis: Summary statistics for the modified triangular graphs for the individual samples.**

The sample sizes of  $dP_4$ s include measurable and unmeasurable specimens, and the sample sizes of  $P_4$ s are only measurable teeth. UW CH is the average unworn crown height of the sample, unless noted otherwise. The percentage of young is the percentage of  $dP_4$ s in the sample, the percentage of prime is the percentage of  $P_4$ s that were less than half worn, and the percentage of old is of teeth that were more than half worn. Crown height measurements were used to determine the degree of wear.

| sample                  | $n$ | $dP_4$ | $n$ | $P_4$              | $dP_4+P_4$ | $P_4$ | UW CH | % young | % prime | % old |
|-------------------------|-----|--------|-----|--------------------|------------|-------|-------|---------|---------|-------|
| <i>Azilian</i>          |     |        |     |                    |            |       |       |         |         |       |
| Urtiaga C               | 9   | 15     | 24  | 18.70              | 37.5       | 58.3  | 4.2   |         |         |       |
| <i>Magdalenian</i>      |     |        |     |                    |            |       |       |         |         |       |
| El Juyo 4               | 28  | 26     | 54  | 19.55              | 51.9       | 44.4  | 3.7   |         |         |       |
| El Juyo 6               | 52  | 81     | 133 | 17.79              | 39.1       | 48.9  | 12.0  |         |         |       |
| Urtiaga D               | 39  | 24     | 63  | 19.31              | 61.9       | 33.3  | 4.8   |         |         |       |
| Urtiaga F               | 5   | 28     | 33  | 19.31 <sup>a</sup> | 15.2       | 72.7  | 12.1  |         |         |       |
| <i>Mousterian</i>       |     |        |     |                    |            |       |       |         |         |       |
| Combe-Grenal 50         | 7   | 32     | 39  | 17.65              | 17.9       | 71.8  | 10.3  |         |         |       |
| Combe-Grenal 52         | 1   | 18     | 19  | 17.65 <sup>b</sup> | 5.3        | 89.5  | 5.3   |         |         |       |
| Gabasa e                | 25  | 11     | 36  | 17.77              | 69.4       | 22.2  | 8.3   |         |         |       |
| Gabasa f                | 28  | 4      | 32  | 17.77 <sup>c</sup> | 87.5       | 12.5  | 0.0   |         |         |       |
| <i>Early Mousterian</i> |     |        |     |                    |            |       |       |         |         |       |
| Lazaret E               | 6   | 16     | 22  | 19.77 <sup>d</sup> | 27.3       | 40.9  | 31.8  |         |         |       |
| <i>Modern</i>           |     |        |     |                    |            |       |       |         |         |       |
| Wolves                  | 45  | 53     | 98  | 23.0               | 45.9       | 24.5  | 29.6  |         |         |       |

<sup>a</sup> estimated from Urtiaga D

<sup>b</sup> estimated from Combe-Grenal 50

<sup>c</sup> estimated from Gabasa e

<sup>d</sup> estimated from other Lazaret levels

**Table 7.4 Second analysis: Grouped samples with more than twenty-five measurable  $dP_4$ s and  $M_1$ s**

The sample sizes are for the number of measurable teeth of each type. UW CH is the average unworn crown height of the sample, unless noted otherwise.

| sample                  | $n$ $dP_4$ | $n$ $M_1$ | $dP_4+M_1$ | $dP_4$ UW CH       | $M_1$ UW CH       | $M_1$ CH median | $M_1$ breadth | median/breadth | % $dP_4$ |
|-------------------------|------------|-----------|------------|--------------------|-------------------|-----------------|---------------|----------------|----------|
| <i>Azilian</i>          |            |           |            |                    |                   |                 |               |                |          |
| N. Spanish Azilian      | 8          | 41        | 49         | 11.93              | 23.02             | 16.90           | 13.12         | 1.29           | 16.3     |
| <i>Magdalenian</i>      |            |           |            |                    |                   |                 |               |                |          |
| El Castillo             | 54         | 61        | 115        | 11.63              | 23.50             | 14.00           | 13.27         | 1.06           | 47.0     |
| El Juyo                 | 85         | 155       | 240        | 11.93              | 22.64             | 16.70           | 13.18         | 1.27           | 35.4     |
| Urtiaga                 | 35         | 64        | 99         | 12.52              | 21.43             | 14.48           | 13.64         | 1.06           | 35.4     |
| <i>Solutrean</i>        |            |           |            |                    |                   |                 |               |                |          |
| La Riera                | 22         | 48        | 70         | 12.77              | 21.86             | 15.44           | 13.49         | 1.14           | 31.4     |
| <i>Mousterian</i>       |            |           |            |                    |                   |                 |               |                |          |
| Gabasa                  | 60         | 38        | 98         | 11.71              | 21.86             | 16.47           | 12.53         | 1.31           | 61.2     |
| Combe-Grenal 1-35       | 9          | 73        | 82         | 11.45              | 26.15             | 9.50            | 13.88         | 0.68           | 11.0     |
| Combe-Grenal 36-54      | 10         | 97        | 107        | 11.71 <sup>a</sup> | 20.58             | 11.10           | 12.76         | 0.87           | 9.3      |
| <i>Early Mousterian</i> |            |           |            |                    |                   |                 |               |                |          |
| Lazaret                 | 25         | 73        | 98         | 13.06              | 21.80             | 8.84            | 13.75         | 0.64           | 25.5     |
| <i>Modern</i>           |            |           |            |                    |                   |                 |               |                |          |
| Recent humans           | 86         | 164       | 250        | 14.0 <sup>b</sup>  | 27.0 <sup>b</sup> | 13.66           | 15.37         | 0.89           | 34.4     |
| Wolves                  | 45         | 53        | 98         | 14.0 <sup>b</sup>  | 27.0 <sup>b</sup> | 4.00            | 15.49         | 0.26           | 45.9     |

<sup>a</sup> estimated from Gabasa

<sup>b</sup> from Klein and Cruz-Urbe (1984:49)

**Table 7.5 Second analysis: Results of the Kolmogorov-Smirnov test for grouped samples with more than twenty-five measurable dP<sub>4s</sub> and M<sub>1s</sub>**

Kolmogorov-Smirnov results for pair-wise comparisons of the histograms constructed from grouped samples with more than twenty-five measurable dP<sub>4s</sub> and M<sub>1s</sub>. The box encloses the Middle to Upper Paleolithic comparisons. (C-G = Combe-Grenal)

| A. Complete age distribution |                 |                 |                 |                 |                 |                 |                 |                 |                |
|------------------------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|----------------|
| sample                       | N Spanish Az    | El Castillo     | El Juyo         | Urriaga         | La Riera        | Gabasa          | C-G 1-35        | C-G 36-54       | Lazaret        |
| El Castillo                  | 0.84            |                 |                 |                 |                 |                 |                 |                 |                |
| El Juyo                      | 0.721           | 0.392           |                 |                 |                 |                 |                 |                 |                |
| Urriaga                      | 0.595           | 0.408           | 0.565           |                 |                 |                 |                 |                 |                |
| La Riera                     | 1.092           | 0.43            | 0.641           | 0.689           |                 |                 |                 |                 |                |
| Gabasa                       | 0.877           | <b>1.458*</b>   | <b>1.709**</b>  | <b>1.74**</b>   | <b>1.573*</b>   |                 |                 |                 |                |
| C-G 1-35                     | <b>3.241***</b> | <b>3.079***</b> | <b>3.589***</b> | <b>3.179***</b> | <b>2.147***</b> | <b>4.237***</b> |                 |                 |                |
| C-G 36-54                    | <b>2.057***</b> | <b>1.867**</b>  | <b>1.988***</b> | <b>1.791**</b>  | 1.198           | <b>3.214***</b> | <b>1.712**</b>  |                 |                |
| Lazaret                      | <b>2.237***</b> | <b>2.027***</b> | <b>2.47***</b>  | <b>2.003***</b> | <b>1.425*</b>   | <b>3.188***</b> | 1.293           | 0.913           |                |
| Humans                       | <b>1.745**</b>  | <b>1.715**</b>  | <b>1.862**</b>  | <b>1.417*</b>   | 0.944           | <b>3.278***</b> | <b>2.924***</b> | 1.015           | <b>2.05***</b> |
| Wolf                         | <b>2.251***</b> | <b>2.177***</b> | <b>2.809***</b> | <b>2.005***</b> | <b>1.768**</b>  | <b>2.912***</b> | <b>2.146***</b> | <b>2.029***</b> | <b>1.395*</b>  |
| Living                       | <b>2.754***</b> | <b>2.672***</b> | <b>3.702***</b> | <b>2.74***</b>  | <b>1.512*</b>   | <b>4.225***</b> | <b>1.644**</b>  | <b>1.488*</b>   | 0.368          |
| Attritional                  | <b>2.199***</b> | <b>2.556***</b> | <b>3.653***</b> | <b>1.997***</b> | <b>1.871**</b>  | <b>3.145***</b> | <b>3.099***</b> | <b>2.26***</b>  | <b>1.893**</b> |

B. Adults only. Age class 1 was deleted. Sample sizes were too small to compare the northern Spanish Azilian and Gabasa samples.

| sample      | El Castillo     | El Juyo         | Urriaga         | La Riera       | C-G 1-35       | C-G 36-54       | Lazaret        |
|-------------|-----------------|-----------------|-----------------|----------------|----------------|-----------------|----------------|
| El Juyo     | 0.428           |                 |                 |                |                |                 |                |
| Urriaga     | 0.574           | 0.529           |                 |                |                |                 |                |
| La Riera    | 0.223           | 0.5             | 0.708           |                |                |                 |                |
| C-G 1-35    | 1.084           | <b>1.638**</b>  | <b>1.39*</b>    | 0.88           |                |                 |                |
| C-G 36-54   | 0.334           | 0.803           | 0.914           | 0.281          | 0.857          |                 |                |
| Lazaret     | 0.973           | <b>1.443*</b>   | 1.146           | 0.743          | 0.372          | 0.743           |                |
| Humans      | 0.211           | 0.531           | 0.755           | 0.31           | <b>1.703**</b> | 0.701           | <b>1.532*</b>  |
| Wolves      | <b>1.84**</b>   | <b>2.53***</b>  | <b>1.779**</b>  | <b>1.615*</b>  | <b>1.404*</b>  | <b>2.113***</b> | <b>1.437*</b>  |
| Living      | 1.121           | <b>2.114***</b> | <b>1.447*</b>   | 0.911          | 0.391          | 1.262           | 0.299          |
| Attritional | <b>2.338***</b> | <b>3.503***</b> | <b>2.022***</b> | <b>1.871**</b> | <b>1.774**</b> | <b>2.735***</b> | <b>1.705**</b> |

\*  $p < 0.05$

\*\*  $p < 0.01$

\*\*\*  $p < 0.001$

**Table 7.6 Second analysis: Summary statistics for the modified triangular graph for the grouped samples**

The sample sizes of  $dP_4$ s include measurable and unmeasurable specimens, and the sample sizes of  $P_4$ s are only measurable teeth. UW CH is the average unworn crown height of the sample. The percentage of young is the percentage of  $dP_4$ s in the sample, the percentage of prime is the percentage of  $P_4$ s that were less than half worn, and the percentage of old is of teeth that were more than half worn. Crown height measurements were used to determine the degree of wear.

| sample                  | $n$ | $dP_4$ | $n$ | $P_4$ | $dP_4+P_4$ | $P_4$ | UW   | CH | % young | % prime | % old |
|-------------------------|-----|--------|-----|-------|------------|-------|------|----|---------|---------|-------|
| <i>Azilian</i>          |     |        |     |       |            |       |      |    |         |         |       |
| N. Spanish Azilian      | 10  | 25     | 35  | 18.6  | 28.6       | 68.6  | 2.9  |    |         |         |       |
| <i>Magdalenian</i>      |     |        |     |       |            |       |      |    |         |         |       |
| El Juyo                 | 85  | 107    | 192 | 18.3  | 44.3       | 45.8  | 9.9  |    |         |         |       |
| Urliaga                 | 46  | 54     | 100 | 19.3  | 46.0       | 46.0  | 8.0  |    |         |         |       |
| <i>Solutrean</i>        |     |        |     |       |            |       |      |    |         |         |       |
| La Riera                | 29  | 42     | 71  | 19.9  | 40.8       | 52.1  | 7.0  |    |         |         |       |
| <i>Mousterian</i>       |     |        |     |       |            |       |      |    |         |         |       |
| Gabasa                  | 75  | 21     | 96  | 17.8  | 78.1       | 16.7  | 5.2  |    |         |         |       |
| Combe-Grenal 1-35       | 11  | 67     | 78  | 19.2  | 14.1       | 55.1  | 30.8 |    |         |         |       |
| Combe-Grenal 36-54      | 14  | 77     | 91  | 17.7  | 15.4       | 72.5  | 12.1 |    |         |         |       |
| <i>Early Mousterian</i> |     |        |     |       |            |       |      |    |         |         |       |
| Lazaret                 | 28  | 88     | 116 | 19.7  | 24.1       | 41.4  | 34.5 |    |         |         |       |
| <i>Modern</i>           |     |        |     |       |            |       |      |    |         |         |       |
| Wolves                  | 45  | 53     | 98  | 23.0  | 45.9       | 24.5  | 29.6 |    |         |         |       |

**Table 7.7 Third analysis: Grouped samples with ten or more measurable  $M_1$  crown heights**  
 The sample sizes of  $dP_4$ s include measurable and unmeasurable specimens, and the sample sizes of  $M_1$ s are all measurable  $M_1$ s.

| sample                   | $n$ | $dP_4$ | $n$ | $M_1$ | $dP_4+M_1$ | $M_1$ | $CH$  | median | $M_1$ | breadth | median/breadth | % $dP_4$ |
|--------------------------|-----|--------|-----|-------|------------|-------|-------|--------|-------|---------|----------------|----------|
| <i>Holocene</i>          |     |        |     |       |            |       |       |        |       |         |                |          |
| German Federmesser       | 5   | 14     | 19  | 15.62 | 13.92      | 1.12  | 26.32 |        |       |         |                |          |
| N. Spanish Azilian       | 10  | 41     | 51  | 16.90 | 13.12      | 1.29  | 19.61 |        |       |         |                |          |
| Star Carr Mesolithic     | 2   | 32     | 34  | 13.3  | 12.88      | 1.03  | 5.88  |        |       |         |                |          |
| <i>Magdalenian</i>       |     |        |     |       |            |       |       |        |       |         |                |          |
| Altamira                 | 10  | 10     | 20  | 13.45 | 13.30      | 1.01  | 50.00 |        |       |         |                |          |
| El Castillo              | 56  | 61     | 117 | 14.00 | 13.27      | 1.06  | 47.86 |        |       |         |                |          |
| El Juyo                  | 85  | 155    | 240 | 16.70 | 13.18      | 1.27  | 35.42 |        |       |         |                |          |
| La Riera                 | 5   | 16     | 21  | 15.00 | 13.27      | 1.13  | 23.81 |        |       |         |                |          |
| Urriaga                  | 46  | 64     | 110 | 14.48 | 13.64      | 1.06  | 41.82 |        |       |         |                |          |
| <i>Solutrean</i>         |     |        |     |       |            |       |       |        |       |         |                |          |
| Altamira                 | 3   | 20     | 23  | 15.50 | 13.51*     | 1.15  | 13.04 |        |       |         |                |          |
| La Riera                 | 29  | 48     | 77  | 15.44 | 13.51      | 1.14  | 37.66 |        |       |         |                |          |
| <i>Châtelperronian</i>   |     |        |     |       |            |       |       |        |       |         |                |          |
| Labeko Koba IX inf.      | 2   | 12     | 14  | 16.85 | 14.02      | 1.20  | 14.29 |        |       |         |                |          |
| <i>Mousterian</i>        |     |        |     |       |            |       |       |        |       |         |                |          |
| Gabasa                   | 75  | 38     | 113 | 16.47 | 12.53      | 1.31  | 66.37 |        |       |         |                |          |
| Combe-Grenal 1-35        | 11  | 73     | 84  | 9.50  | 13.88      | 0.68  | 13.10 |        |       |         |                |          |
| Combe-Grenal 36-54       | 14  | 97     | 111 | 11.10 | 12.76      | 0.87  | 12.61 |        |       |         |                |          |
| <i>Early Mousterian</i>  |     |        |     |       |            |       |       |        |       |         |                |          |
| Lazaret                  | 28  | 73     | 101 | 8.84  | 13.75      | 0.64  | 27.72 |        |       |         |                |          |
| Piegu                    | 2   | 18     | 20  | 12.12 | 13.74      | 0.88  | 10.00 |        |       |         |                |          |
| <i>Acheulo-Yabrudian</i> |     |        |     |       |            |       |       |        |       |         |                |          |
| Tabun                    | 2   | 10     | 12  | 11.55 | 13.58      | 0.85  | 16.67 |        |       |         |                |          |
| <i>Modern</i>            |     |        |     |       |            |       |       |        |       |         |                |          |
| Recent humans            | 86  | 164    | 250 | 13.66 | 15.37      | 0.89  | 34.40 |        |       |         |                |          |
| Wolves                   | 45  | 53     | 98  | 4.00  | 15.49      | 0.26  | 45.92 |        |       |         |                |          |

\* estimated from La Riera

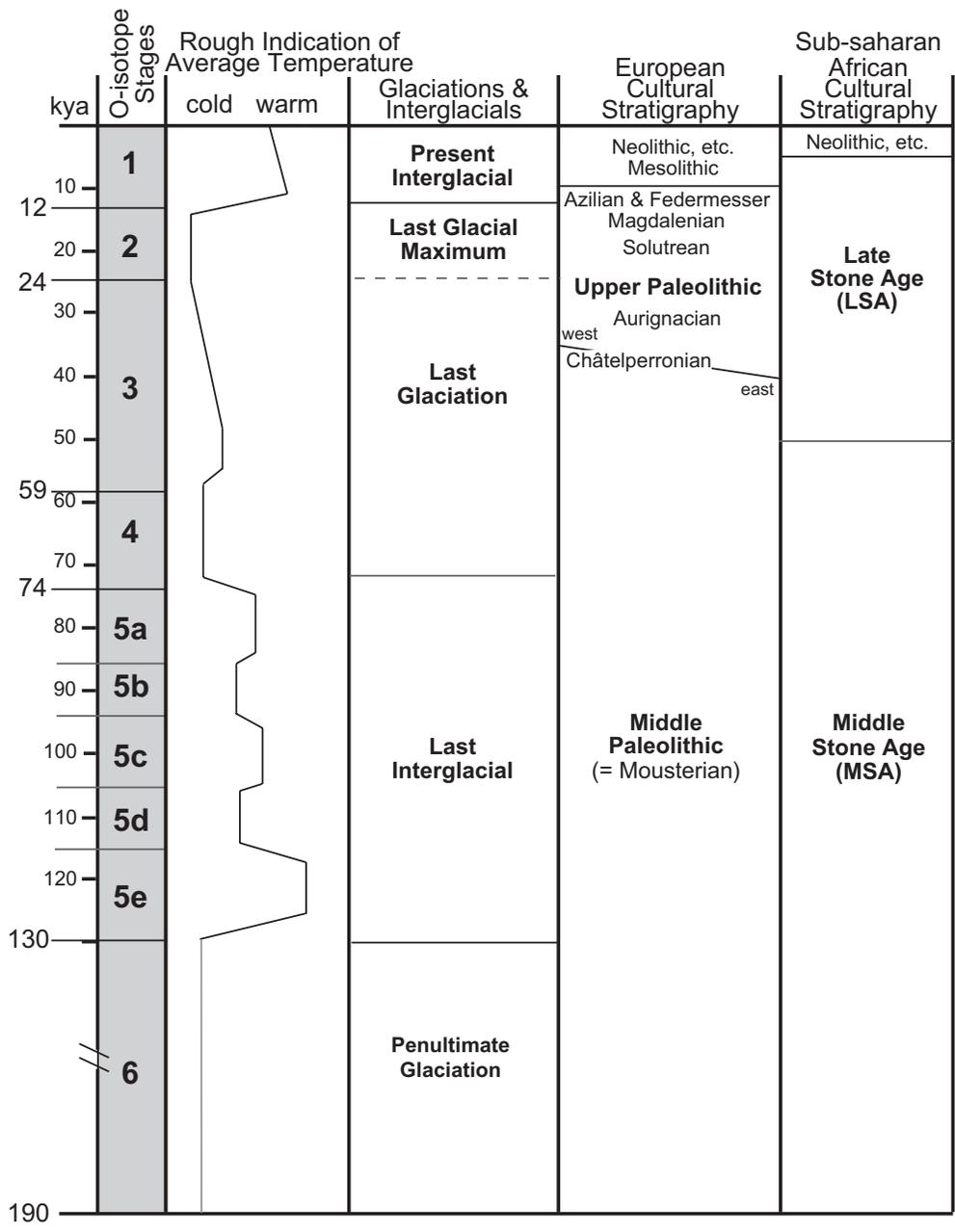
**Table 7.8 Third analysis: Individual samples with ten or more measurable M<sub>1</sub> crown heights**

The sample sizes of dP<sub>4</sub>s include measurable and unmeasurable specimens, and the sample sizes of M<sub>1</sub>s are all measurable M<sub>1</sub>s. More details for each sample, including references, are provided in Appendices C and D. Confidence intervals around the dates are not considered, and the dates are primarily used to place samples in relative positions on the graph.

| sample                   | n dP <sub>4</sub> | n M <sub>1</sub> | total | % dP <sub>4</sub> | M <sub>1</sub> CH median | M <sub>1</sub> breadth | median/breadth | % C. e | temperature | O/S    | date   |
|--------------------------|-------------------|------------------|-------|-------------------|--------------------------|------------------------|----------------|--------|-------------|--------|--------|
| <i>Holocene</i>          |                   |                  |       |                   |                          |                        |                |        |             |        |        |
| Majolicas Azilian        | 0                 | 12               | 12    | 0.00              | 16.95                    | 12.34                  | 1.37           |        |             | 1      | 8700   |
| Urtiaga C Azilian        | 9                 | 24               | 33    | 27.27             | 16.99                    | 13.56                  | 1.25           | 63.2   |             | 1      | 8700   |
| German Federmesser       | 5                 | 14               | 19    | 26.32             | 15.62                    | 13.92                  | 1.12           |        |             | 1      | 11300  |
| Star Carr Mesolithic     | 2                 | 32               | 34    | 5.88              | 13.30                    | 12.88                  | 1.03           | 51.0   | temperate   | 1      | 9600   |
| <i>Final Magdalenian</i> |                   |                  |       |                   |                          |                        |                |        |             |        |        |
| La Riera 21-23           | 1                 | 13               | 14    | 7.14              | 15.00                    | 13.30                  | 1.13           | 84.3   | cold        | 2      | 11000  |
| Urtiaga D                | 39                | 33               | 72    | 54.17             | 15.86                    | 13.65                  | 1.16           | 47.0   |             | 2      | 10280  |
| <i>Early Magdalenian</i> |                   |                  |       |                   |                          |                        |                |        |             |        |        |
| Altamira                 | 10                | 10               | 20    | 50.00             | 13.45                    | 13.30                  | 1.01           | 95.4   |             | 2      | 15000  |
| El Castillo              | 56                | 61               | 117   | 47.86             | 14.00                    | 13.27                  | 1.06           | 38.1   | cold        | 2      | 16850  |
| El Juyo 4                | 28                | 32               | 60    | 46.67             | 16.95                    | 13.01                  | 1.30           | 90.1   |             | 2      | 13920  |
| El Juyo 6                | 52                | 97               | 149   | 34.90             | 16.50                    | 13.22                  | 1.25           | 93.1   |             | 2      | 11400  |
| El Juyo 8                | 5                 | 26               | 31    | 16.13             | 16.85                    | 13.21                  | 1.28           | 90.3   |             | 2      | 14440  |
| Urtiaga F                | 5                 | 28               | 33    | 15.15             | 14.46                    | 13.67                  | 1.06           | 67.5   |             | 2      | 17050  |
| <i>Solutrean</i>         |                   |                  |       |                   |                          |                        |                |        |             |        |        |
| Altamira                 | 3                 | 20               | 23    | 13.04             | 15.50                    | 13.66*                 | 1.13           |        |             | 2      | 18000  |
| La Riera 16              | 5                 | 14               | 19    | 26.32             | 15.33                    | 13.66                  | 1.12           | 79.1   | temperate   | 2      | 18200  |
| La Riera 8               | 6                 | 16               | 22    | 27.27             | 18.37                    | 13.44                  | 1.37           | 70.2   | cold        | 2      | 20690  |
| <i>Châtelperronian</i>   |                   |                  |       |                   |                          |                        |                |        |             |        |        |
| Labeko Koba IX inf.      | 2                 | 12               | 14    | 14.29             | 16.85                    | 14.02                  | 1.20           | 68.4   | temperate   | 3      | 34125  |
| <i>Mousterian</i>        |                   |                  |       |                   |                          |                        |                |        |             |        |        |
| Combe-Grenal 25          | 2                 | 10               | 12    | 16.67             | 10.40                    | 14.38                  | 0.72           | 22.9   | cold        | 4      | 66500  |
| Combe-Grenal 35          | 4                 | 12               | 16    | 25.00             | 8.41                     | 13.41                  | 0.63           | 49.8   | cold        | 4      | 74000  |
| Combe-Grenal 50          | 7                 | 38               | 45    | 15.56             | 11.76                    | 12.51                  | 0.94           | 83.1   | temperate   | 5      | 100000 |
| Combe-Grenal 52          | 1                 | 27               | 28    | 3.57              | 12.16                    | 12.57                  | 0.97           | 76.7   | temperate   | 5      | 100000 |
| Combe-Grenal 54          | 0                 | 11               | 11    | 0.00              | 11.02                    | 12.78                  | 0.86           | 74.1   | temperate   | 5      | 110000 |
| Gabasa e                 | 25                | 17               | 42    | 59.52             | 15.39                    | 12.34                  | 1.25           | 27.1   | cold        | 3      | 46000  |
| Gabasa g                 | 13                | 11               | 24    | 54.17             | 16.20                    | 12.51                  | 1.30           | 31.2   | cold        | 3      | 46000  |
| <i>Early Mousterian</i>  |                   |                  |       |                   |                          |                        |                |        |             |        |        |
| Lazaret A                | 9                 | 15               | 24    | 37.50             | 8.43                     | 13.62                  | 0.62           | 75.9   | cold        | 6      | 130000 |
| Lazaret C                | 4                 | 14               | 18    | 22.22             | 7.35                     | 14.13                  | 0.52           | 76.9   | cold        | 6      | 130000 |
| Lazaret D                | 6                 | 13               | 19    | 31.58             | 12.03                    | 13.85                  | 0.87           | 81.4   | cold        | 6      | 130000 |
| Lazaret E                | 6                 | 22               | 28    | 21.43             | 9.06                     | 13.59                  | 0.67           | 85.6   | cold        | 6      | 170000 |
| Piegu                    | 2                 | 18               | 20    | 10.00             | 12.12                    | 13.74                  | 0.88           |        |             | 6 or 7 | 190000 |
| <i>Acheulo-Yabrudian</i> |                   |                  |       |                   |                          |                        |                |        |             |        |        |
| Tabun                    | 2                 | 10               | 12    | 16.67             | 11.55                    | 13.58                  | 0.85           |        |             | 7 or 8 | 245000 |

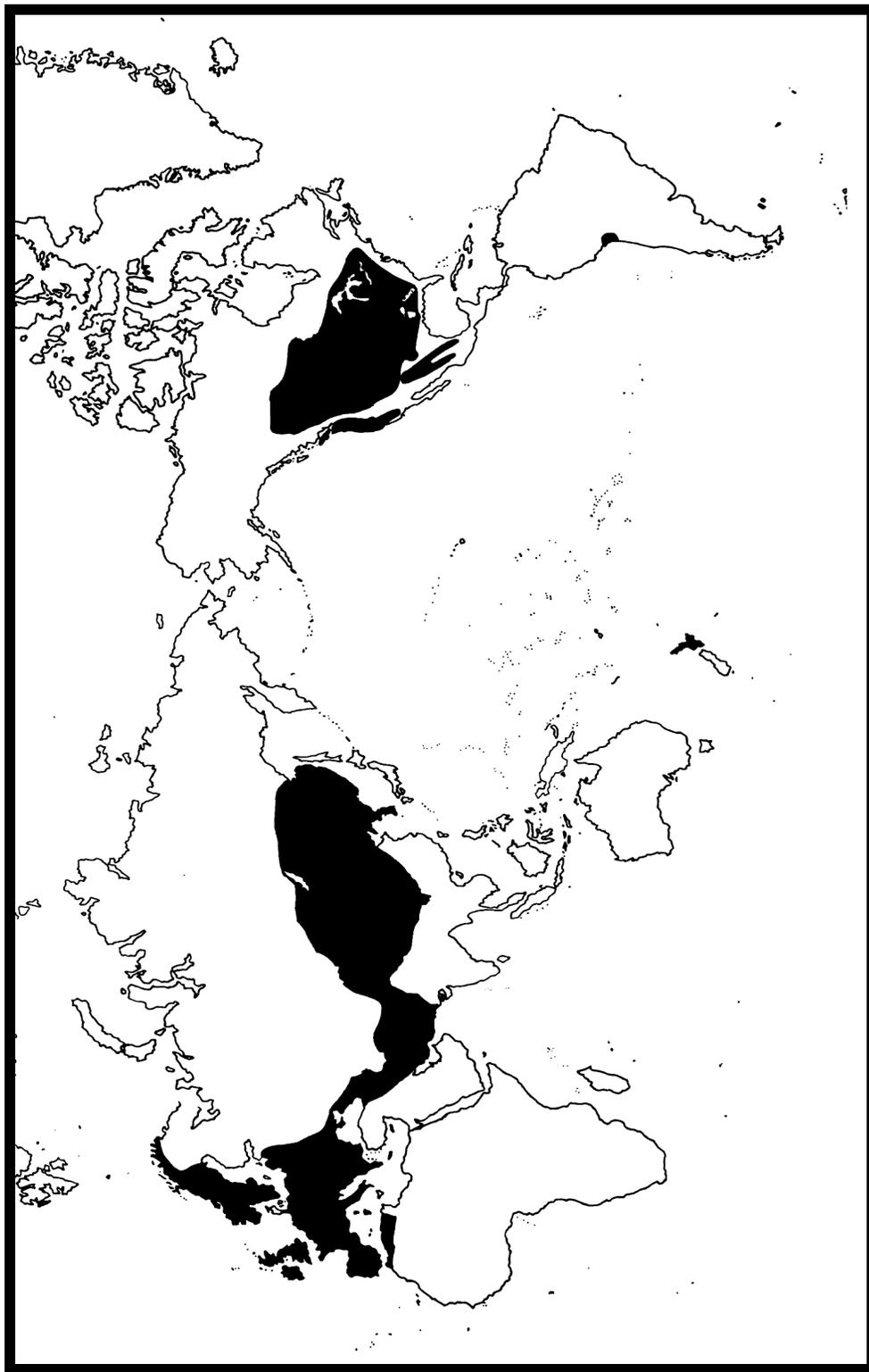
\* estimated from La Riera 16

## **Appendix B Illustrations**



**Figure 1.1 Later Pleistocene climatic and cultural stratigraphy**

Modified from Klein (1999:523). Dates for the Oxygen Isotope Stages are from Martinson *et al.* (1987) as in Bradley (1999:212). kya = thousands of years ago.



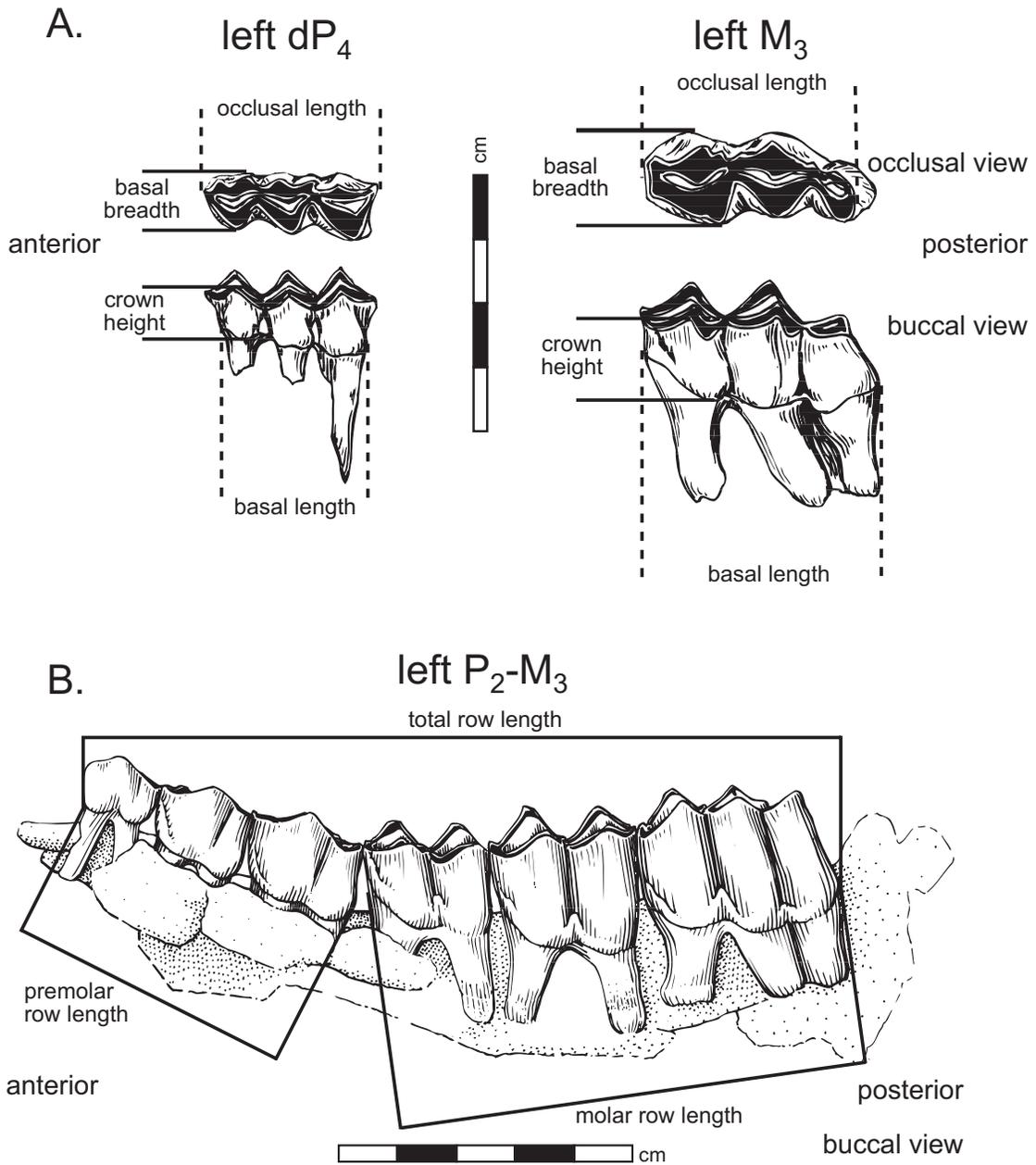
**Figure 2.1 Global distribution of *C. elaphus***

The darkened areas of the map show the global distribution of *C. elaphus*, including extinct and introduced populations. Map is modified from Bryant and Maser (1982:15).

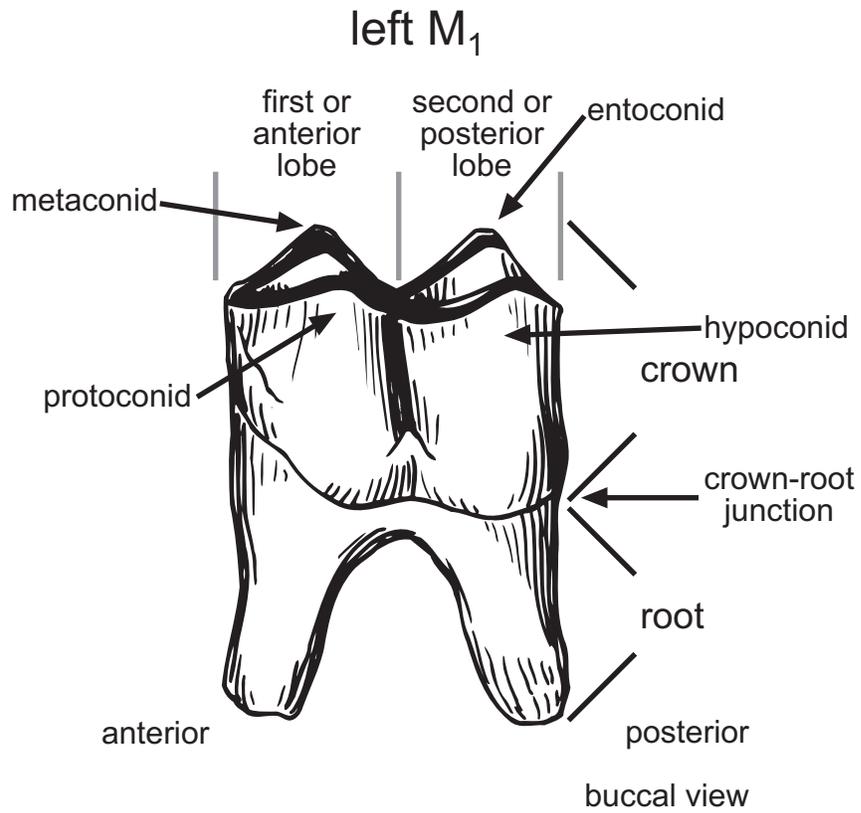


**Figure 3.1 Map of fossil sites included in this study**

Appendices C and D provide detailed information about each site. Map is courtesy of R. G. Klein.

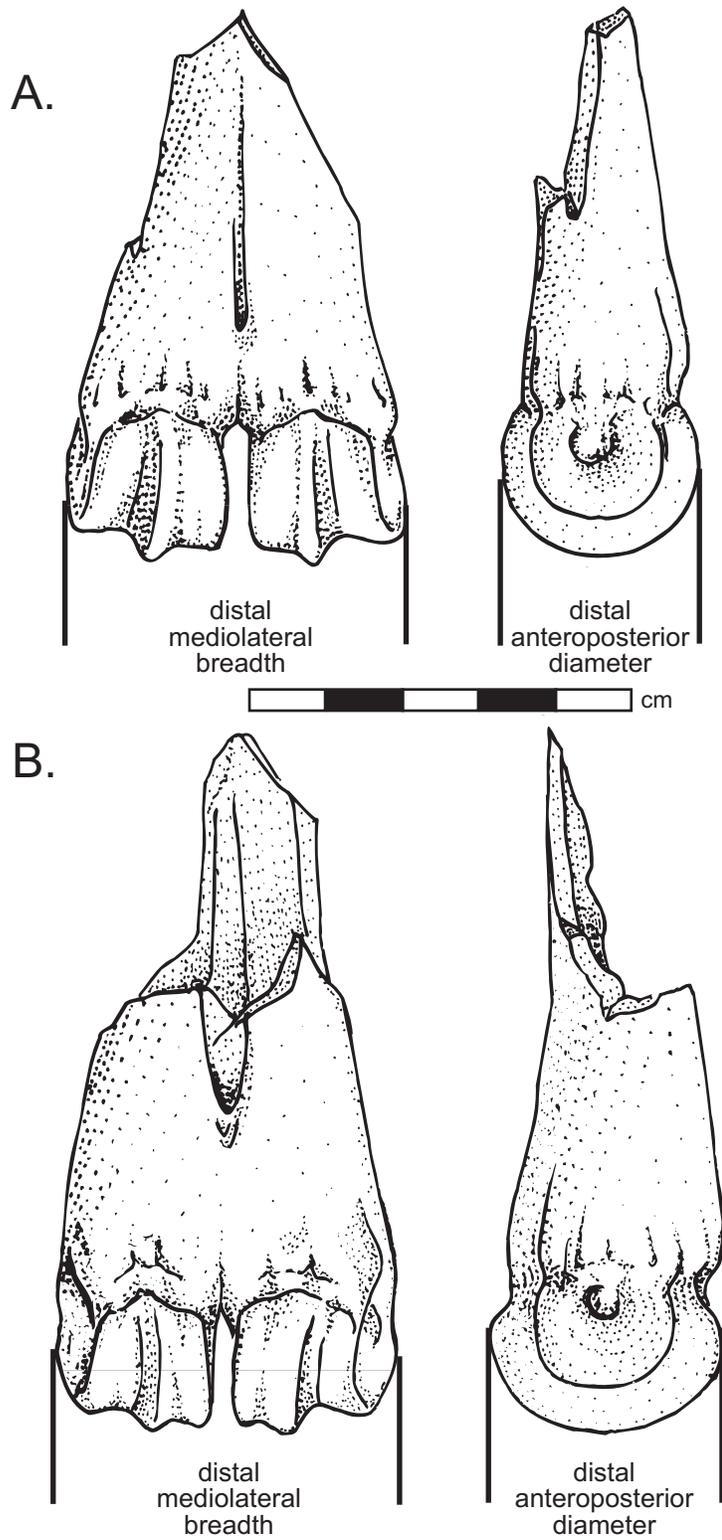


**Figure 3.2 Dental measurements used in this study**  
 Measurements taken on *C. elaphus* teeth (A) and mandibles (B) following Klein and Cruz-Urbe (1984:46-47) and von den Driesch (1976:56). Drawings are courtesy of R. G. Klein.



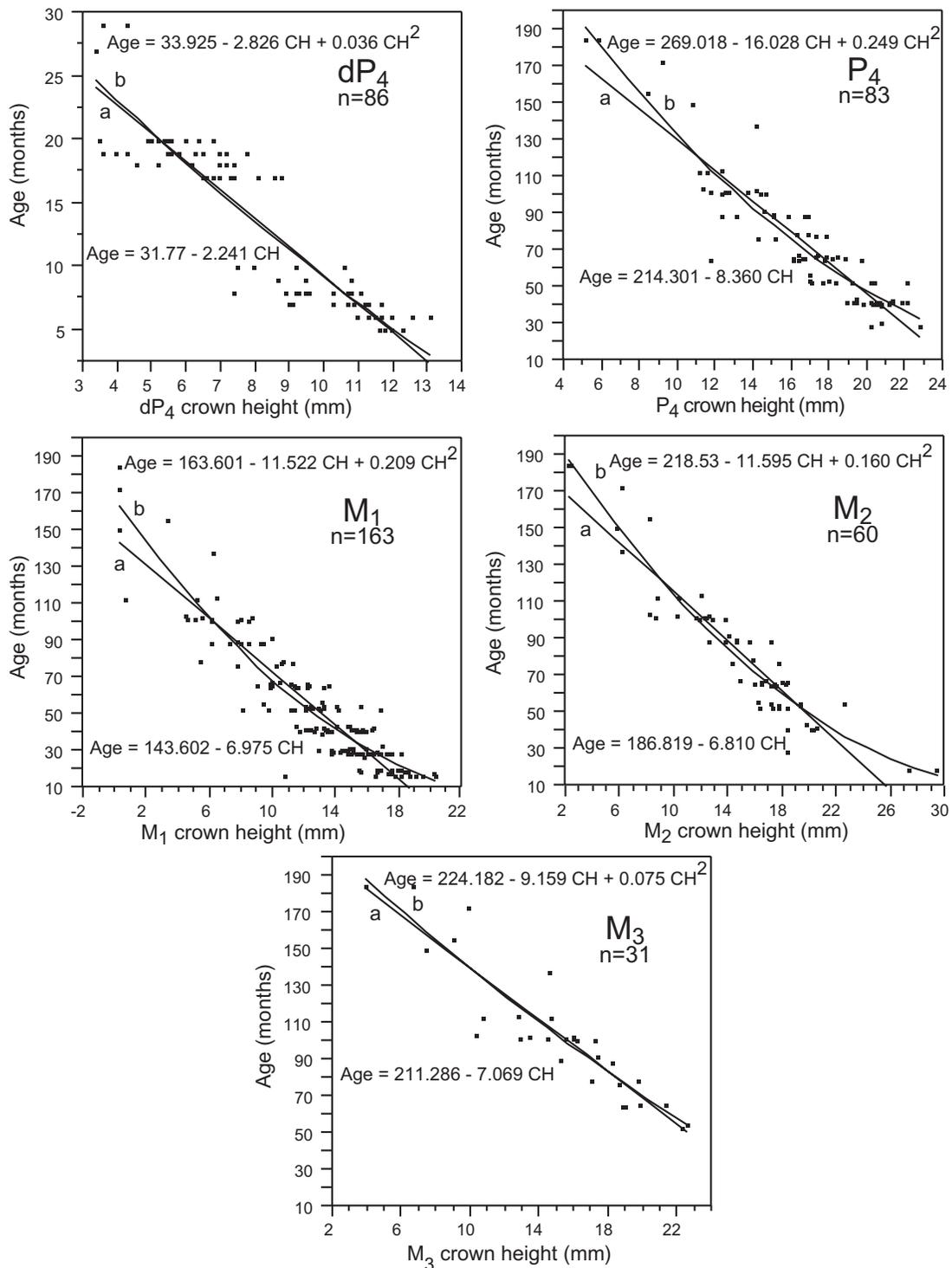
**Figure 3.3 *C. elaphus* tooth nomenclature**

The *C. elaphus* tooth nomenclature used in this study. Based on Lister (1981:Figure 2.2). Drawing is courtesy of R. G. Klein.



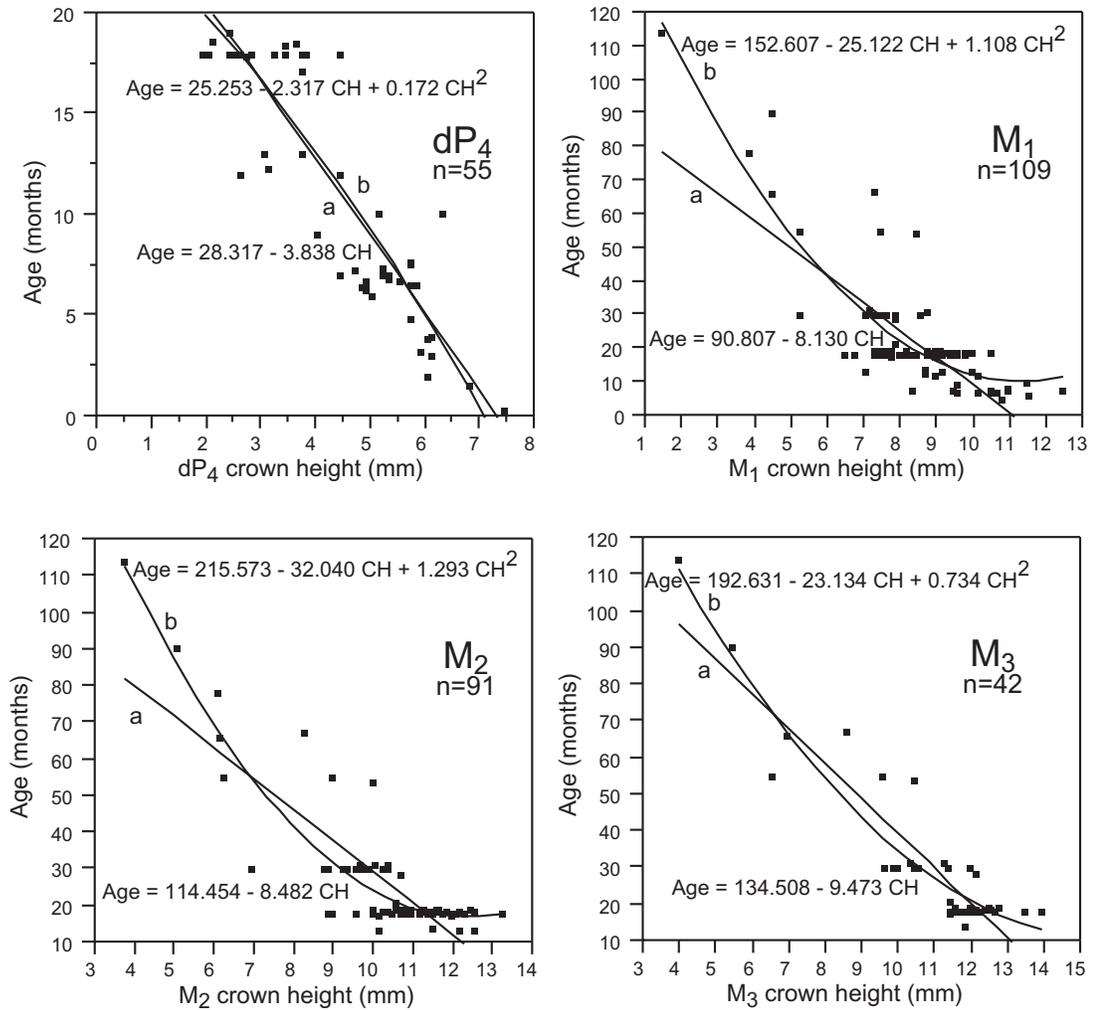
**Figure 3.4 Postcranial measurements used in this study**

Measurements taken on *C. elaphus* distal metacarpals (A) and metatarsals (B) following Klein and Cruz-Urbe (1984:20) and von den Driesch (1976:92). Drawings are courtesy of R. G. Klein.



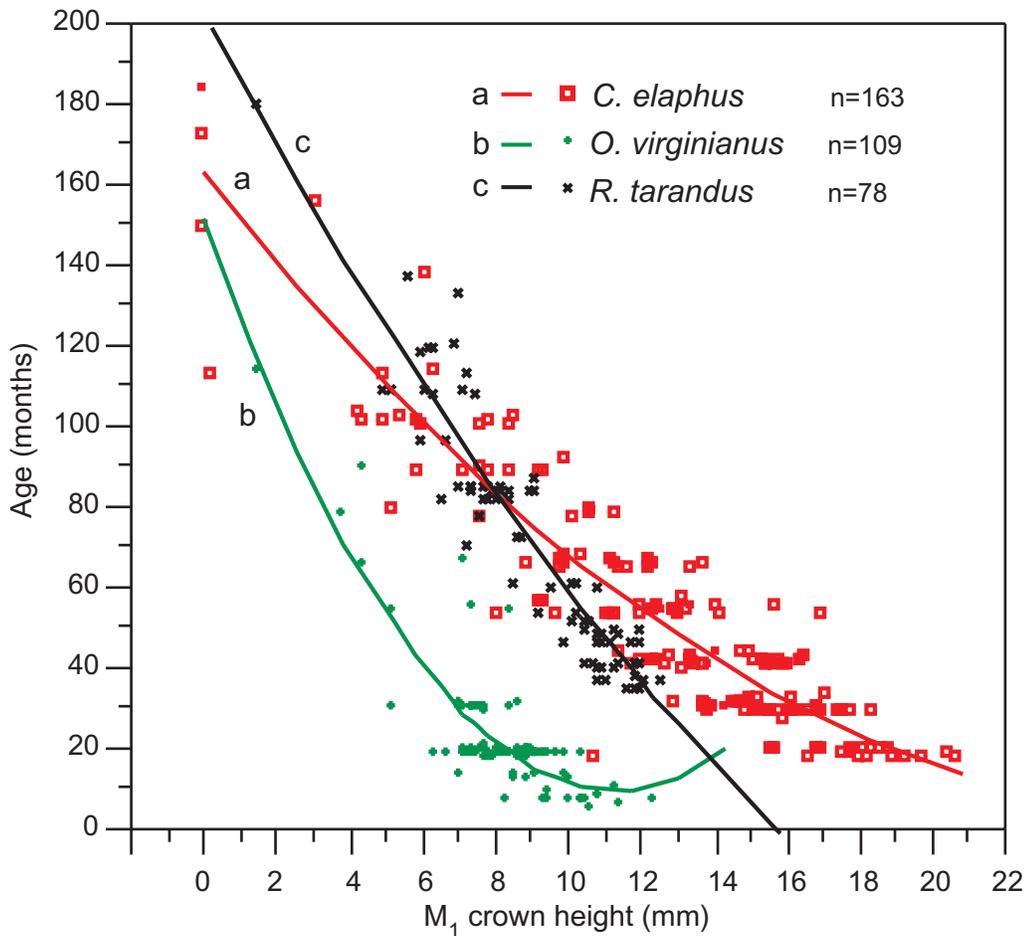
**Figure 4.1 Regression of age on crown height for elk**

Linear (a) and quadratic (b) regressions of age on crown height for the known-age sample of elk. Summary statistics are in Table 4.2. R. G. Klein provided some of these data as indicated in Table 4.1.



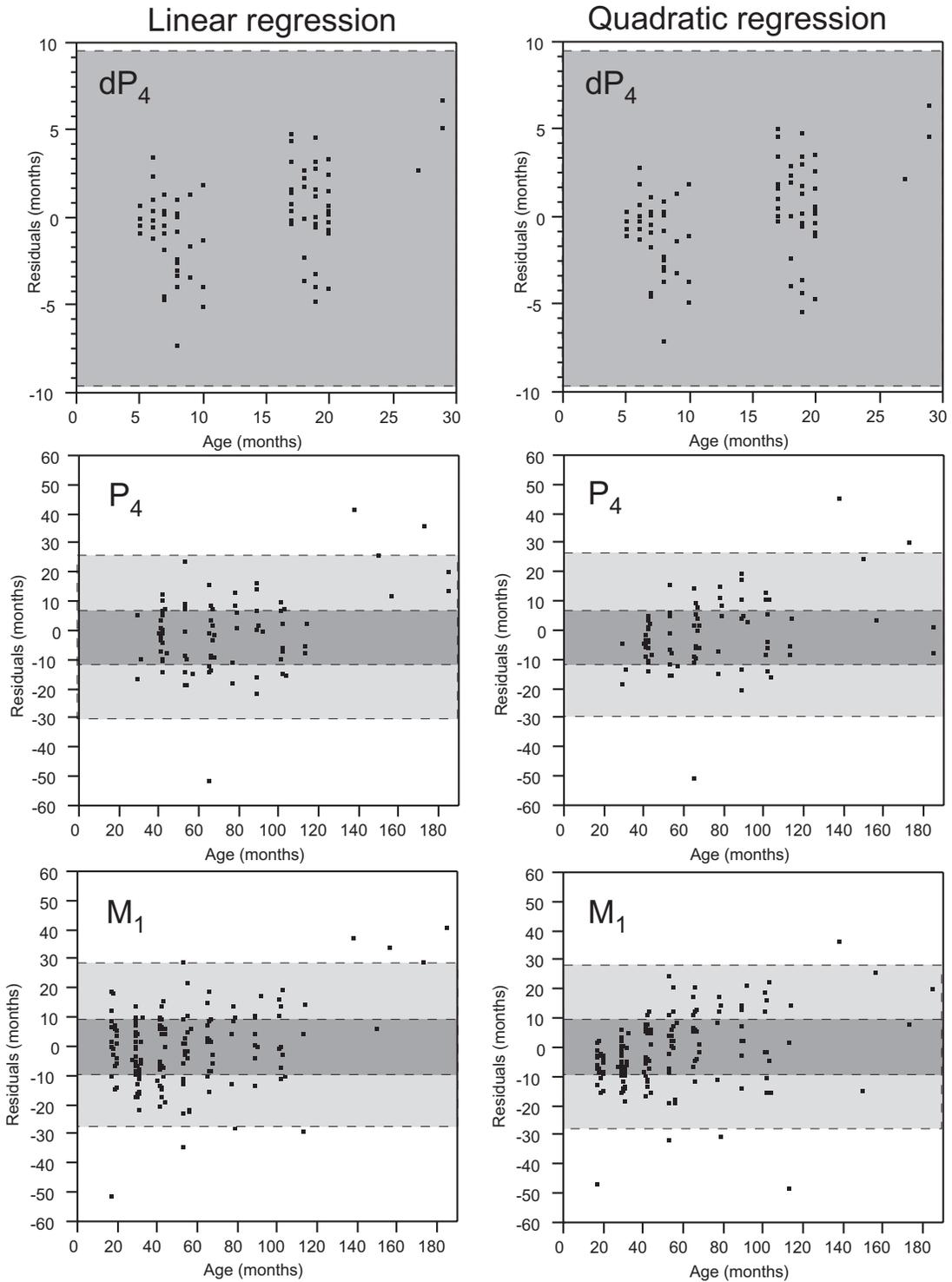
**Figure 4.2 Regression of age on crown height for white-tailed deer**

Linear (a) and quadratic (b) regressions of age on crown height for a known-age sample of white-tailed deer. Summary statistics are in Table 4.3. Data were collected by C. Wolf and provided by R. G. Klein.



|                       |   |
|-----------------------|---|
| <i>C. elaphus</i>     | Age = 163.601 - 11.522 M <sub>1</sub> CH + 0.209 M <sub>1</sub> CH <sup>2</sup> |
| <i>O. virginianus</i> | Age = 152.607 - 25.122 M <sub>1</sub> CH + 1.108 M <sub>1</sub> CH <sup>2</sup> |
| <i>R. tarandus</i>    | Age = 204.746 - 17.056 M <sub>1</sub> CH + 0.263 M <sub>1</sub> CH <sup>2</sup> |

**Figure 4.3 Comparison of wear rates between elk, white-tailed deer, and reindeer**  
 Quadratic regressions of age in months on M<sub>1</sub> crown height for three species: *C. elaphus* (a), *O. virginianus* (b), and *R. tarandus* (c). *C. elaphus* data are from Klein *et al.* (1983) and this study, white-tailed deer data are unpublished data collected by C. Wolf, and *R. tarandus* data are from Morrison and Whitridge (1997:1105-6).



**Figure 4.4 Residuals of age predictions using the regression equations**

Known age plotted against known age minus the age estimated from the linear (left) and quadratic (right) regressions shown in Figure 4.1 for elk. Age was estimated correctly for the specimens that have a residual of '0'. The darkly shaded regions approximate  $\pm 9.6$  months (one 10% of life span age class), while the lightly shaded regions approximate the adjacent 10% of life span age classes.

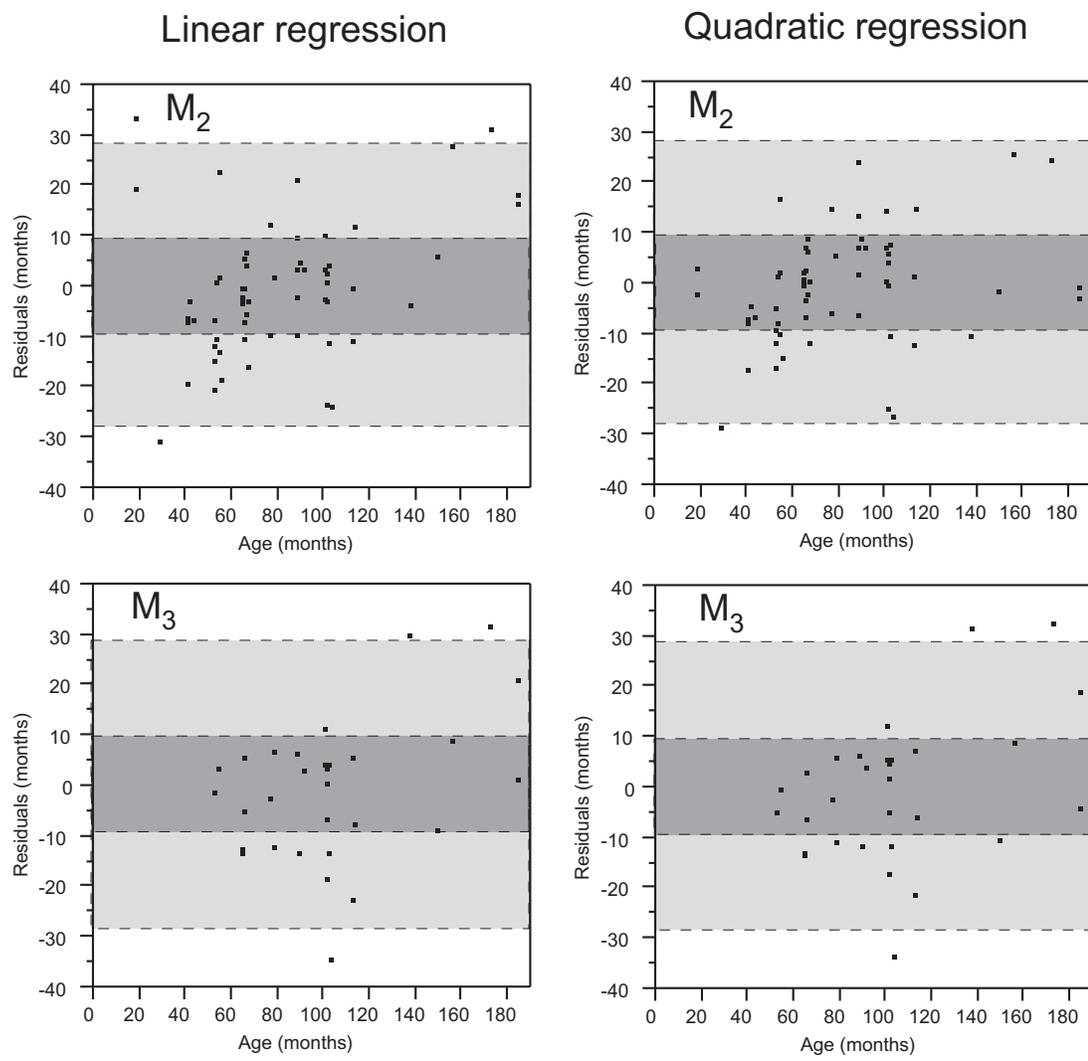
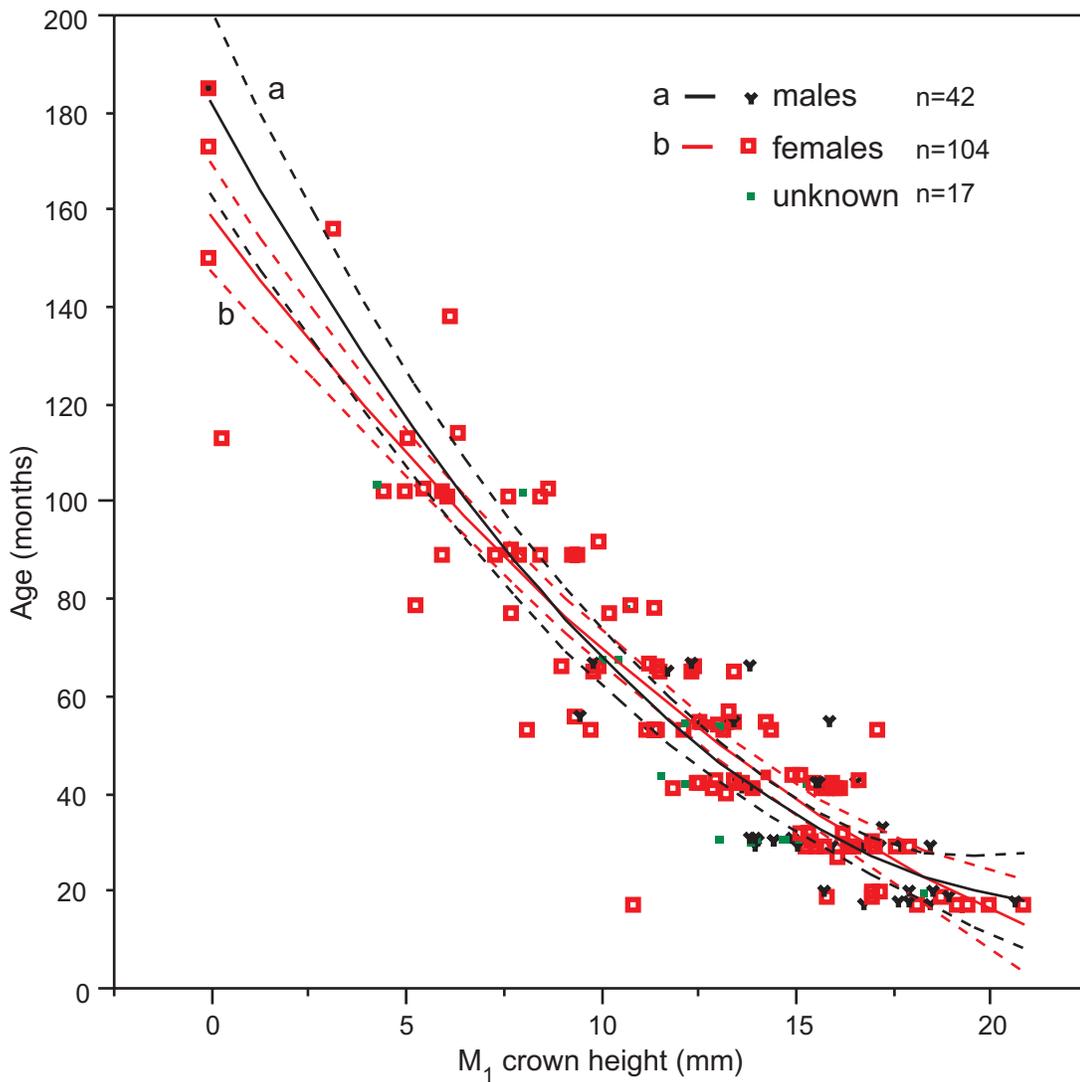


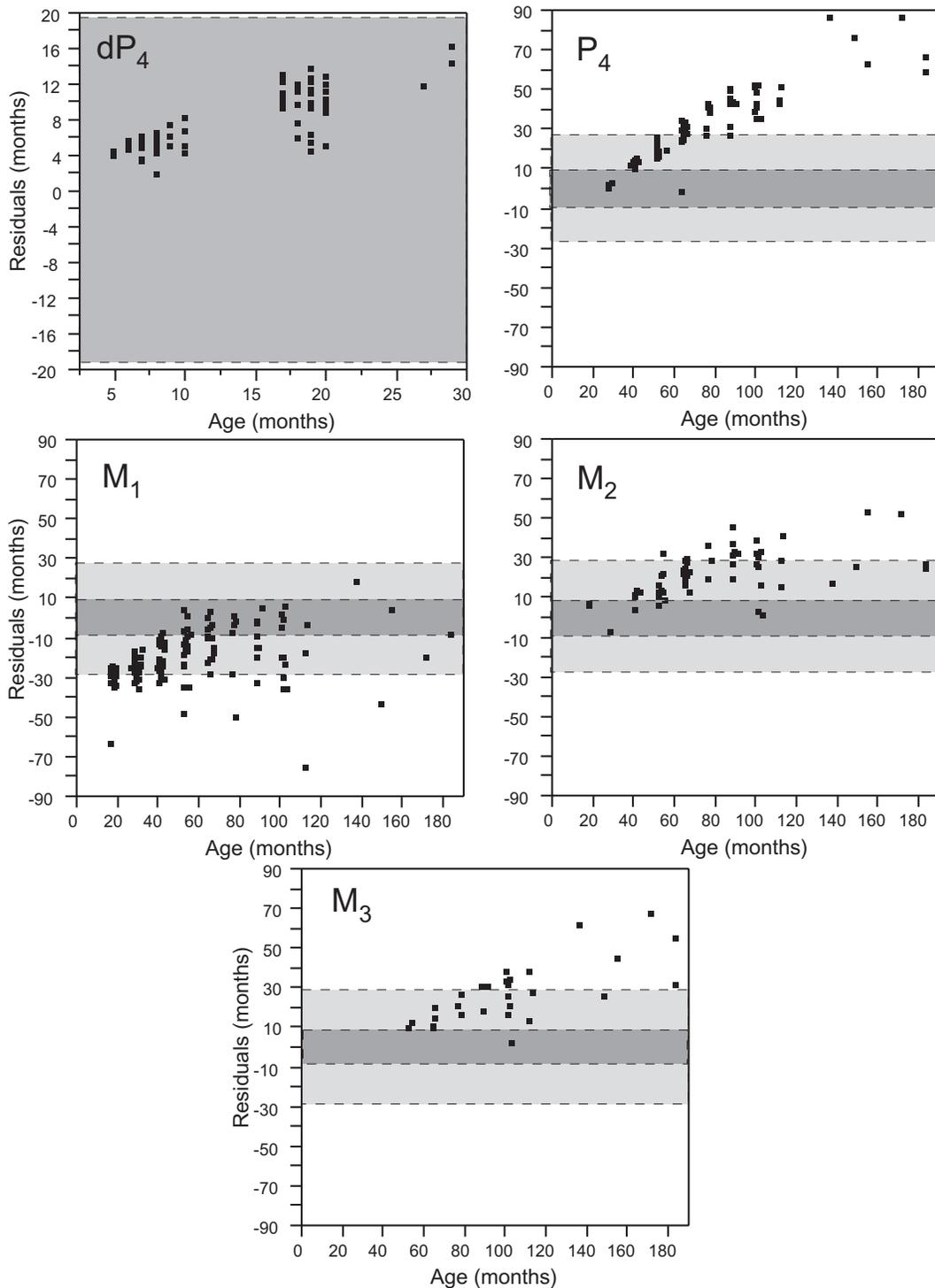
Figure 4.4 con't



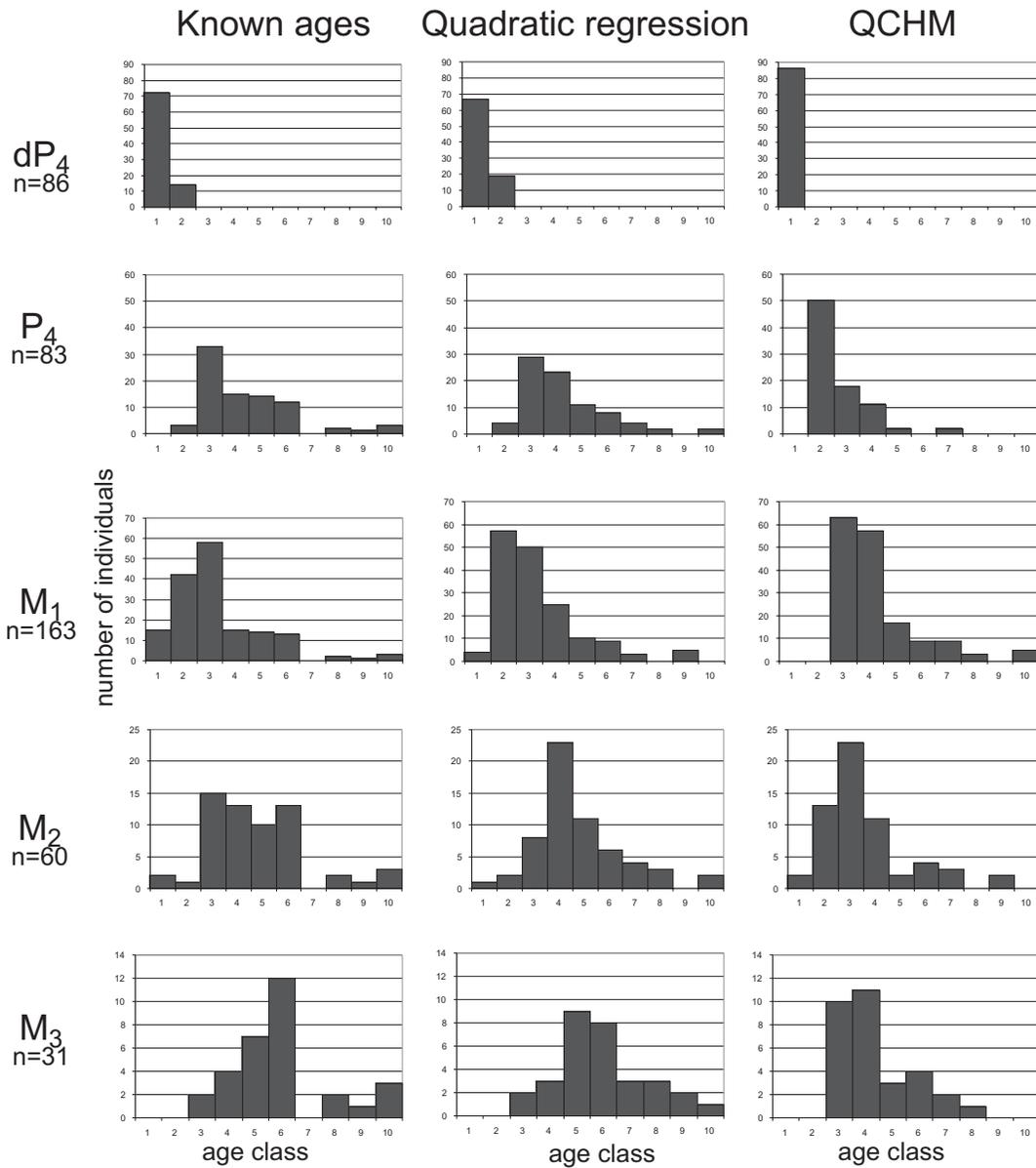
Females      Age = 159.158 - 10.589 M<sub>1</sub> CH + 0.172 M<sub>1</sub> CH<sup>2</sup>  
 Males         Age = 182.649 - 14.607 M<sub>1</sub> CH + 0.322 M<sub>1</sub> CH<sup>2</sup>

**Figure 4.5 Differences in wear rates between male and female elk**

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



**Figure 4.6 Residuals of ages predicted using the Quadratic Crown Height Method**  
 Known age plotted against known age minus the age estimated from the theoretical formulas (listed in Table 4.5) for the known-age elk sample. The darkly shaded regions approximate  $\pm 9.6$  months (one 10% of life span age class), while the lightly shaded regions approximate the adjacent 10% of life span age classes.



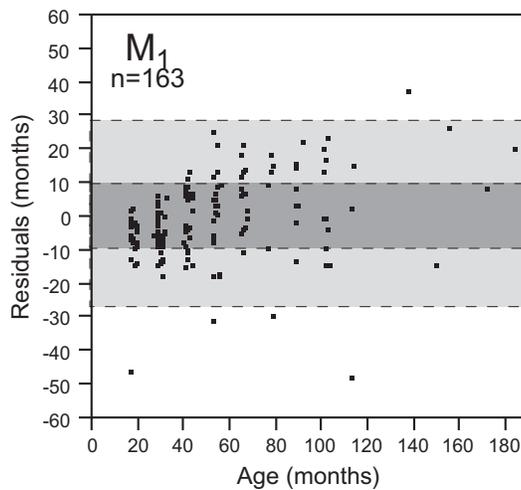
Results of the Kolmogorov-Smirnov test comparing known ages to estimated ages.

| Method               | $dP_4$ | $P_4$  | $M_1$  | $M_2$ | $M_3$ |                |
|----------------------|--------|--------|--------|-------|-------|----------------|
| Quadratic regression | 0.38   | 0.39   | 0.61   | 0.64  | 0.38  | * $p < 0.01$   |
| QCHM                 | 1.07   | **3.65 | **3.16 | *1.83 | *1.91 | ** $p < 0.001$ |

**Figure 4.7 Comparisons of the two age estimation methods**

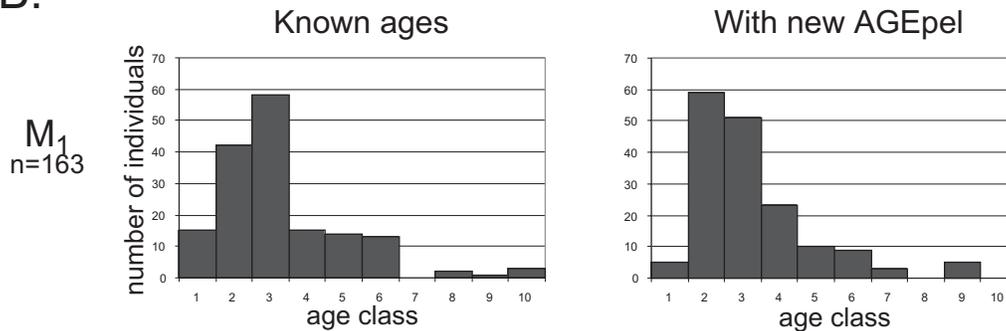
Histograms comparing the number of individuals in each age class for each tooth type. Age classes were assigned for the elk sample using known ages (left), the quadratic regression formula (center), and the theoretical formulas of the Quadratic Crown Height Method (right). The Kolmogorov-Smirnov test was used to see if the distributions created from the estimation techniques were similar to the known ages. The formulas used here are listed in Table 4.5.

A.



$$\text{Age} = 163.6 - 11.674 M_1 \text{ CH} + 0.216 M_1 \text{ CH}^2$$

B.

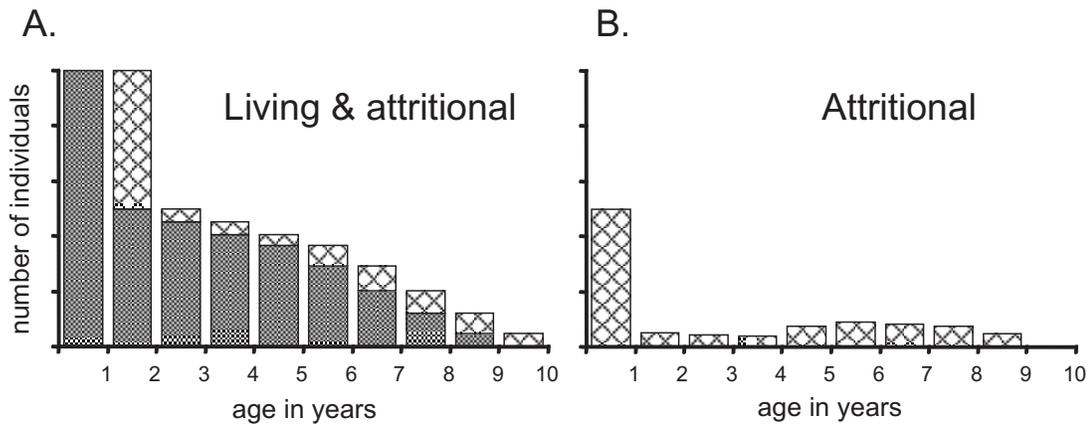


Results of the Kolmogorov-Smirnov test comparing known ages to estimated ages.

| Method               | $M_1$  |              |
|----------------------|--------|--------------|
| Quadratic regression | 0.61   | ** p < 0.001 |
| QCHM                 | **3.16 |              |
| With new AGEpel      | 0.56   |              |

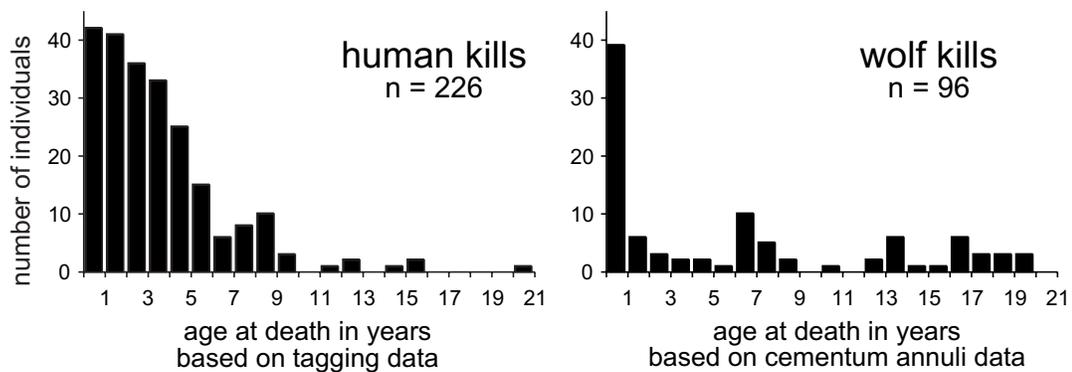
#### Figure 4.8 Adjusted method for estimating age from $M_1$ s

(A) Known age plotted against known age minus the age estimated for  $M_1$ s in the known-age elk sample. Age was estimated using the Quadratic Crown Height Method where the y-intercept value of the regression equation was substituted for AGEpel, because  $M_1$  crown height could reach '0' before the animal dies. The y-intercept value predicts the age at which  $M_1$  crown height will reach '0', here 163.6 months. The resulting equation used to estimate age is shown. The darkly shaded region approximates  $\pm 9.6$  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. (B) Histograms comparing the number of individuals in each age class for  $M_1$  as calculated from the known ages and from the modified quadratic crown height equation. When age classes are calculated using the potential longevity of the tooth not of individuals of the species, the histogram does not differ significantly from the histogram based on known ages.



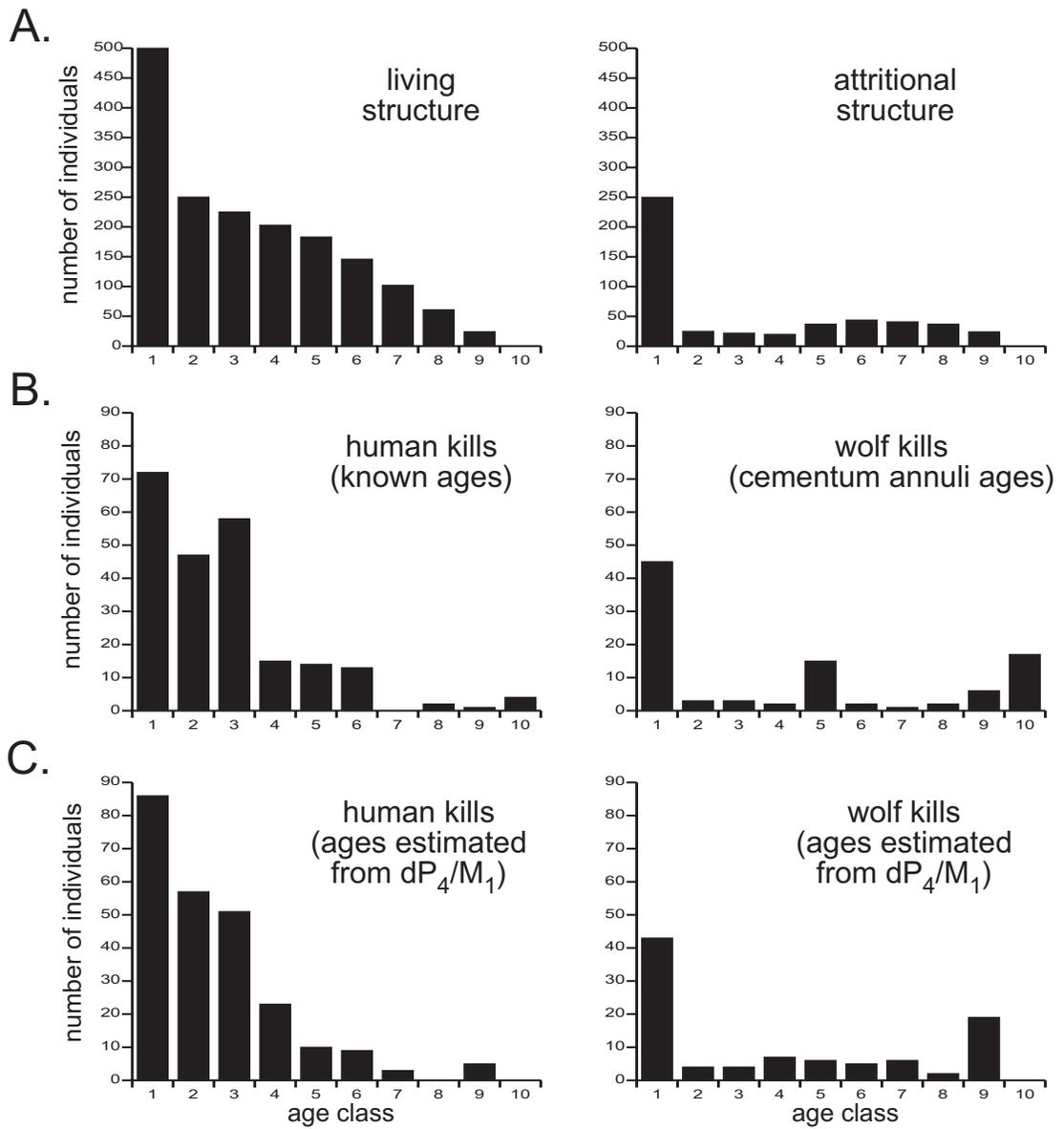
**Figure 5.1 Model age structures**

Theoretical living (left) and attritional (right) age structures for a population of large mammals that gives birth to one offspring per year and is not changing in population size. The dark bars refer to the number of individuals in each age class in a living herd. The hatched bars represent the number of individuals that died in between each age class, the attrition on the herd. The hatched bars correspond directly between the two histograms. These theoretical structures provide guidelines for comparisons of mortality profiles constructed from a faunal assemblage. Taken from Klein (1982:51) and Voorhies (1969). See Table 5.1 for data and more details.



**Figure 5.2 Differences in prey age-at-death between human and wolf hunters**

Histograms showing the differences in the ages of the animals killed by human and wolf hunters. The mortality profile of the human kills more closely resembles the model living structure in Figure 5.1.A, while the profile of the wolf kills resembles the attritional structure in Figure 5.1.B. The human kill ages are based on ear tags of animals that were marked shortly after birth, and the wolf kill ages are based on cementum annuli counts of incisors from the dead animals. D. Smith provided the cementum annuli ages of the wolf kills.



Age estimated for  $dP_4$  using:  $\text{Age} = 26 - 3.714 dP_4 \text{ CH} + 0.133 dP_4 \text{ CH}^2$   
 Age estimated for  $M_1$  using:  $\text{Age} = 163.6 - 11.674 M_1 \text{ CH} + 0.216 M_1 \text{ CH}^2$

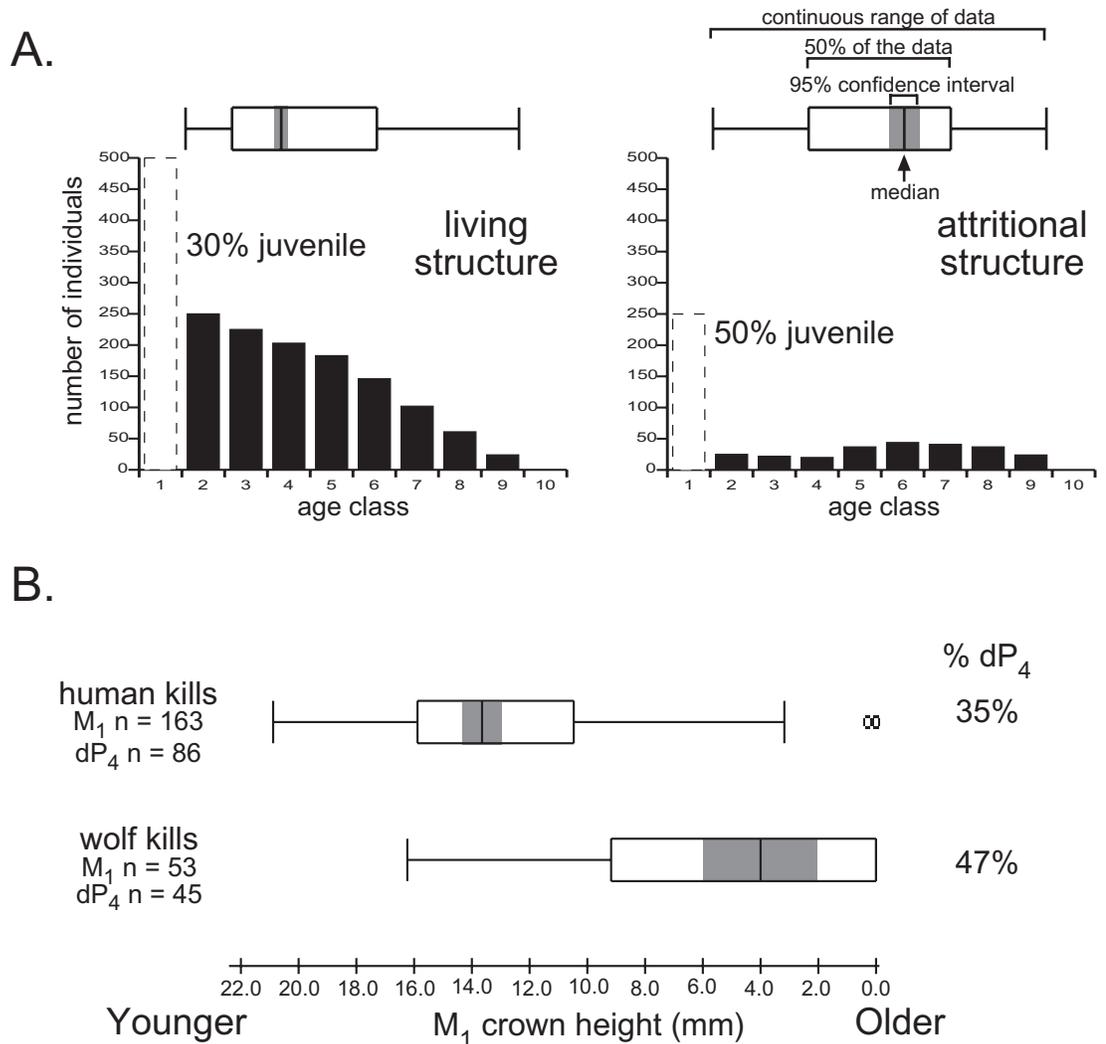
Results of the Kolmogorov-Smirnov test comparing mortality distributions.

|                  | living | attritional | human known | human $dP_4/M_1$ | wolf c.a. ages |
|------------------|--------|-------------|-------------|------------------|----------------|
| human known      | 2.93** | 2.69**      |             |                  |                |
| human $dP_4/M_1$ | 3.21** | 3.27**      | 0.64        |                  |                |
| wolf c.a. ages   | 2.15** | 1.72*       | 2.44**      | 2.80**           |                |
| wolf $dP_4/M_1$  | 1.75*  | 1.35        | 2.07**      | 2.37**           | 1.23           |

\*  $p < 0.01$   
 \*\*  $p < 0.001$

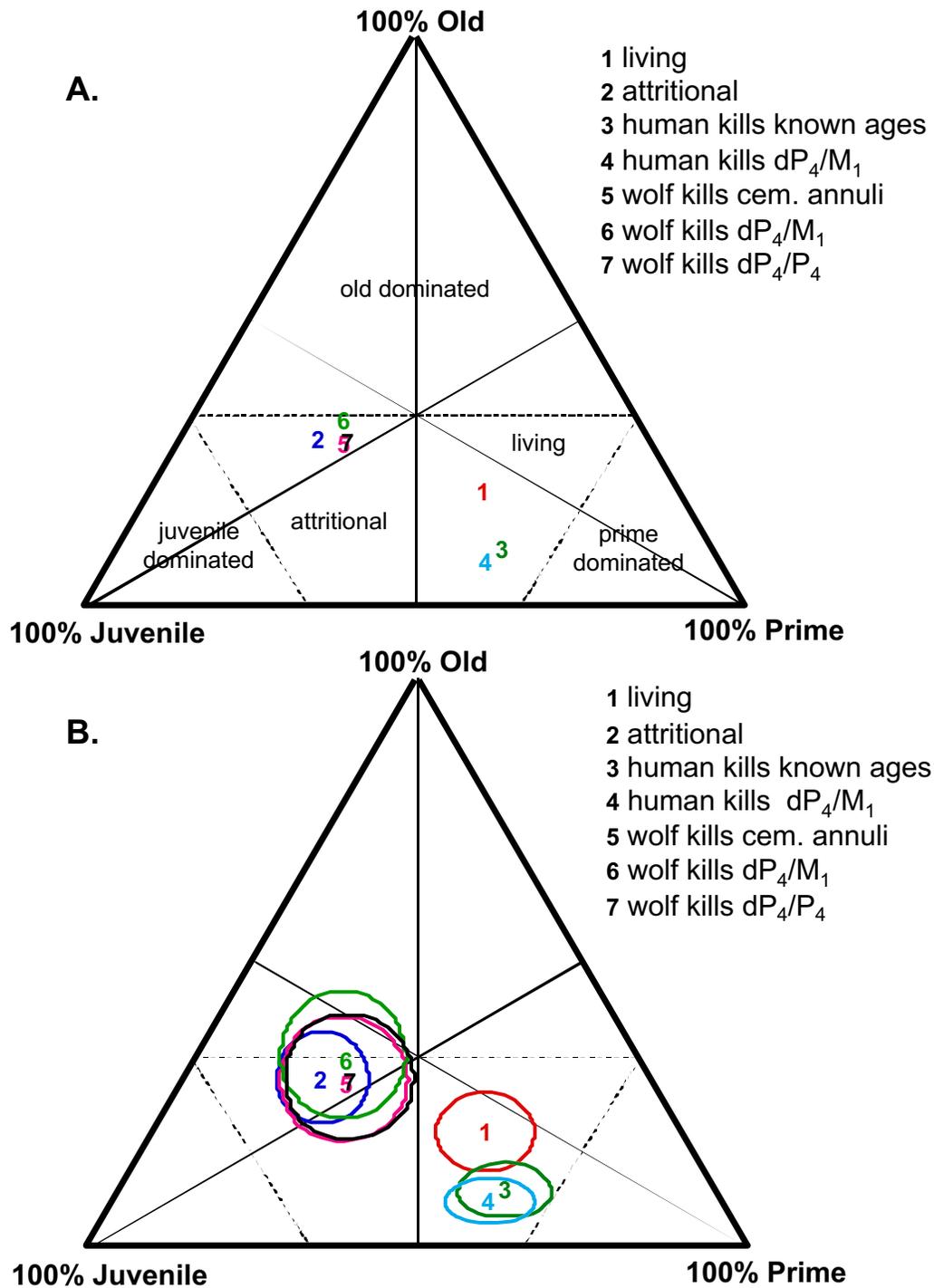
**Figure 5.3 First method: Histograms**

Mortality distributions shown as histograms. Histograms were created from a model life table (A, Table 5.1), known ages for two elk samples (B), and estimated ages for the same two samples (C).



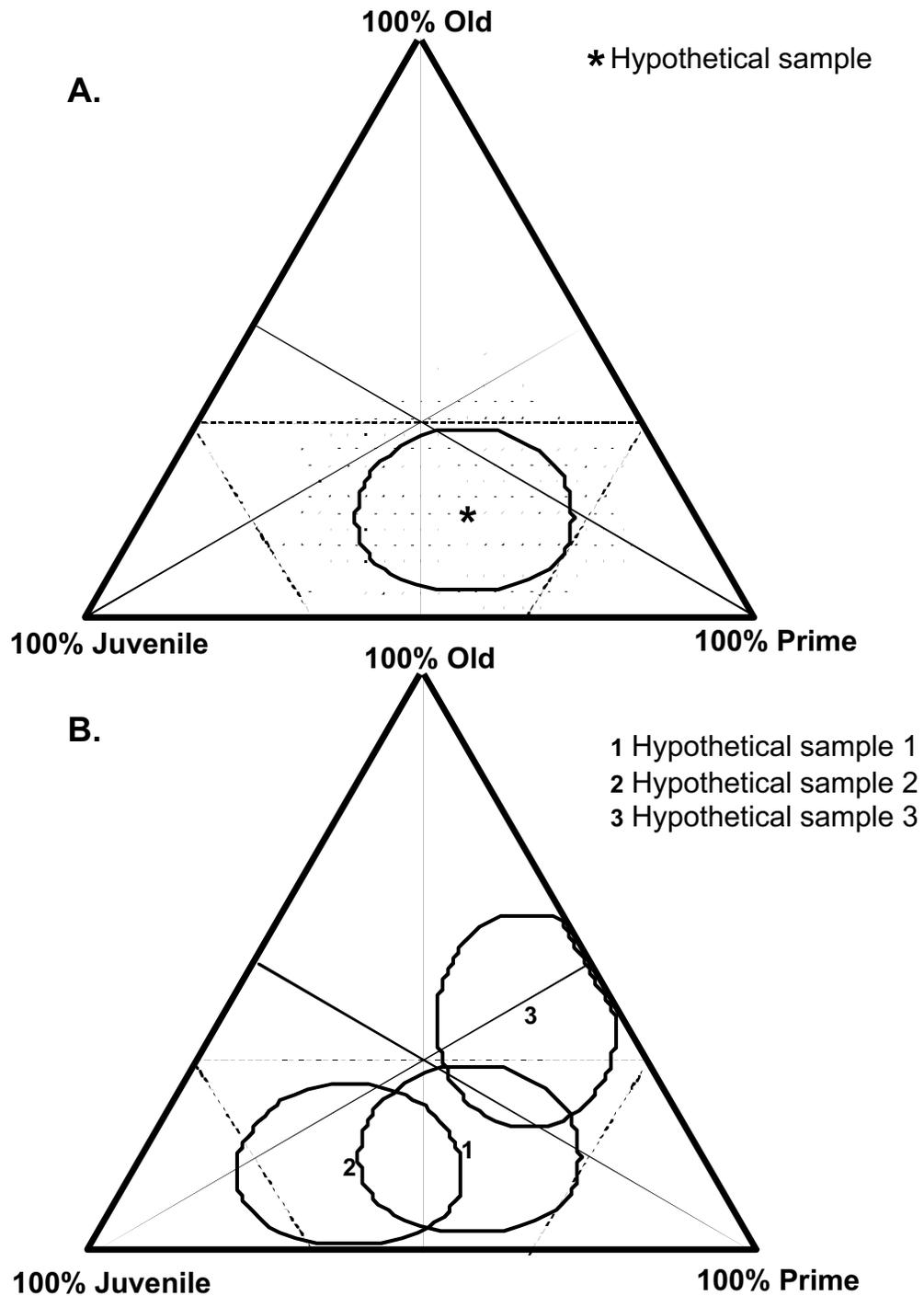
**Figure 5.4 Second method: Boxplots**

(A) The model histograms are the same as in Figure 5.3.A, and the adults from the “samples” are translated into boxplots above them. The juveniles are represented as percentages and as dashed bars in the histograms. The boxplots show the higher number of old individuals in the attritional model than in the living age structure model (after Klein and Cruz-Urbe 1996a:323). (B) The boxplots show the median  $M_1$  crown height for the wolf- and human-killed samples. Because the shaded areas do not overlap, the two medians are significantly different. The wolf-kill sample has many more heavily worn teeth, and, therefore contains more old individuals than the human-kill sample. The percentages of juveniles are shown as the percentages of  $dP_4$ s.



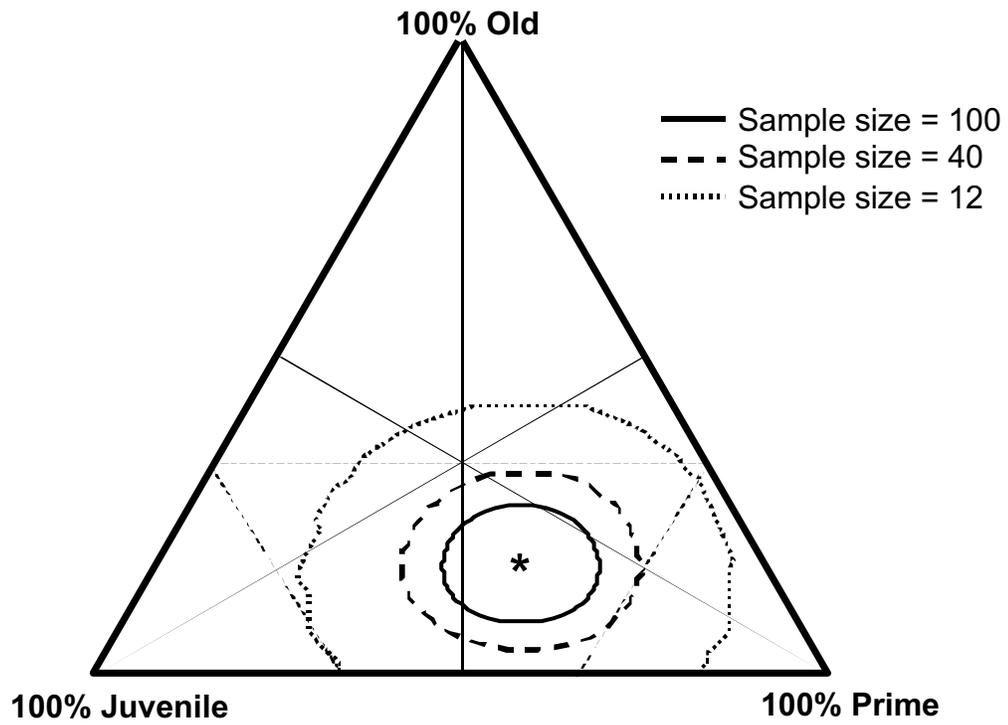
**Figure 5.5 Third method: Triangular graphs**

(A) The human and wolf-kill samples and model profiles plotted on a triangular graph following Stiner (1990). (B) The same samples plotted on a modified triangular graph following Steele and Weaver (2002). The ovals can be interpreted as 95% confidence intervals around the points.



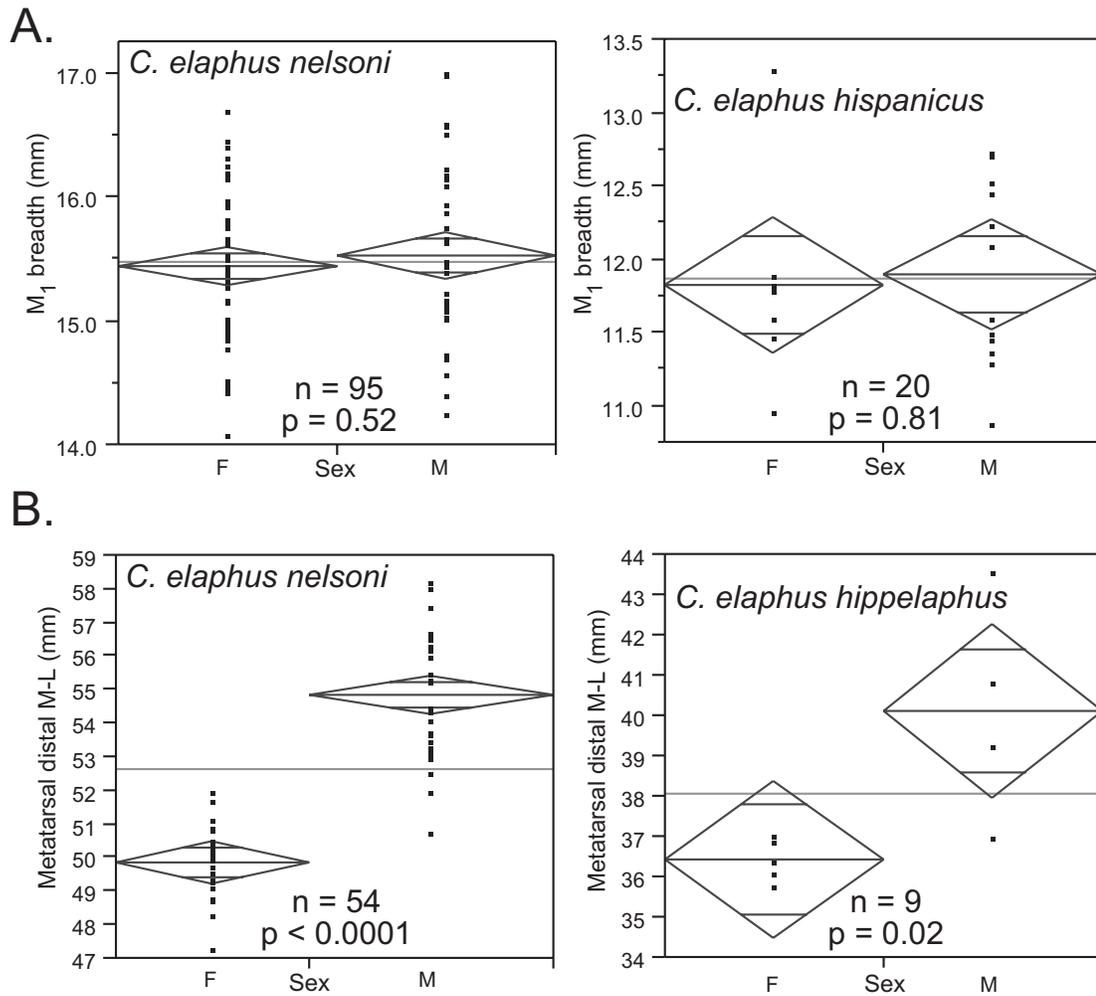
**Figure 5.6 Modified triangular graphs**

(A) A modified triangular graph showing the distribution of the 10,000 re-samples and the 95% density contour for a hypothetical sample. (B) A modified triangular graph with the 95% density contours for three hypothetical samples. Although each sample plots within a different zone on the graph, and therefore should have different age structures, not all the samples can be separated.



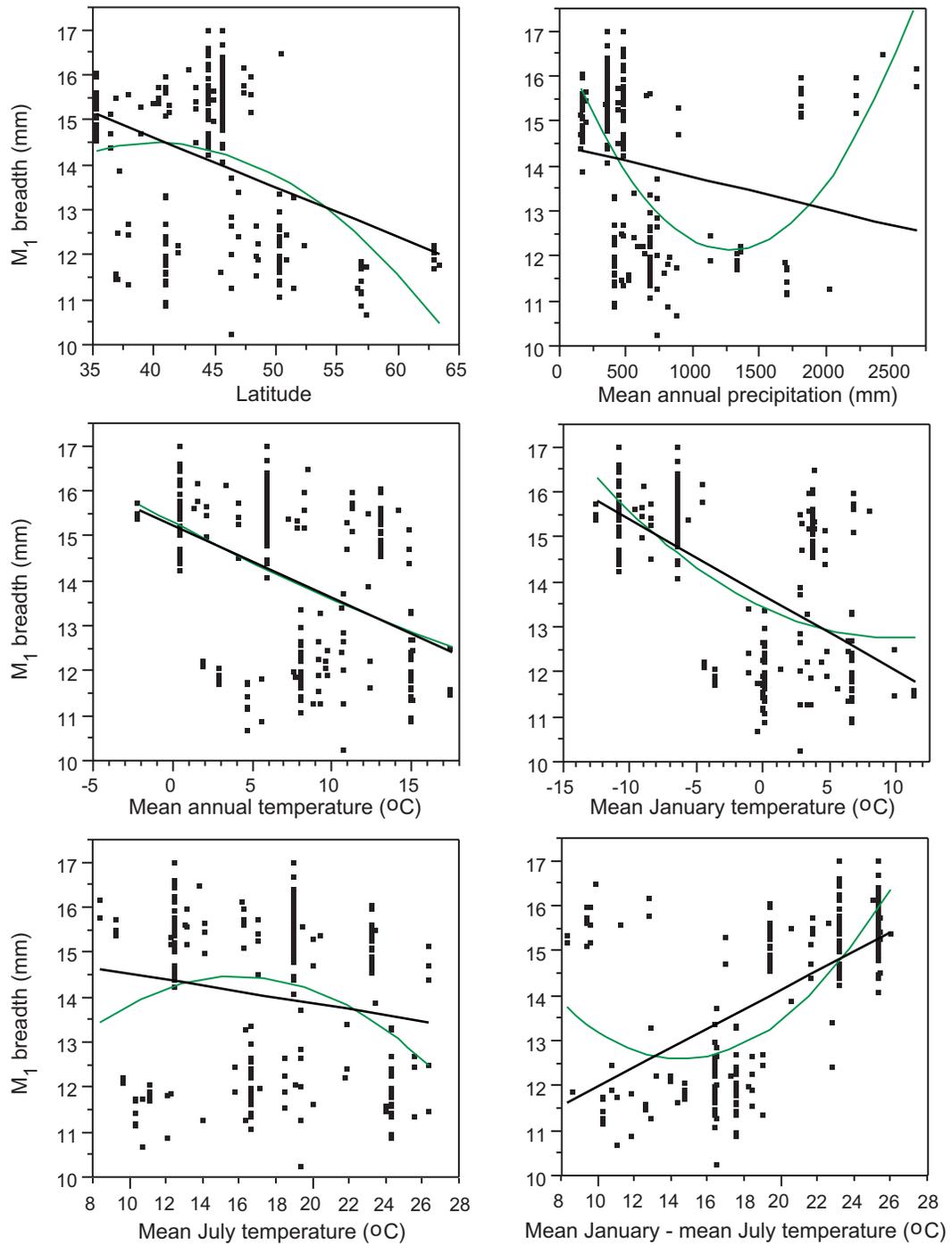
**Figure 5.7 The effects of sample size in modified triangular graphs**

A modified triangular graph demonstrating the effects of sample size on the ability to distinguish age structures, because the 95% density contours increase with smaller sample sizes. The percentages of each age class remained the same and only the total sample size changed.



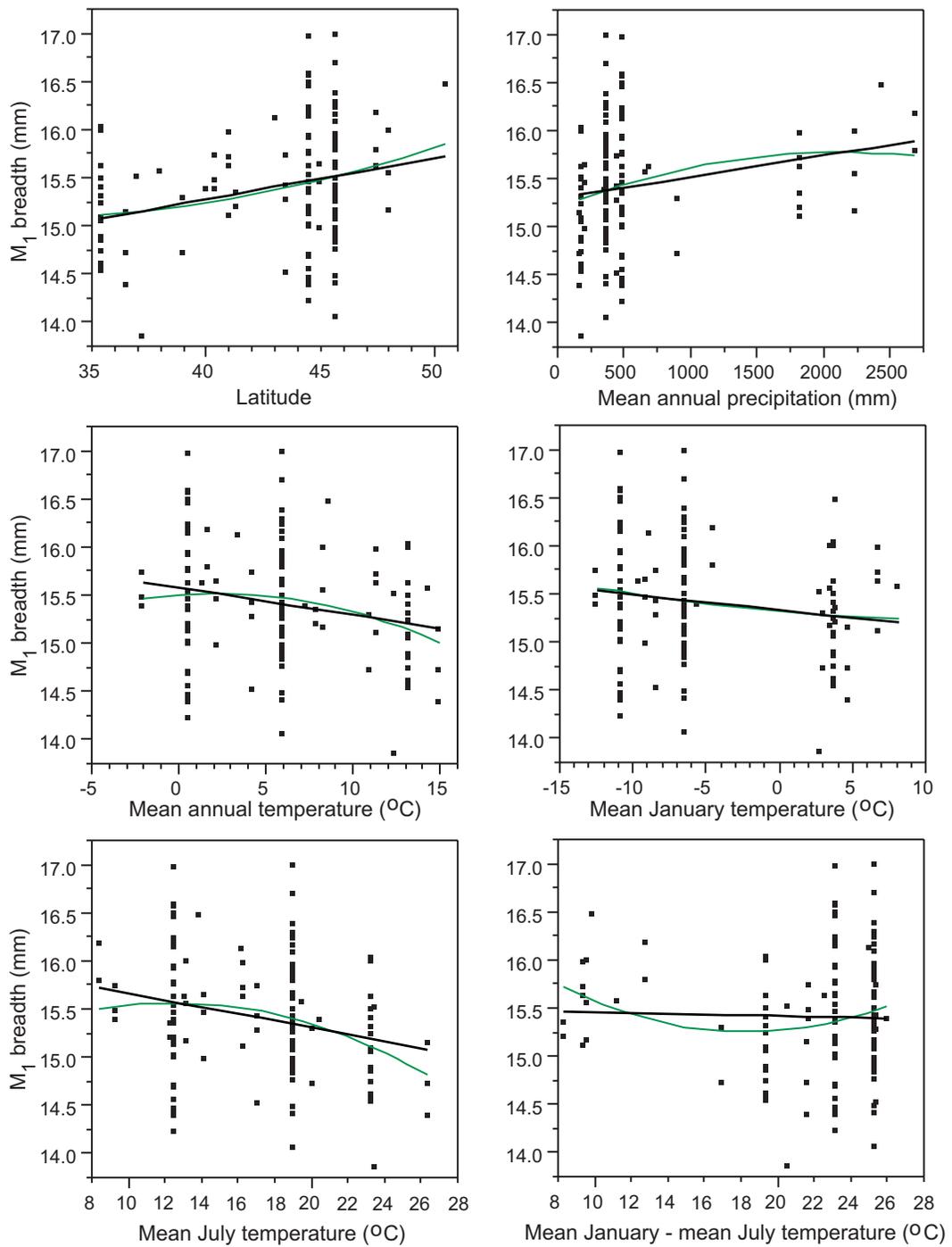
**Figure 6.1 Sexual dimorphism in *C. elaphus***

Graphs showing the difference in sexual dimorphism between two different elements in three subspecies of *C. elaphus*: *C. elaphus nelsoni* (Rocky Mountain elk), *C. elaphus hippelaphus* (western European red deer) and *C. elaphus hispanicus* (Spanish red deer). (A)  $M_1$  breadth by sex. (B) Distal metatarsal breadth by sex. The centers of the diamonds show the mean, and the top and bottom lines show the 95% confidence interval around that mean.

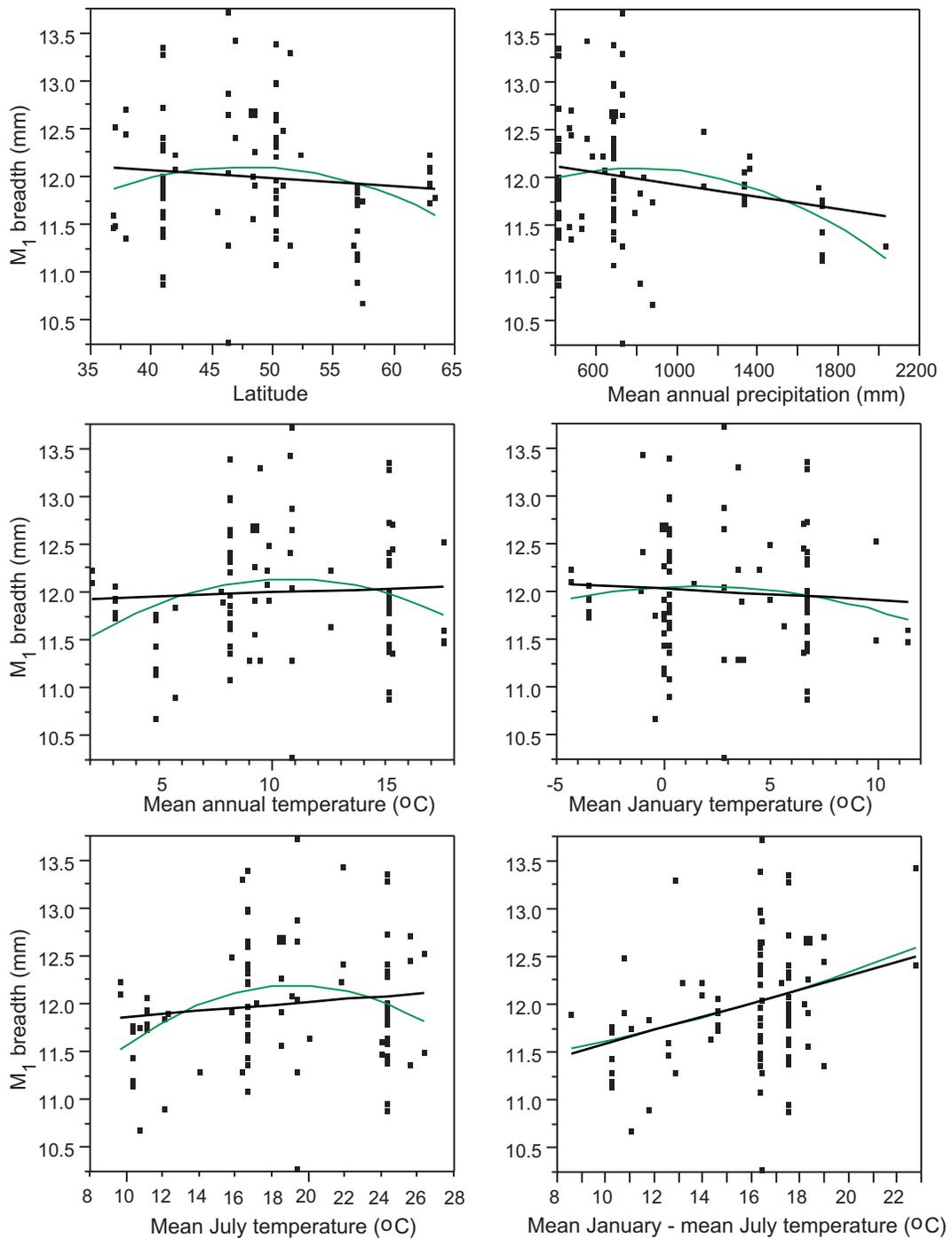


**Figure 6.2** The relationship between  $M_1$  tooth breadth and climatic variables in modern *C. elaphus*

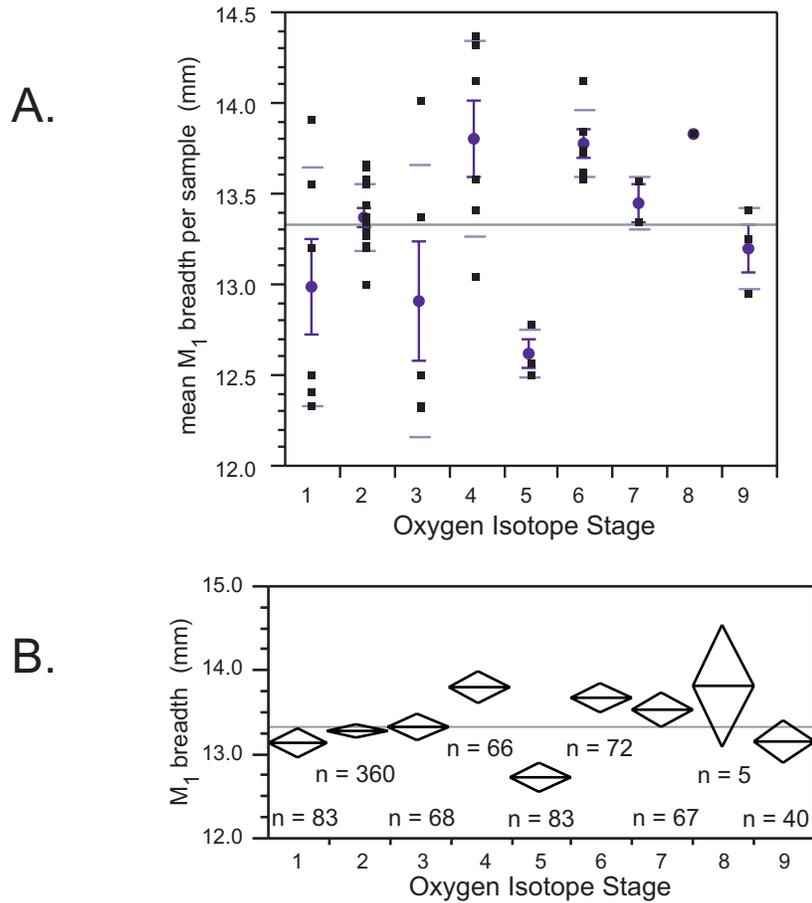
Significance values are provided in Table 6.3. Sample size is 220 in each case. In all plots, the larger specimens are North American elk.



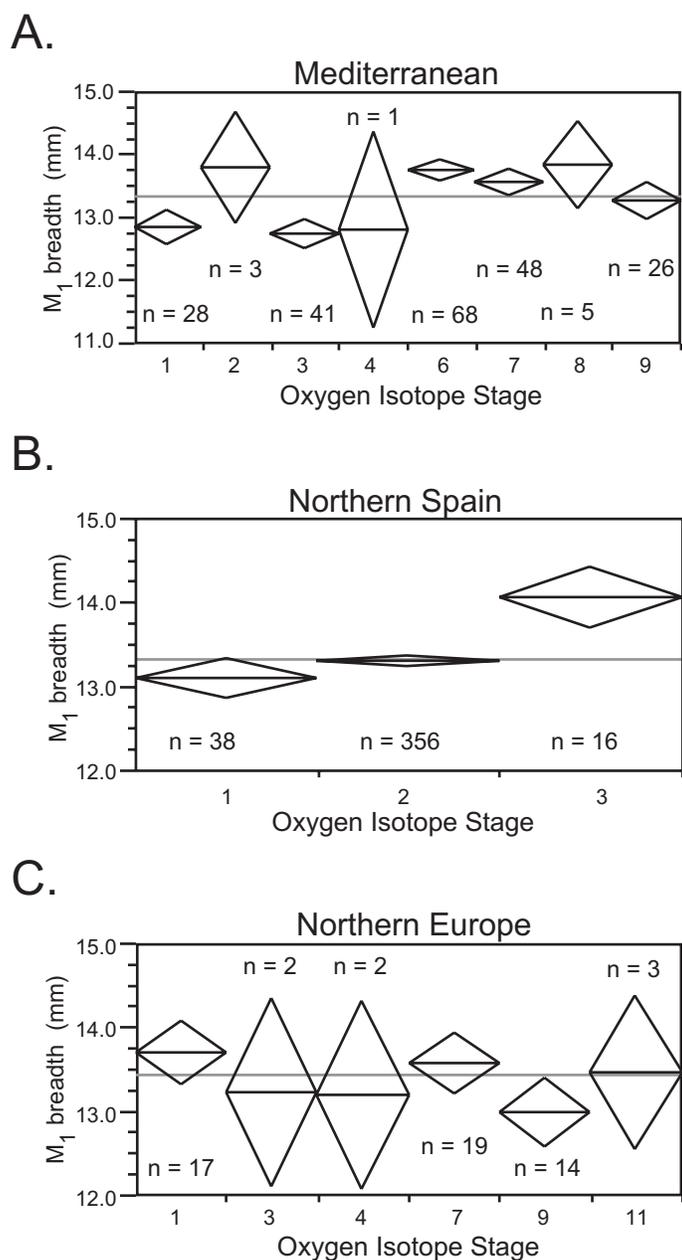
**Figure 6.3** The relationship between  $M_1$  tooth breadth and climatic variables in modern *C. elaphus* from North America  
 Significance values are provided in Table 6.3. Sample size is 131 in each case.



**Figure 6.4** The relationship between  $M_1$  tooth breadth and climatic variables in modern *C. elaphus* from western Europe  
 Significance values are provided in Table 6.3. Sample size is 89 in each case.

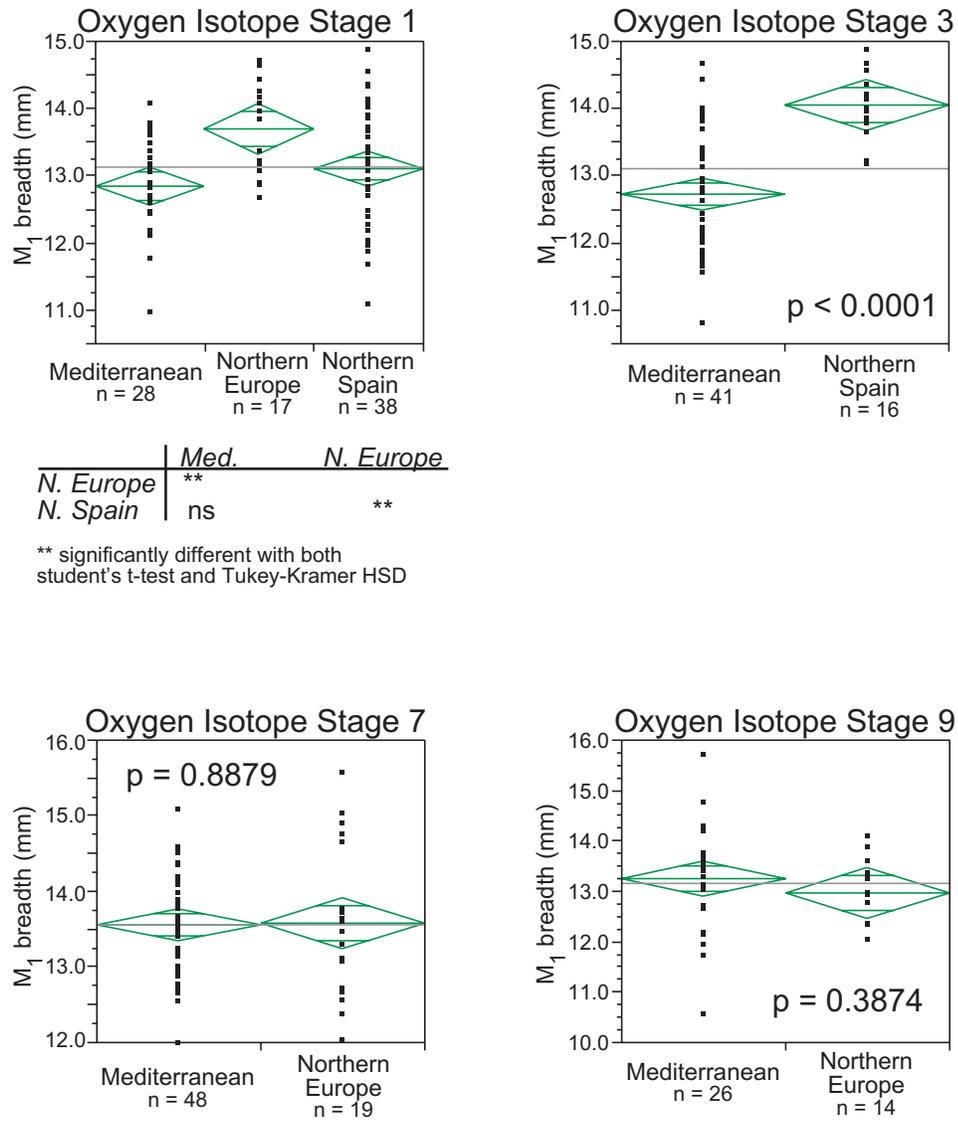


**Figure 6.5 The relationship between tooth breadth and glacial/interglacial climates in fossil red deer**  
 (A) Sample means plotted by Oxygen Isotope Stage (OIS). 45 samples are included. Samples and their sizes, means, standard deviations, and coefficients of variation are listed in Table 6.4. In general, glacial samples (even numbered stages) tend to be larger than the grand mean (shown by the line through the middle of the graph), while interglacial samples are smaller. (B) Individual  $M_1$  breadth plotted by OIS. 852 teeth are included. The central line of the mean's diamond shows the mean of the OIS, and the points of the diamond show the limits of the 95% confidence intervals. Statistical comparisons using the Tukey-Kramer Honestly Significant Difference test are in Table 6.5.A.

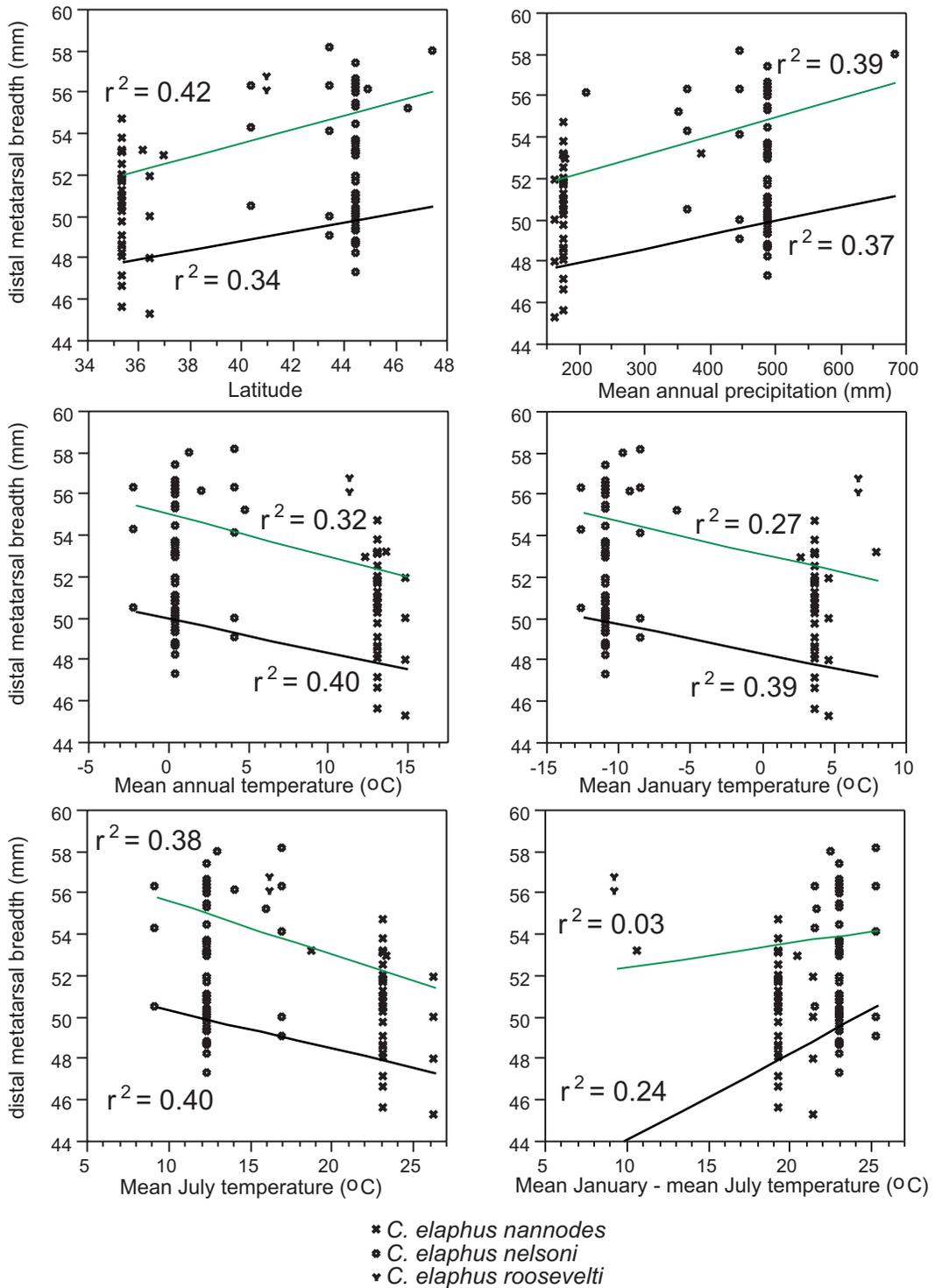


**Figure 6.6 The relationship between fossil red deer tooth breadth and glacial/interglacial climates in various regions of western Europe**

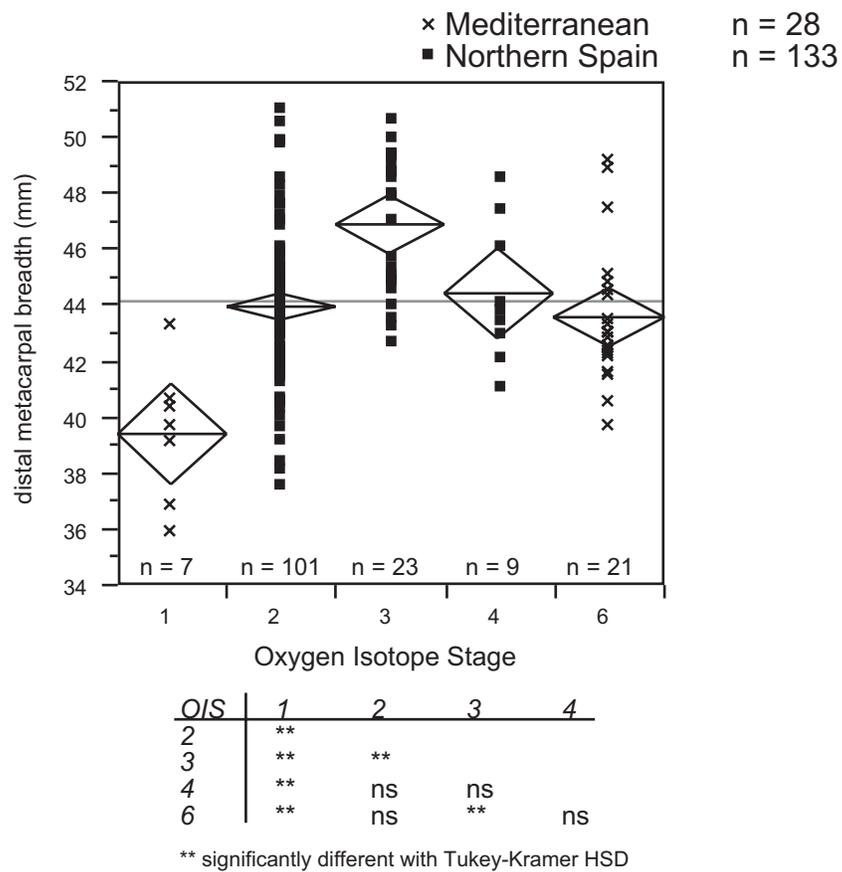
Comparison of mean  $M_1$  breadth for each OIS calculated from individual fossil teeth. The regions, Mediterranean (A,  $n = 220$ ), northern Spain (B,  $n = 410$ ), and northern Europe (C,  $n = 57$ ), are defined in the text. Statistical comparisons using the Tukey-Kramer Honestly Significant Difference test are in Tables 6.5.B-C.



**Figure 6.7 Variation in fossil red deer M<sub>1</sub> breadth during different Oxygen Isotope Stages**  
 Comparisons of tooth breadth between regions during individual Oxygen Isotope Stages. The regions, Mediterranean, northern Spain, and northern Europe, are defined in the text.

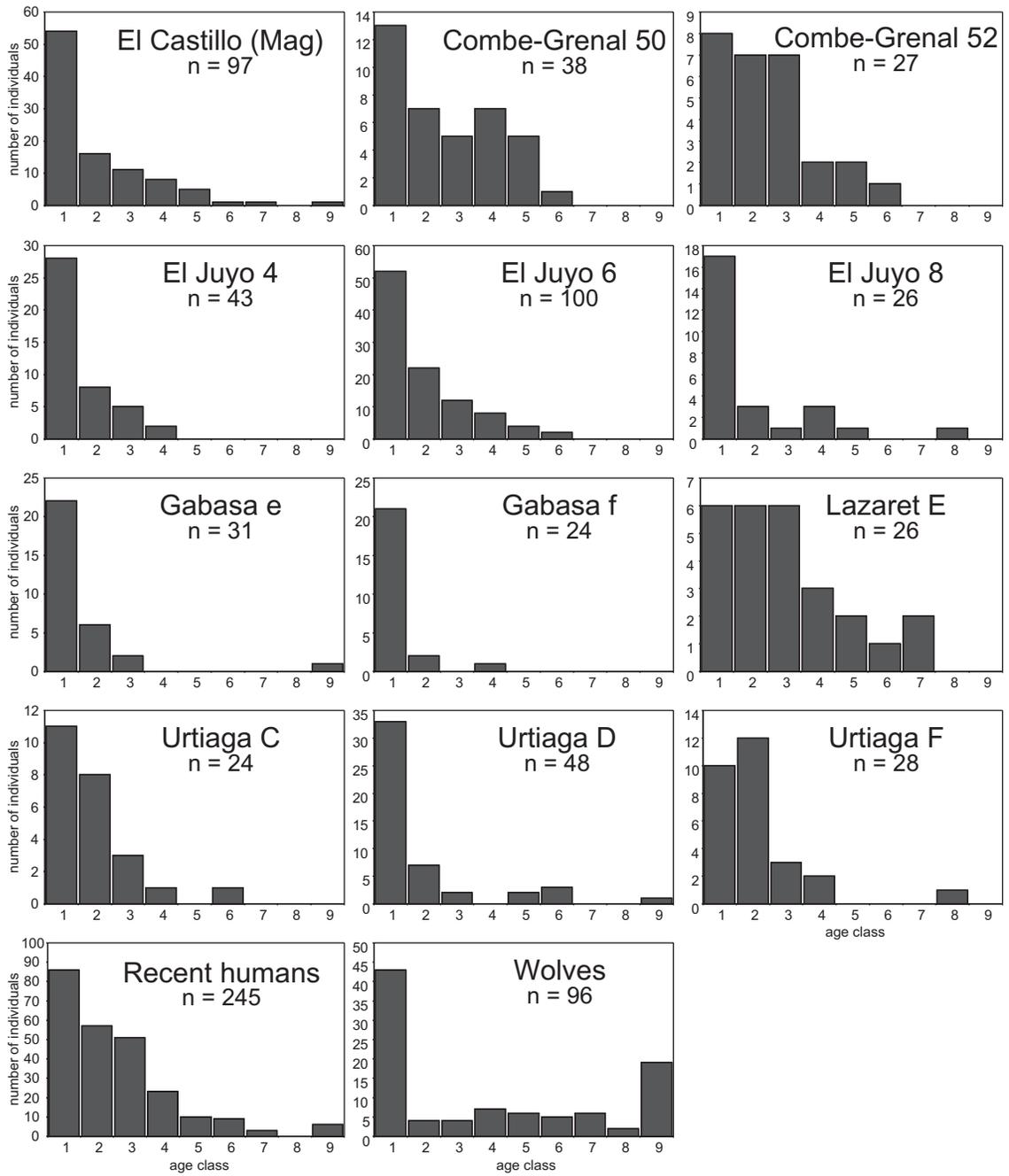


**Figure 6.8** The relationship between distal metatarsal breadth and climatic variables in modern *C. elaphus* from North America  
 Regression lines are calculated separately for males (n = 50) and females (n = 35); in all cases the males are the upper line. Climatic data are in Table 6.2, and summary statistics are in Table 6.6.



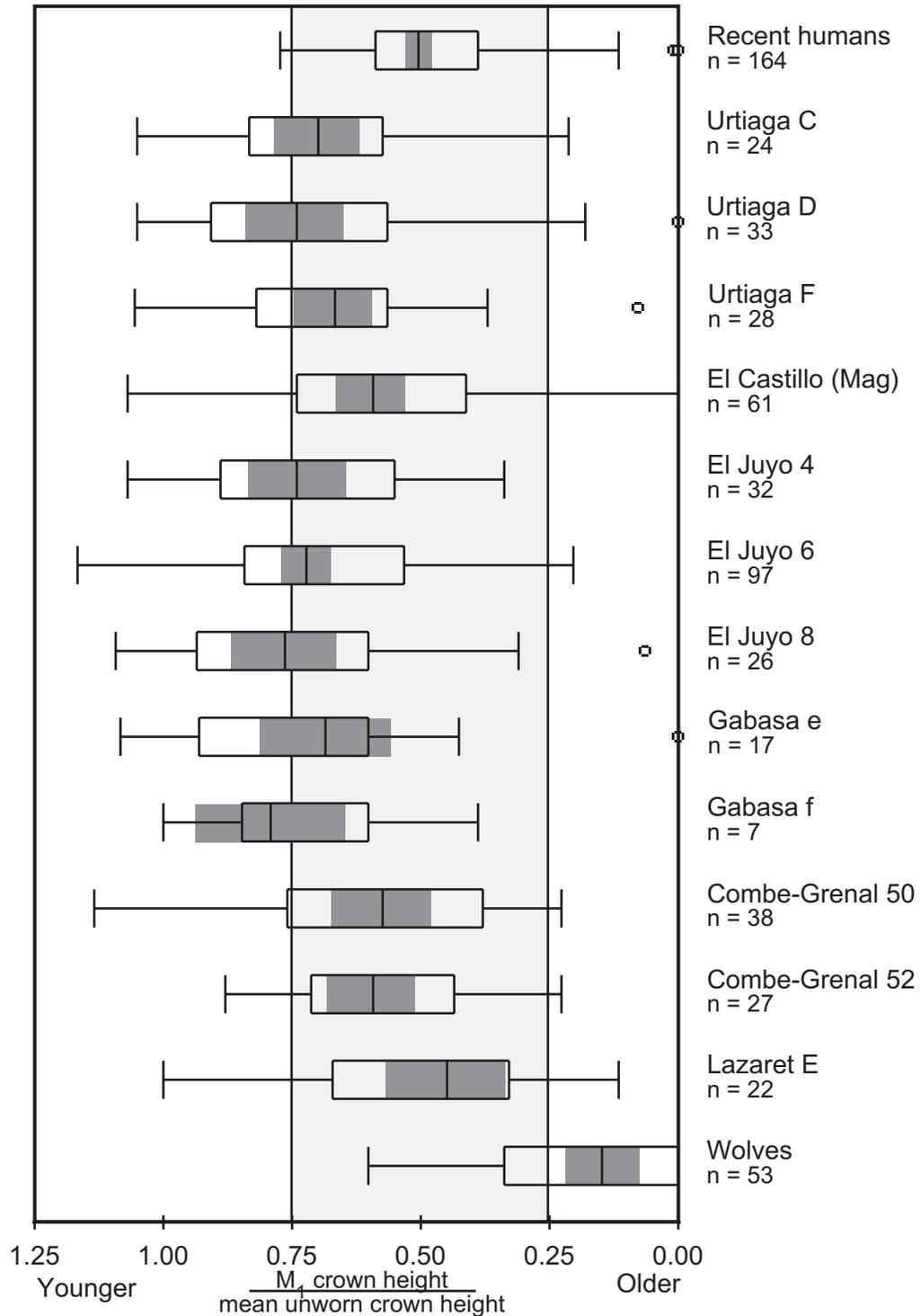
**Figure 6.9 Variation in fossil red deer distal metacarpal breadth during different Oxygen Isotope Stages**

The central line of the means diamond shows the mean of the OIS, and the points of the diamond show the limits of the 95% confidence intervals. The samples total 161 individuals.



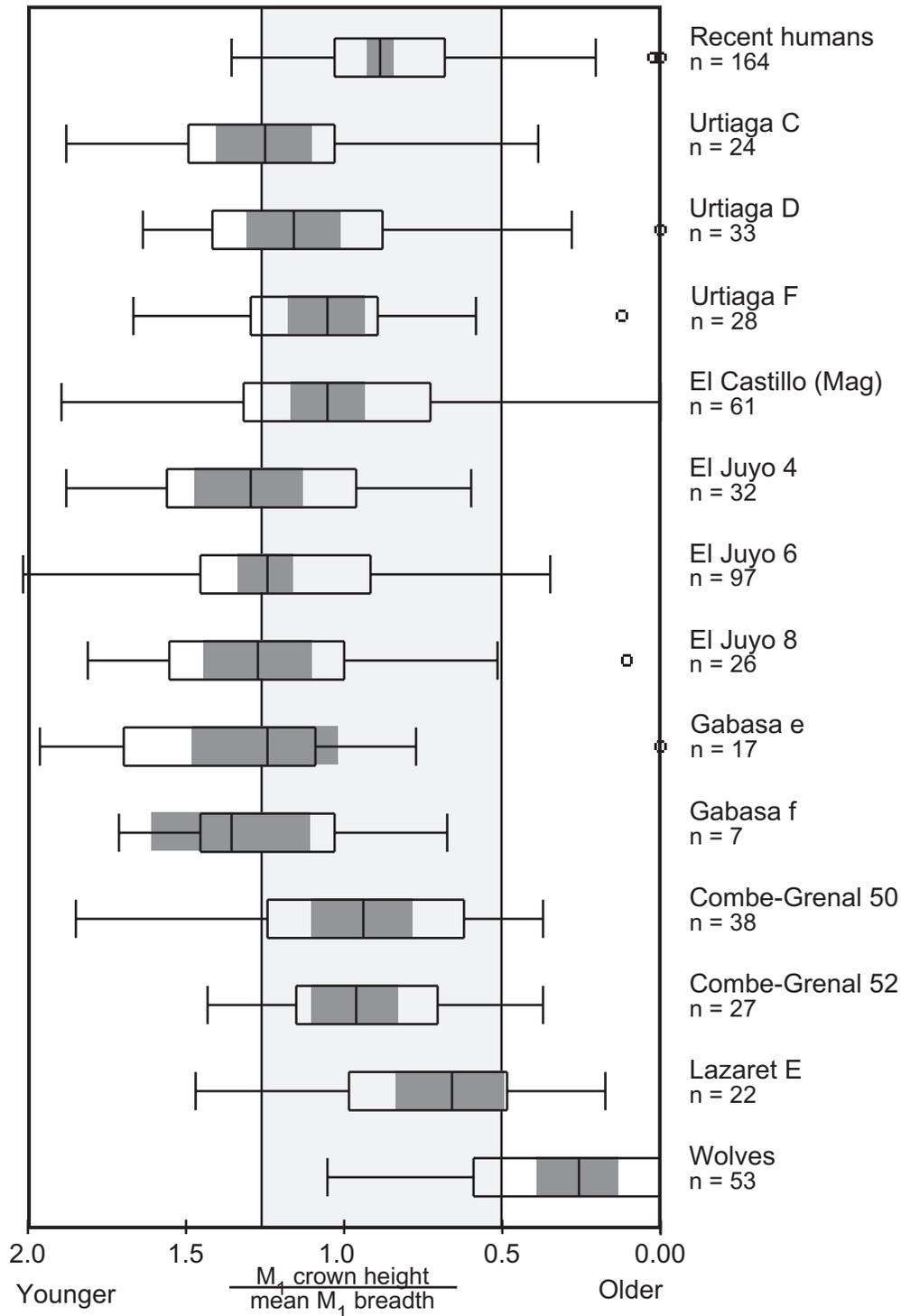
**Figure 7.1 First analysis: Histograms of individual samples**

Samples with a combined total of measurable  $dP_4$ s and  $M_1$ s of greater than 25. Age classes are based on 10% of life span (19.2 months for *C. elaphus*), but no individuals plotted in the oldest age class. Kolmogorov-Smirnov results are listed in Table 7.2.



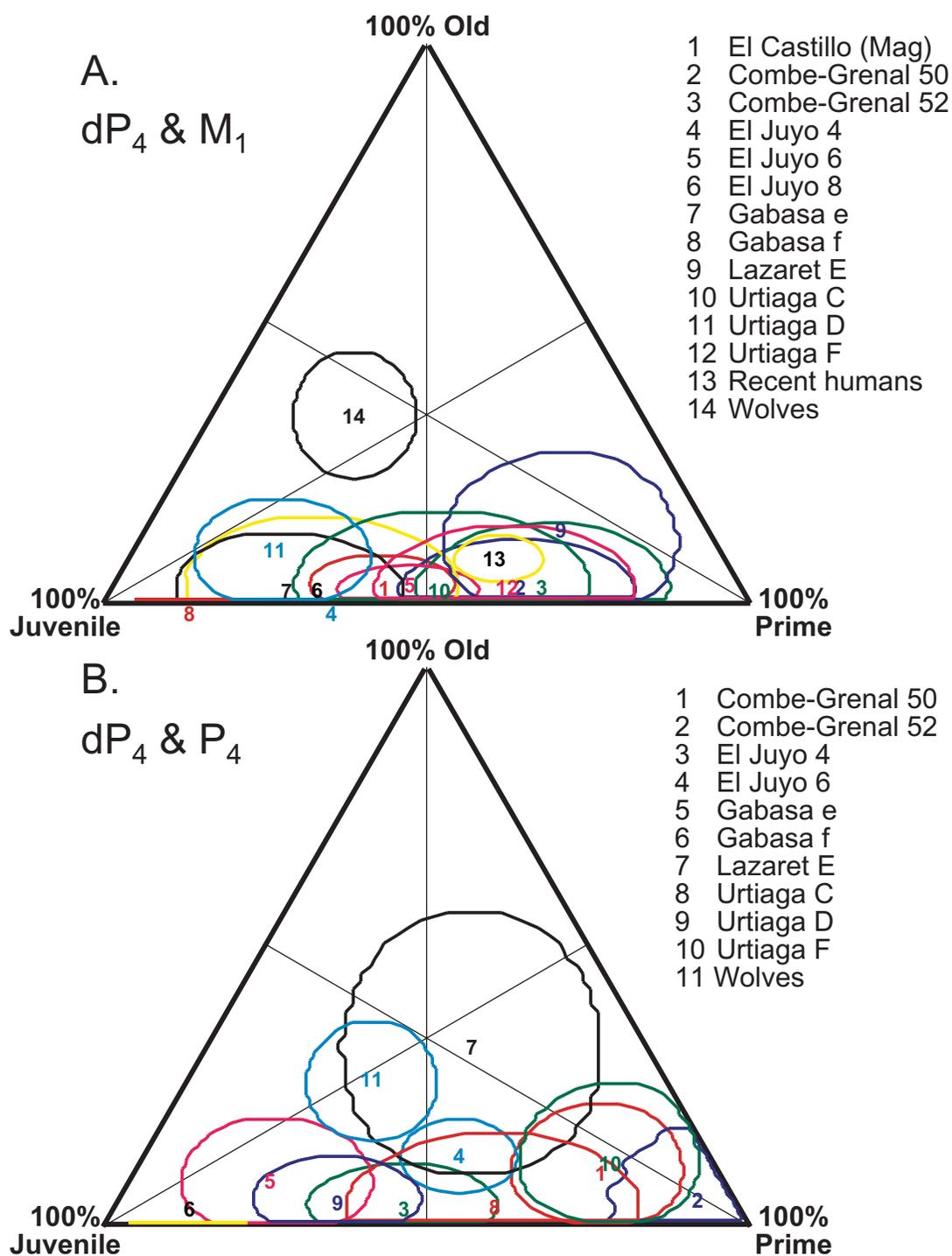
**Figure 7.2 First analysis: Boxplots of individual samples**

Samples have a combined total of  $dP_4$  and  $M_1$  of greater than 25 and are standardized by the mean unworn crown height of that sample. The darkly shaded area for each sample approximates the 95% confidence intervals around each median, and if these regions for two samples do not overlap, they can be considered significantly different. The central lightly shaded area approximates the region for prime adult animals.



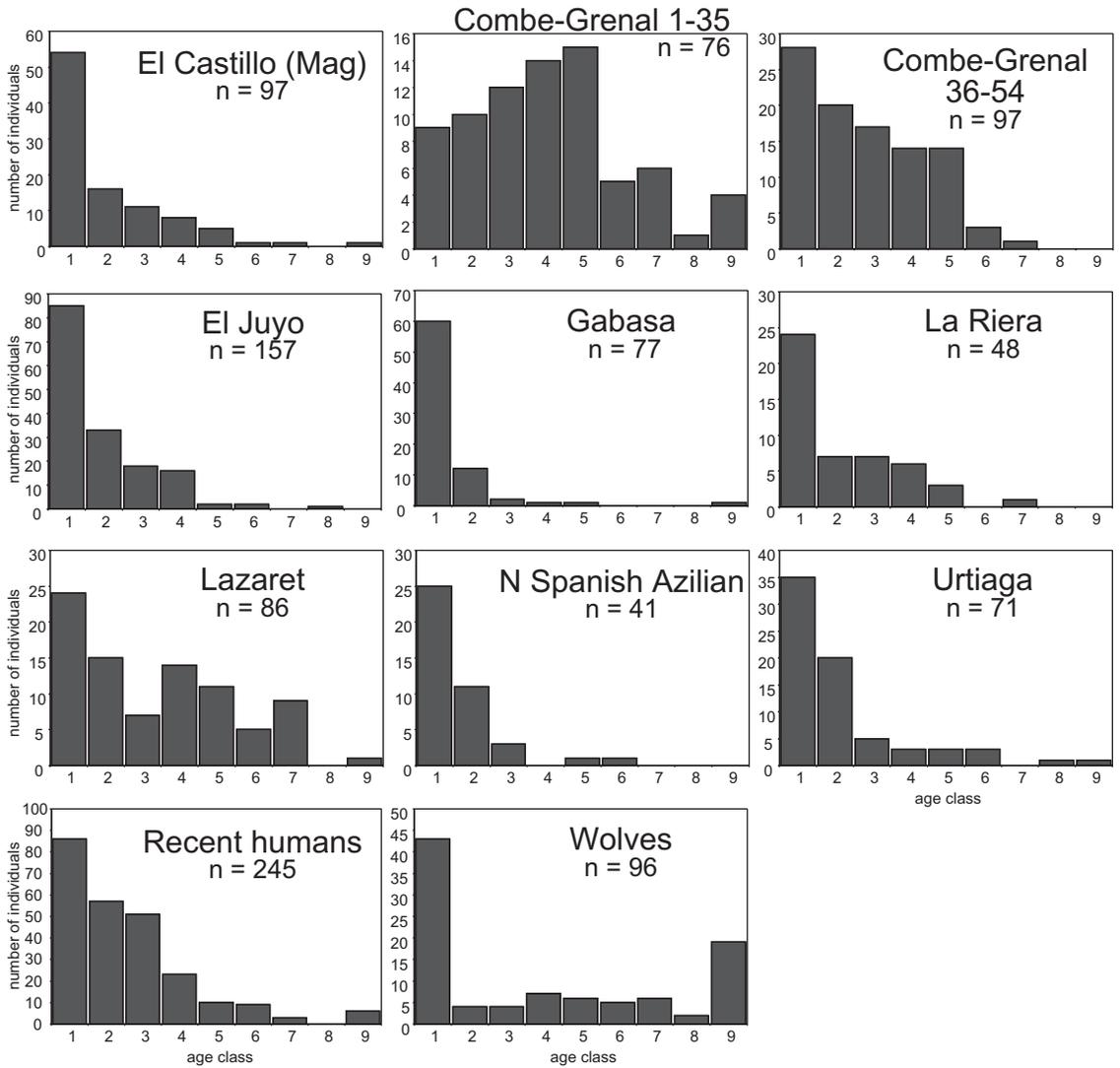
**Figure 7.3 First analysis: Boxplots of individual samples**

Samples have a combined total of  $dP_4$  and  $M_1$  of greater than 25 and are standardized by the mean  $M_1$  breadth of that sample. The darkly shaded area for each sample approximates the 95% confidence intervals around each median, and if these regions for two samples do not overlap, they can be considered significantly different. The central lightly shaded area approximates the region for prime adult animals.



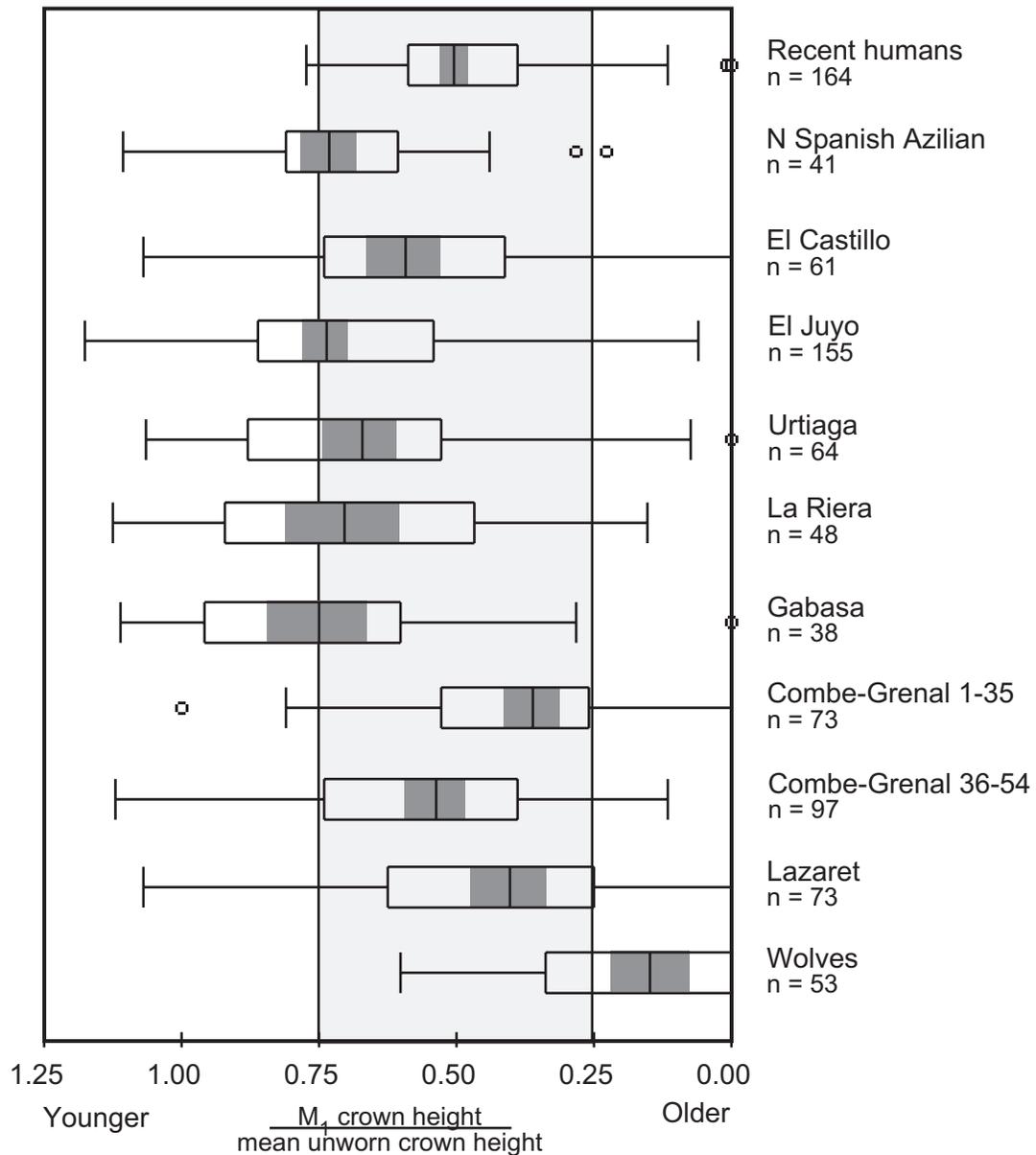
**Figure 7.4 First analysis: Modified triangular graphs of individual samples**

Circles around the points approximate 95% confidence intervals. (A) Age classes were assigned using the modified QCHM for dP<sub>4</sub> and M<sub>1</sub> discussed in Chapter 4. I used the same results here as I used in the histogram analysis. I assigned Age Class 1 as “young,” Age Classes 2-5 as “prime,” and 6-10 as “old.” (B) I assigned ages following Stiner (1990) where all dP<sub>4</sub>s were “young,” P<sub>4</sub>s less than 50% worn were “prime,” and P<sub>4</sub>s over 50% worn were “old.”



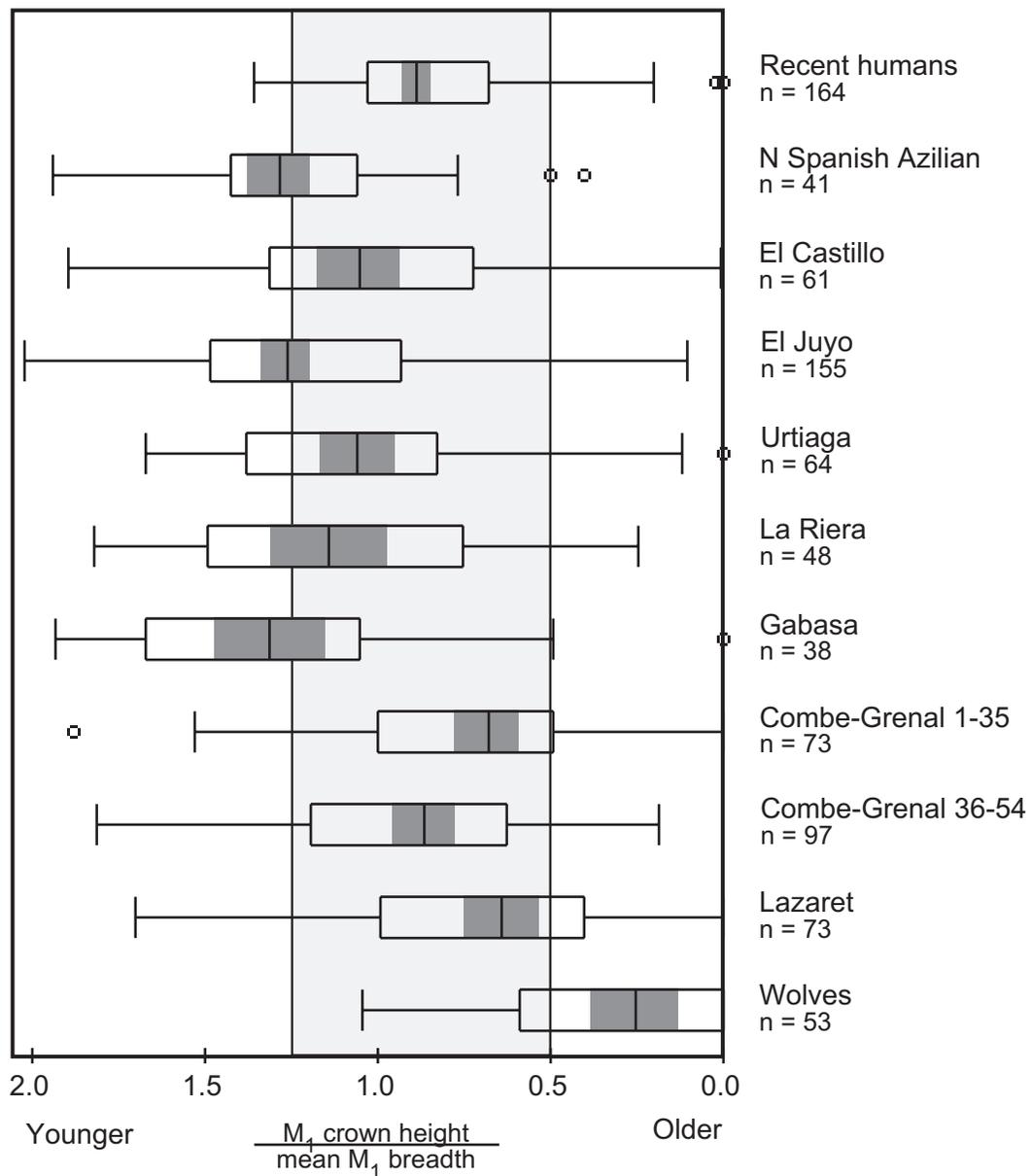
**Figure 7.5 Second analysis: Histograms of grouped samples**

Samples are groups of individual layers that have a combined total of  $dP_4$  and  $M_1$  of greater than 25. Age classes are 10% of life span (19.2 months for *C. elaphus*), but no individuals plotted in the oldest age class. Kolmogorov-Smirnov results are listed in Table 7.5.



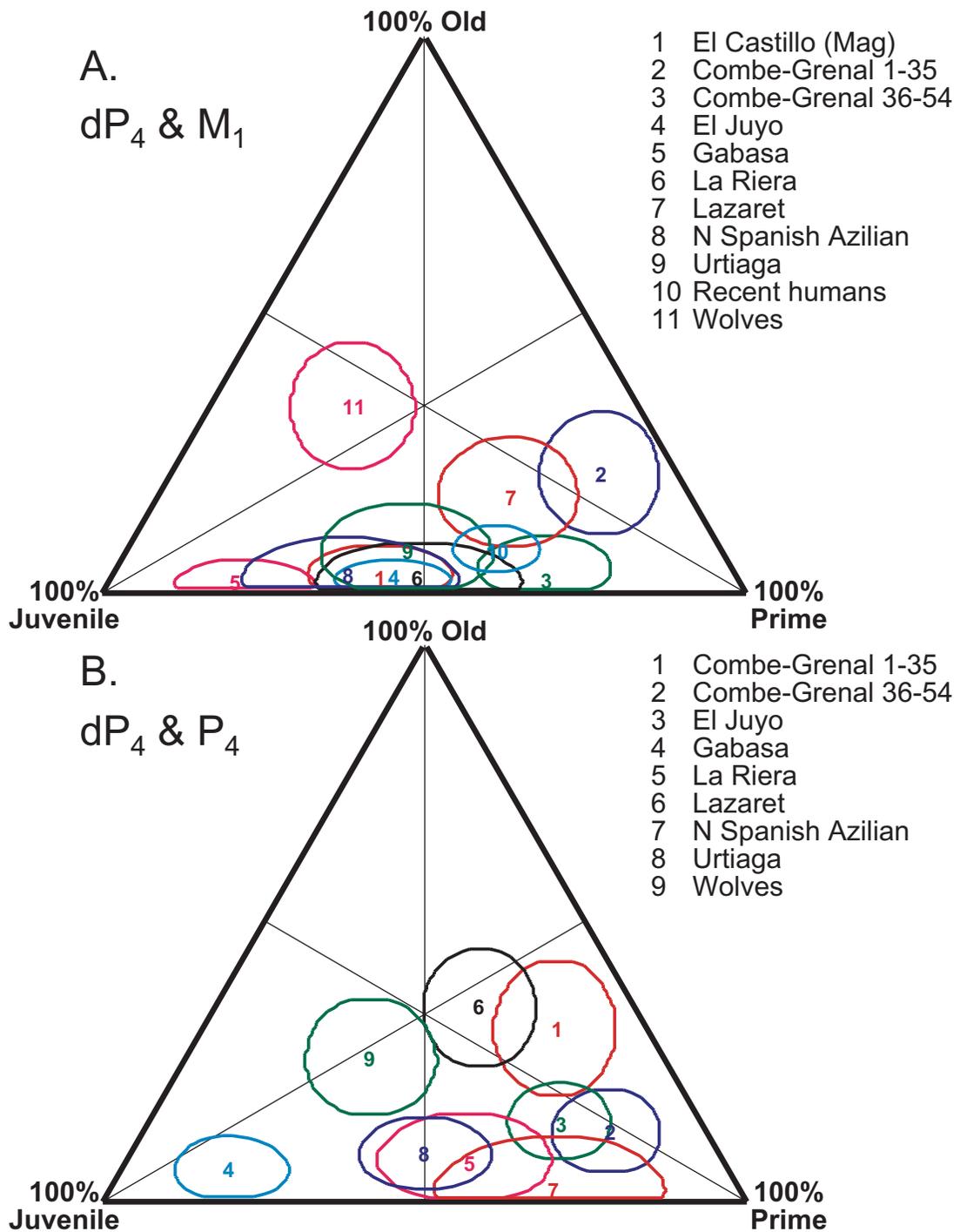
**Figure 7.6 Second analysis: Boxplots of grouped samples**

Samples are groups of individual layers that have a combined total of  $dP_4$  and  $M_1$  of greater than 25. Samples are standardized by the mean unworn  $M_1$  crown height of each sample. The darkly shaded area for each sample approximates the 95% confidence intervals around each median, and if these regions for two samples do not overlap, they can be considered significantly different. The central lightly shaded area approximates the region for prime adult animals.



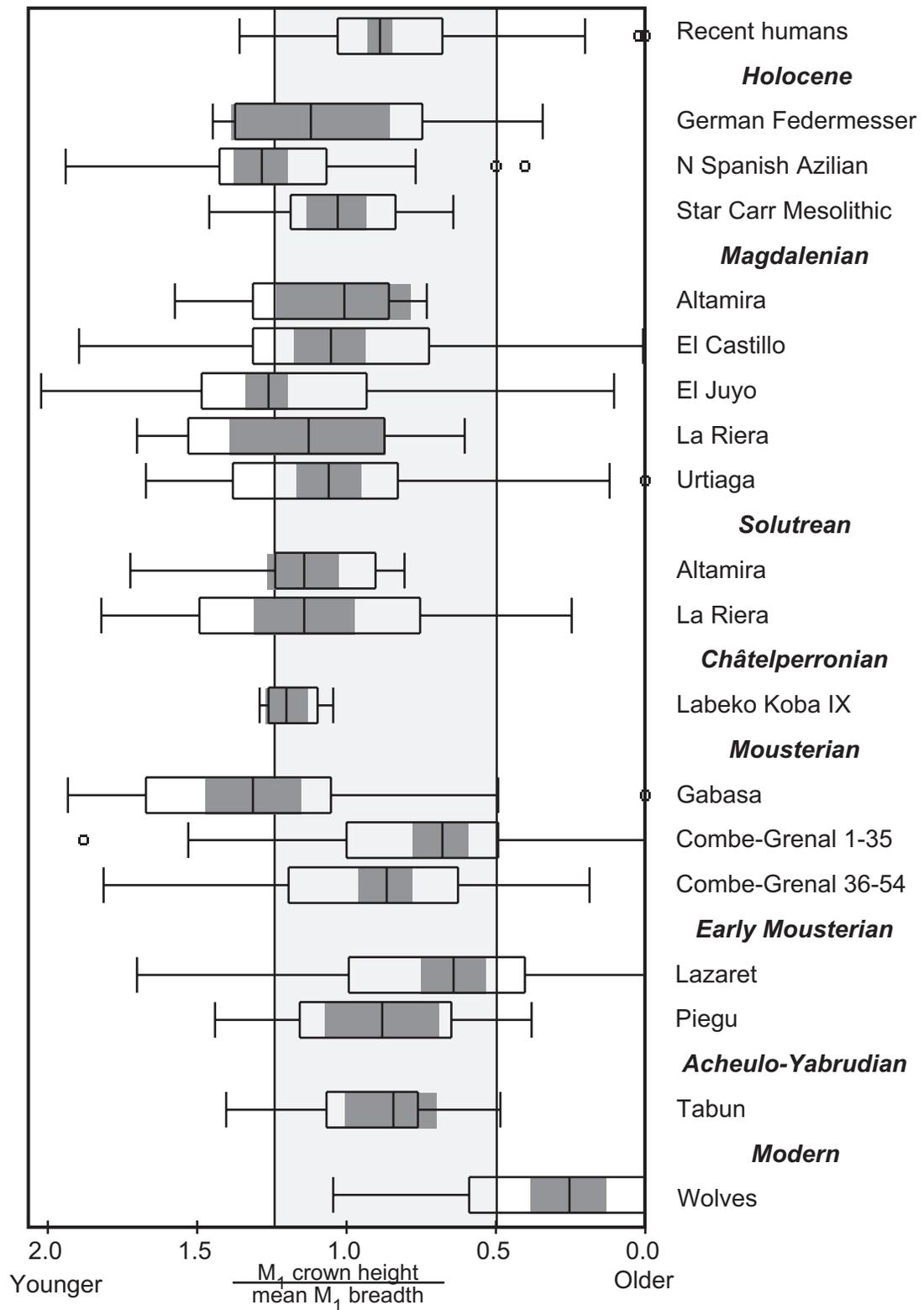
**Figure 7.7 Second analysis: Boxplots of grouped samples**

Samples are groups of individual layers that have a combined total of  $dP_4$  and  $M_1$  of greater than 25. Samples are standardized by the mean  $M_1$  breadth of each sample. The darkly shaded area for each sample approximates the 95% confidence intervals around each median, and if these regions for two samples do not overlap, they can be considered significantly different. The central lightly shaded area approximates the region for prime adult animals.



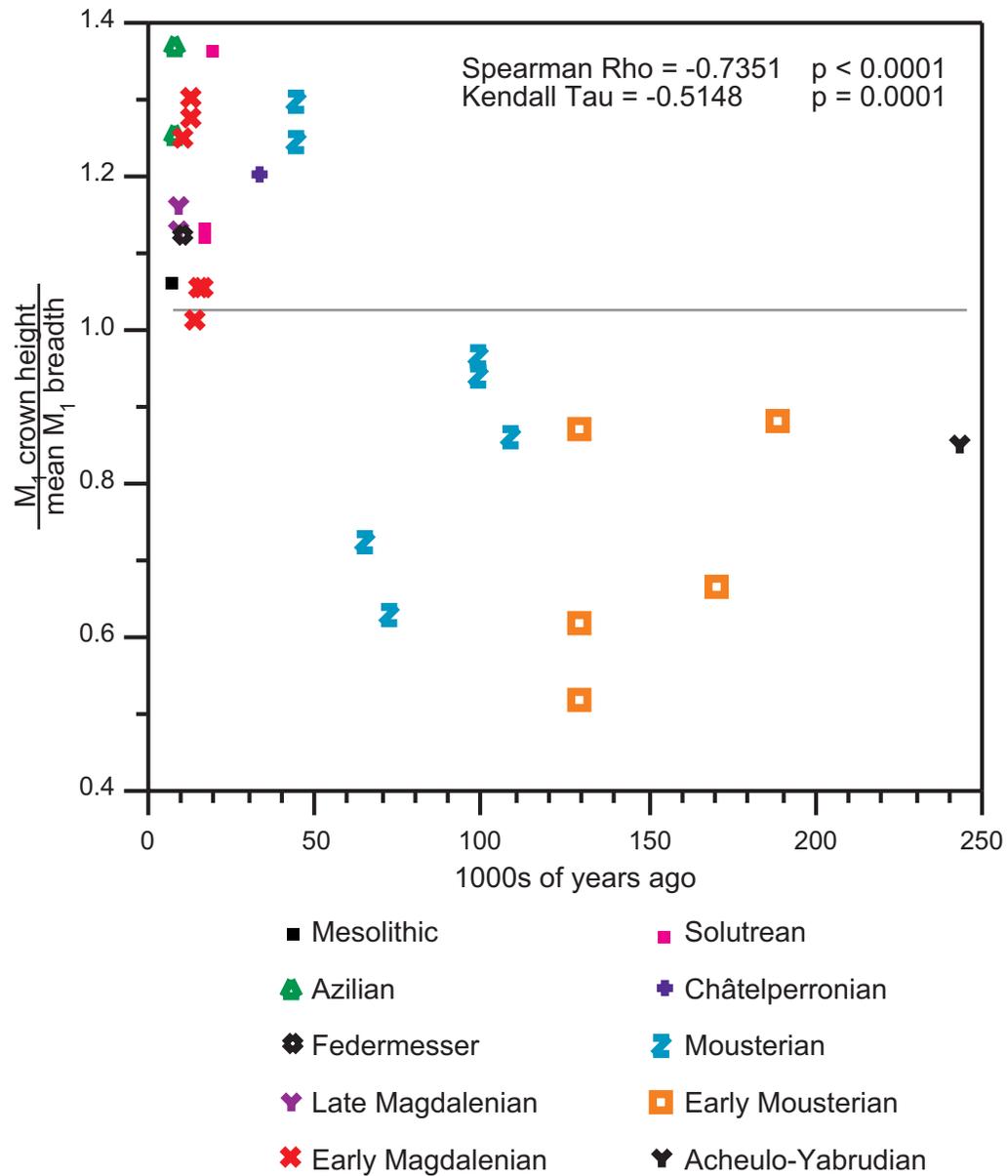
**Figure 7.8 Second analysis: Modified triangular graphs of grouped samples**

Circles around the points approximate 95% confidence intervals. (A) Age classes were assigned using the modified QCHM for  $dP_4$  and  $M_1$  as discussed in Chapter 4. I used the same results here as I used in the histogram analysis. I assigned Age Class 1 as “young,” Age Classes 2-5 as “prime,” and 6-10 as “old.” (B) I assigned ages following Stiner (1990) where all  $dP_4$ s were “young,”  $P_4$ s less than 50% worn were “prime,” and  $P_4$ s over 50% worn were “old.”



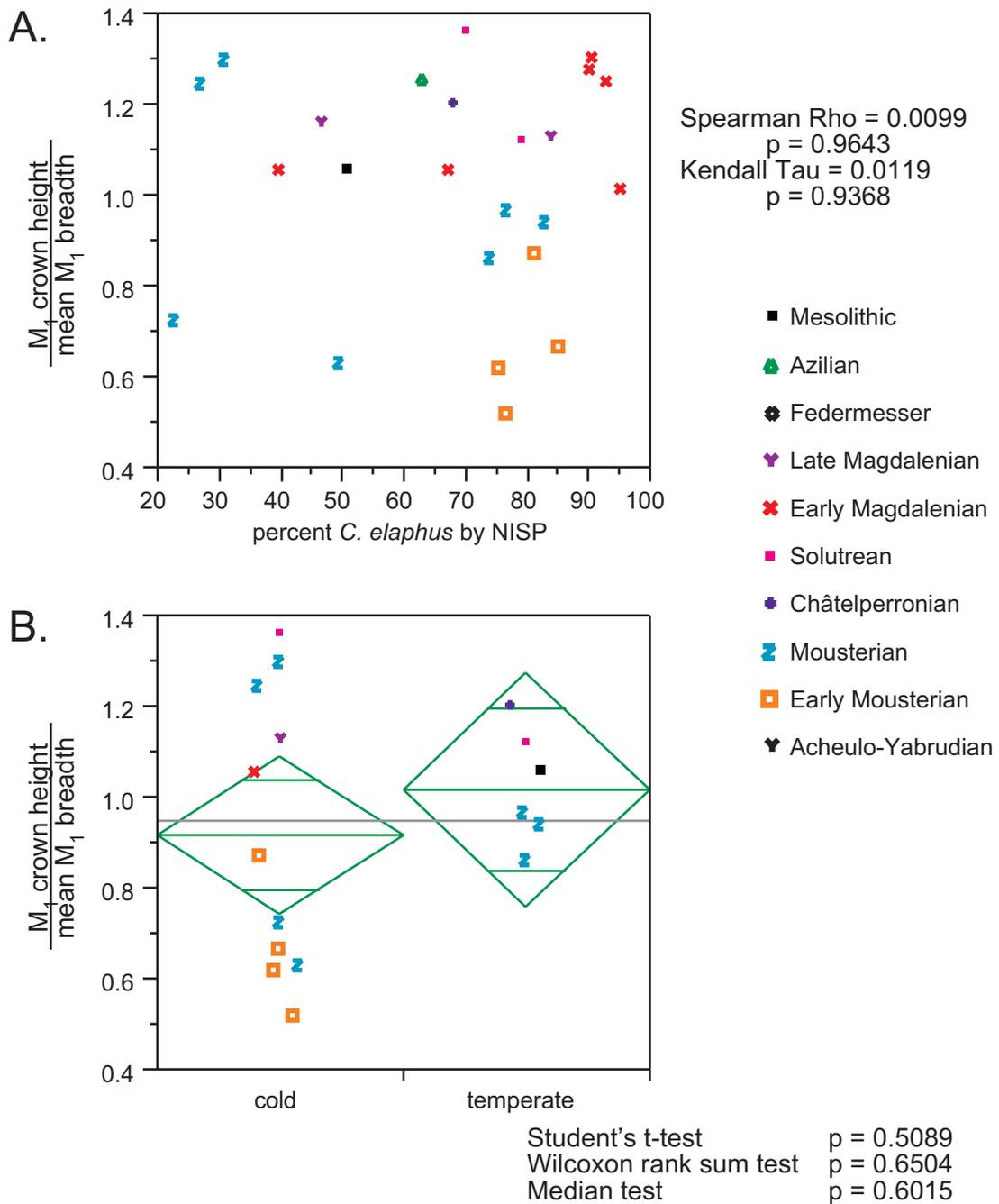
**Figure 7.9 Third analysis: Boxplots of small grouped samples**

Grouped samples with ten or more measurable M<sub>1</sub>s are included. Samples are arranged in approximately chronological order, grouped by tool technology, and standardized by the mean M<sub>1</sub> breadth of that sample.



**Figure 7.10 Third analysis: Bivariate plot of median crown height by time**

Points are median crown heights for individual samples with ten or more measurable  $M_1$  crown heights and are standardized by the mean  $M_1$  breadth for that sample (same as in Figure 7.9). The line across the center of the graph shows the grand mean of all the samples. There is a significant negative relationship between time and median height indicating that more ancient samples have higher proportions of older red deer.



**Figure 7.11 Third analysis: Bivariate plots of median crown height by environment**  
 (A) Median age is considered in terms of the percentage of red deer present in the assemblages. The percentage is based on NISP of only the ungulates in the assemblage. (B) Median age is considered in terms of temperature: cold versus temperate. Cold versus temperate designation was obtained from site reports and is based on various sources, including sedimentology, large or small faunal remains, and pollen analysis.

## Appendix C Archaeological sites that provided samples for this study

| <i>site</i>        | <i>region</i> | <i>location</i>                           | <i>latitude*</i> | <i>longitude</i> |
|--------------------|---------------|---|------------------|------------------|
| Altamira           | N Spain       | Cantabria                                 | 43°21'           | 4°03' W          |
| Andernach          | W Germany     | Neuwied Basin, Central Rhineland          | 50°26'           | 7°24' E          |
| Biache-Saint-Vaast | N France      | Pas-de-Calais, Nord-Pas-de-Calais         | 50°17'           | 2°47' E          |
| Bockstein          | S Germany     |   | 48°31'           | 9°02' E          |
| Cagny-l'Épinette   | N France      | Somme, Picardie                           | 49°42'           | 2°48' E          |
| Castillo           | N Spain       | Cantabria                                 | 43°15'           | 4°03' W          |
| Chaves             | E Spain       | Huesca, Aragón                            | 42°08'           | 0°25' W          |
| Clacton            | SE England    | Essex                                     | 51°48'           | 1°09' E          |
| Combe-Grenal       | SW France     | Dordogne, Aquitaine                       | 44°53'           | 1°13' E          |
| Conty              | N France      | Somme, Picardie                           | 49°44'           | 2°09' E          |
| Ekain              | N Spain       | Guipúzcoa, País Vasco                     | 43°14'           | 2°16' W          |
| El Juyo            | N Spain       | Cantabria                                 | 43°28'           | 3°55' W          |
| Erralla            | N Spain       | Guipúzcoa, País Vasco                     | 43°14'           | 2°16' W          |
| Forcas 1           | E Spain       | Huesca, Aragón                            | 42°08'           | 0°25' W          |
| Forcas 2           | E Spain       | Huesca, Aragón                            | 42°08'           | 0°25' W          |
| Fossellone         | C Italy       | Lazio                                     | 41°17'           | 13°15' E         |
| Fumane             | NE Italy      | Veneto                                    | 45°33'           | 11°33' E         |
| Gabasa             | E Spain       | Huesca, Aragón                            | 42°00'           | 0°25' W          |
| Gough's Cave       | SW England    | Cheddar, Somerset                         | 51°16'           | 2°45' W          |
| Grays              | SE England    | Essex                                     | 51°29'           | 0°20' E          |
| Hortus             | S France      | Hérault, Languedoc-Roussillon             | 43°36'           | 3°53' E          |
| Hoxne              | SE England    | Suffolk                                   | 52°24'           | 1°18' E          |
| Hummerich          | W Germany     | Neuwied Basin, Central Rhineland          | 50°25'           | 7°27' E          |
| Ilford             | SE England    | Essex                                     | 51°33'           | 0°05' E          |
| Kärlich            | W Germany     | Neuwied Basin, Central Rhineland          | 50°25'           | 7°27' E          |
| Kebara             | Israel        |   | 32°33'           | 34°57' E         |
| Kent's Cavern      | SW England    | Torquay, Devon                            | 50°28'           | 3°30' W          |
| Kettig             | W Germany     | Neuwied Basin, Central Rhineland          | 50°25'           | 7°27' E          |
| l'Abri Pataud      | SW France     | Dordogne, Aquitaine                       | 45°11'           | 0°43' E          |
| l'Arago            | S France      | Pyrénées-Orientales, Languedoc-Roussillon | 42°41'           | 2°53' E          |
| La Crouzade        | S France      | Aude, Languedoc-Roussillon                | 43°11'           | 3°0' E           |
| La Riera           | N Spain       | Asturias                                  | 43°25'           | 4°52' W          |
| Labeko Koba        | N Spain       | Guipúzcoa, País Vasco                     | 43°03'           | 2°40' W          |
| Lazaret            | SE France     | Alpes-Maritimes, PACA                     | 43°42'           | 7°15' E          |
| Le Portel          | S France      | Ariège, Midi-Pyrénées                     | 43°07'           | 1°36' E          |
| les Conques        | S France      | Pyrénées-Orientales, Languedoc-Roussillon | 42°41'           | 2°53' E          |
| Majolicas          | N Spain       |   |                  |                  |
| Marizulo           | N Spain       | Guipúzcoa, País Vasco                     | 43°13'           | 1°58' W          |
| Miesenheim I       | W Germany     | Neuwied Basin, Central Rhineland          | 50°25'           | 7°27' E          |
| Miesenheim II      | W Germany     | Neuwied Basin, Central Rhineland          | 50°25'           | 7°27' E          |
| Niederbieber       | W Germany     | Neuwied Basin, Central Rhineland          | 50°25'           | 7°27' E          |
| Orgnac             | S France      | Ardèche, Rhône-Alpes                      | 43°57'           | 4°21' E          |
| Piégu              | N France      | Côtes-d'Armor, Bretagne                   | 48°31'           | 2°47' W          |
| Ramandils          | S France      | Aude, Languedoc-Roussillon                | 43°02'           | 2°59' E          |
| Romain-la-Rochette | E France      | Doubs, Franche-Comté                      | 47°15'           | 6°02' E          |
| Romanelli          | S Italy       | Puglia                                    | 40°23'           | 18°11' E         |
| Rouquette          | S France      | Gard, Languedoc-Roussillon                | 44°08'           | 4°05' E          |
| San Bernardino     | NE Italy      | Veneto                                    | 45°25'           | 11°53' E         |
| Schweinskopf       | W Germany     | Neuwied Basin, Central Rhineland          | 50°25'           | 7°27' E          |
| Skhul              | Israel        |   | 32°40'           | 35°05' E         |
| Soman              | N Italy       | Trentino-Alto Adige                       | 45°35'           | 10°50' E         |
| Star Carr          | N England     | Yorkshire                                 | 54°17'           | 0°24' W          |

| <i>site</i>    | <i>region</i> | <i>location</i>                  | <i>latitude*</i> | <i>longitude</i> |
|----------------|---------------|----------------------------------|------------------|------------------|
| Swanscombe     | SE England    | Kent                             | 51°26'           | 0°18' E          |
| Tabun          | Israel        |                                  | 32°40'           | 35°05' E         |
| Tito Bustillo  | N Spain       | Asturias                         | 43°28'           | 5°04' W          |
| Tönchesberg    | W Germany     | Neuwied Basin, Central Rhineland | 50°25'           | 7°27' E          |
| Tournal à Bize | S France      | Aude, Languedoc-Roussillon       | 43°11'           | 3°0' E           |
| Urbar          | W Germany     | Neuwied Basin, Central Rhineland | 50°25'           | 7°27' E          |
| Urtiaga        | N Spain       | Guipúzcoa, País Vasco            | 43°16'           | 2°18' W          |
| Vogelherd      | S Germany     |                                  | 48°31'           | 9°02' E          |
| West Renton    | SE England    | Norfolk                          | 52°35'           | 1°0' E           |
| Wad            | Israel        |                                  | 32°40'           | 35°05' E         |
| Wannen         | W Germany     | Neuwied Basin, Central Rhineland | 50°25'           | 7°27' E          |
| Zuttiyeh       | Israel        |                                  | 32°51'           | 35°30' E         |

\* all latitudes are North

| <i>site</i>        | <i>excavator<sup>a</sup></i>  | <i>curation<sup>f</sup></i>  |
|--------------------|---|--|
| Altamira           | Obermaier <sup>b</sup> ; Freeman & González Echegaray   | R. G. Klein <sup>c</sup>   |
| Andernach          |   | RGZM – Neuwied <sup>d</sup>  |
| Biache-Saint-Vaast | A. Tuffreau (1976-82)   | Arras, France  |
| Bockstein          |   | Universität Tübingen   |
| Cagny-l'Épinette   | A. Tuffreau (1980-95)   | Arras, France  |
| Castillo           | Obermaier & IPH (1910-1914) <sup>b</sup> ; Freeman (1963); Cabrera (1980-present)   | R. G. Klein <sup>c</sup>   |
| Chaves             | V. Baldellou (1975); P. Utrilla (1984-90)   | Museo de Huesca  |
| Clacton            |   | British Museum of Natural History  |
| Combe-Grenal       | F. Bordes (1953-1965)   | Université Bordeaux I (now at the Musée National de Préhistoire in Les Eyzies)               |
| Conty              | T. Ducrocq & P. le Guen (1994-95)   | Université des Sciences et Technologies de Lille   |
| Ekain              | Grupo Cultural Antxieta, Sdad. de Ciencias Aranzadi, J. M. de Barandiarán, & J. Altuna (6 seasons during the 1970s)   | Dpto. Prehistoria, Sdad. de Ciencias Aranzadi  |
| El Juyo            | Janssens and Echegaray (1955-57), Freeman and Echegaray (1978-79, 82-83)  | R. G. Klein <sup>c</sup>   |
| Erralla            | J. Altuna (1977-78)   | Dpto. Prehistoria, Sdad. de Ciencias Aranzadi  |
| Forcas 1           | P. Utrilla and C. Mazo (1990-recently)  | Museo de Huesca  |
| Forcas 2           | P. Utrilla and C. Mazo (1991-92, 96-recently)   | Museo de Huesca  |
| Fossellone         | A. C. Blanc (1936-40, 47, 52-54)  | Museo Preistorico-Etnografico "L. Pigorini"  |
| Fumane             | G. Solinas (1964); Bartolomei, Broglio, Cassoli, Castelletti, Cattani, Cremaschi, Giacobini, Malerba, Maspero, Peresani, Sartorelli & Tagliacozzo (1988-recently) | Museo Preistorico-Etnografico "L. Pigorini"  |
| Gabasa             | P. Utrilla & L. Montes (1984-94)  | Museo de Huesca  |
| Gough's Cave       | R. C. Gough (1903); R. F. Parry (1927-29); Workman (1950)   | British Museum of Natural History  |
| Grays Hortus       | H. & M. A. de Lumley (1960-64)  | British Museum of Natural History<br>Centre européen de Recherches préhistoriques - Tautavel |
| Hoxne              | J. Frere (1797); Evans & Prestwich (1859); Belt (1876); Evans (1895-); R. Moir (1920-34); R.G. West (1951-54); Singer & Wymer (1972-74, 78)                       | British Museum of Natural History  |
| Hummerich Ilford   | K. Kröger (1983-86)   | RGZM - Koblenz<br>British Museum of Natural History  |
| Kärlich            | G. Bosinski, K. Happe, J. Kulemeyer, K. Kröger (1980-82, 1987-92)   | RGZM - Koblenz   |
| Kebara             | F. Turville-Petre (1931) <sup>b</sup> ; M. Stekelis (1951-65); O Bar-Yosef & B. Vandermeersch (1982-90)   | British Museum of Natural History  |
| Kent's Cavern      |   | British Museum of Natural History  |
| Kettig             |   | RGZM - Neuwied   |
| l'Abri Pataud      | H. Movius (1953, 58-64), H. de Lumley   | Musée de l'Abri Pataud   |
| l'Arago            | H. de Lumley (1964-present)   | Centre européen de Recherches préhistoriques - Tautavel                                      |
| La Crouzade        | T. & P. Hélène (1946-61)  | Centre européen de Recherches préhistoriques - Tautavel                                      |
| La Riera           | Vega del Sella (1917-18); Clark (1969); G. Tabanera & Pérez (1972); Clark & Straus (1976-79)  | Museo Arqueologico de Asturias   |
| Labeko Koba        | A. Arrizabalaga & J. Altuna (1987-88)   | Dpto. Prehistoria, Sdad. de Ciencias Aranzadi  |
| Lazaret            | Octobon (1950-65); H. de Lumley (1967-present)  | Laboratoire Départemental de Préhistoire du Lazaret  |

| <i>site</i>     | <i>excavator</i> <sup>a</sup>   | <i>curation</i> <sup>f</sup>                            |
|-----------------|---|---|
| Le Portel       | M. J. & J. Vézian (1949-85)   | Centre européen de Recherches préhistoriques - Tautavel |
| les Conques     | H. Baills & P. Campmajo (1972); H. Baills (1992-95)   | Centre européen de Recherches préhistoriques - Tautavel |
| Majolicas       |   | R. G. Klein <sup>c</sup>                                |
| Marizulo        | J. Merino (1961); J. M. de Barandiarán (1962-67)  | Dpto. Prehistoria, Sdad. de Ciencias Aranzadi           |
| Miesenheim I    | (1982-91)   | RGZM - Neuwied  |
| Miesenheim II   |   | RGZM - Neuwied  |
| Niederbieber    |   | RGZM - Neuwied  |
| Orgnac          | J. Combiér (1967-72)  | Centre européen de Recherches préhistoriques - Tautavel |
| Piégu           | J-L. Monnier (1970s-80s)  | Université des Sciences et Technologies de Lille        |
| Ramandils       | M.P. Boutié (1983-recently)   | Centre européen de Recherches préhistoriques - Tautavel |
| Romain-la-Roche | P. Paupe (1983-84)  | Université des Sciences et Technologies de Lille        |
| Romanelli       | G. A. Blanc (1914); L. Cardini & Instituto Italiano Paleontologia Umana (1954, 58, 61, 63, 64, 70)                          | Museo Preistorico-Etnografico "L. Pigorini"             |
| Rouquette       |   | Centre européen de Recherches préhistoriques - Tautavel |
| San Bernardino  | R. Fabiani (1902-3); A. Allegranzi & Gruppo Grotte "G. Trevisiol" del C.A.I. di Vicenza; A. Broglio & M. Peresani (1986-93) | Museo Preistorico-Etnografico "L. Pigorini"             |
| Schweinskopf    | G. Bosinski, M. Street, & J. Schäfer (1985-88)  | RGZM - Neuwied  |
| Skhul           | T. D. McCown (1930-32)  | British Museum of Natural History                       |
| Soman           | University of Ferrara   | Museo Preistorico-Etnografico "L. Pigorini"             |
| Star Carr       | J.G.D. Clark (1949-1951)  | British Museum of Natural History <sup>e</sup>          |
| Swanscombe      |   | British Museum of Natural History                       |
| Tabun           | D. A. E. Garrod, the British School of Archaeology in Jerusalem & the American School of Prehistoric Research (1929-34)     | British Museum of Natural History                       |
| Tito Bustillo   | G. Guinea (1970); J. A. Moure Romanillo (1972, 74-75)   | Museo Arqueologico de Asturias                          |
| Tönchesberg     | J. Tinnes (1986); N. Conard (1987-89)   | RGZM - Neuwied  |
| Tournal à Bize  | A. Tavoso (1970-87)   | Centre européen de Recherches préhistoriques - Tautavel |
| Urbar           |   | RGZM - Neuwied  |
| Urtiaga         | T. de Aranzadi & J. M. de Barandiarán (1928-36); J. M. de Barandiarán (1954-55, 59)   | Dpto. Prehistoria, Sdad. de Ciencias Aranzadi           |
| Vogelherd       |   | Universität Tübingen                                    |
| West Renton     |   | British Museum of Natural History                       |
| Wad             | D. A. E. Garrod, the British School of Archaeology in Jerusalem & the American School of Prehistoric Research (1929-34)     | British Museum of Natural History                       |
| Wannen          | A. Justus (1986-90)   | RGZM - Koblenz  |
| Zuttiyeh        | F. Turnville-Petre (1925)   | British Museum of Natural History                       |

<sup>a</sup> Unless otherwise noted, I studied the more recent excavations

<sup>b</sup> Date are from this excavation campaign

<sup>c</sup> Data provided by R.G. Klein

<sup>d</sup> RGZM = Römisch-Germanisches Zentralmuseums Mainz

<sup>e</sup> Data provided by K. Cruz-Urbe

<sup>f</sup> Date were collected only from the listed museums; material may also be housed elsewhere

| <i>site</i>        | <i>references</i>  |
|--------------------|--|
| Altamira           | (Freeman et al., 1988; Straus, 1992)   |
| Andernach          | (Street & Baales, 1999; Turner, 1990)  |
| Biache-Saint-Vaast | (Auguste, 1995a; Auguste, 1995b)   |
| Bockstein          | (Müller-Beck, 1988)  |
| Cagny-l'Épinette   | (Auguste, 1995c:147; Tuffreau et al., 1995)  |
| Castillo           | (Klein & Cruz-Urbe, 1994)  |
| Chaves             | (Castaños, 1993; Utrilla & Mazo, 1997)   |
| Clacton            | (Currant, personal communication; Schreve, 2001)   |
| Combe-Grenal       | (Bordes & Prat, 1965; Chase, 1986; Delpech, 1996; Delpech & Prat, 1995; Guadelli, 1996; Mellars, 1996) |
| Conty              | (Fagnart, 1997)  |
| Ekain              | (Altuna and Mariezkurrena (1984) as in Straus, 1992; Altuna & Merino, 1980)                            |
| El Juyo            | (Freeman et al., 1988; Klein et al., 1981)   |
| Erralla            | (Altuna et al., 1985; Altuna & Mariezkurrena, 1993)  |
| Forcas 1           | (Utrilla & Mazo, 1997)   |
| Forcas 2           | (Utrilla & Mazo, 1997)   |
| Fossellone         | (Alhaique et al., 1995; Alhaique et al., 1996)   |
| Fumane             | (Bartolomei et al., 1994; Cassoli & Tagliacozzo, 1994a)  |
| Gabasa             | (Blasco, 1997; Blasco Sancho, 1995)  |
| Gough's Cave       | (Campbell, 1977; Currant & Jacobi, 2001; Oakley, 1971)   |
| Grays              | (Currant, personal communication; Schreve, 1997; Schreve, 2001)  |
| Hortus             | (Moigne, personal communication; Petit-Marie et al., 1971)   |
| Hoxne              | (Grün & Schwarcz, 2000; Lister, 1993; Schreve, 1997; Schreve, 2001; Wymer & Singer, 1993)              |
| Hummerich          | (Gaudzinski et al., 1995)  |
| Ilford             | (Currant, personal communication; Schreve, 1997; Schreve, 2001)  |
| Kärlich            | (Gaudzinski et al., 1996; Gaudzinski, 1999)  |
| Kebara             | (Howell & Fritz, 1975; Speth & Tchernov, 1998; Tchernov, 1998)   |
| Kent's Cavern      | (Currant & Jacobi, 2001; Lister, 1987)   |
| Kettig             | (Street & Baales, 1999)  |
| l'Abri Pataud      | (Cho, 1998; El Mansouri et al., 1996; Fellag, 1998; Movius, 1975; Sekhr, 1998)                         |
| l'Arago            | (Moigne, personal communication; Petit-Marie et al., 1971)   |
| La Crouzade        | (Patou-Mathis, 1996)   |
| La Riera           | (Altuna, 1986; Straus, 1986)   |
| Labeko Koba        | (Altuna & Mariezkurrena, 2000; Arrizabalaga, 2000)   |
| Lazaret            | (Valensi, 1996; Valensi, 2000; Valensi & Abbassi, 1998)  |
| Le Portel          | (Gardeisen, 1997; Gardeisen, 1999)   |
| les Conques        | (Moigne et al., 1998)  |
| Majolicas          | (Klein, personal communication)  |
| Marizulo           | (Altuna, 1972)   |
| Miesenheim I       | (Turner, 1999)   |
| Miesenheim II      | (Gaudzinski et al., 1995; Street & Baales, 1999)   |
| Niederbieber       | (Street & Baales, 1999)  |
| Orgnac             | (Aouraghe, 1992; Aouraghe, 1999)   |
| Piégu              | (Auguste, 1995a:561-562; Monnier, 1985; Monnier, 1991:53-54)   |
| Ramandils          | (Banes, 1998; Patou-Mathis, 1996)  |
| Romain-la-Roche    | (Paupe, 1985; Paupe, 1995)   |
| Romanelli          | (Cassoli et al., 1997)   |
| Rouquette          | (Moigne, personal communication)   |
| San Bernardino     | (Cassoli & Tagliacozzo, 1994b)   |
| Schweinskopf       | (Gaudzinski et al., 1995)  |
| Skhul              | (Bar-Yosef, 1998; Howell & Fritz, 1975)  |
| Soman              | (Tagliacozzo & Cassoli, 1994)  |
| Star Carr          | (Clark, 1954; Dark, 2000)  |
| Swanscombe         | (Currant, personal communication; Schreve, 2001)   |
| Tabun              | (Bar-Yosef, 1998; Garrod & Bate, 1937; Howell & Fritz, 1975; Tchernov, 1998)                           |
| Tito Bustillo      | (Altuna, 1976; Altuna & Merino, 1980)  |
| Tönchesberg        | (Conard, 1992; Gaudzinski et al., 1995; Turner, 1990)  |
| Tournal à Bize     | (Patou-Mathis, 1994; Patou-Mathis, 1996; Tavoso, 1987)   |
| Urbar              | (Street & Baales, 1999; Turner, 1990)  |

| <i>site</i> | <i>references</i>                                       |
|-------------|---|
| Urtiaga     | (Altuna, 1972)  |
| Vogelherd   | (Müller-Beck, 1988)                                     |
| West Renton | (Lister, 1993; Schreve, 2001)                           |
| Wad         | (Garrod & Bate, 1937; Howell & Fritz, 1975)             |
| Wannen      | (Gaudzinski et al., 1995; Justus, 1992)                 |
| Zuttiyeh    | (Bar-Yosef, 1998; Howell & Fritz, 1975; Tchernov, 1998) |

## Appendix D Data on each layer of each site included in this study

See Appendix C for information on each site, including references. Tool industry was determined from published site descriptions. NISP is the number of identified *C. elaphus* specimens in the assemblage. % NISP is the percentage of *C. elaphus* in the total ungulate assemblage as quantified by NISP. NISP and % NISP do not include counts of shed antlers unless otherwise noted. Climate is as described in site reports and is from multiple sources of data, including analyses large mammals, microfauna, pollen, and sediments. All <sup>14</sup>C dates are uncalibrated and, therefore, are not directly comparable to TL, ESR, and U-series dates.

| site               | layer       | tool industry                   | NISP             | % NISP |
|--------------------|-------------|---------------------------------|------------------|--------|
| Altamira           | Magdalenian | Magdalenian                     | 972              | 95.4   |
| Altamira           | Solutrean   | Solutrean                       |                  |        |
| Andernach          | 2           | Federmesser                     | 13+              |        |
| Biache-Saint-Vaast |             | Mousterian                      |                  |        |
| Bockstein          | h III a+b   | Micoque                         |                  |        |
| Cagny-l'Épinette   |             | Acheulean                       | 276              | 25.1   |
| Castillo           | Mag β       | Magdalenian                     | 755              | 38.1   |
| Chaves             | 2           | Final Magdalenian               | 33               | 1.9    |
| Clacton            |             | Clactonian                      |                  |        |
| Combe-Grenal       | 4           | Typical Mousterian              | 9                | 47.4   |
| Combe-Grenal       | 5           | Typical Mousterian              | 2                | 25.0   |
| Combe-Grenal       | 6           | Typical Mousterian              | 16               | 29.1   |
| Combe-Grenal       | 7           | Typical Mousterian              | 15               | 27.8   |
| Combe-Grenal       | 8           | Denticulate Mousterian          | 9                | 39.0   |
| Combe-Grenal       | 9           | ?                               | 24               | 70.6   |
| Combe-Grenal       | 10          | Typical Mousterian?             | 8                | 25.8   |
| Combe-Grenal       | 11          | Denticulate Mousterian          | 14               | 8.8    |
| Combe-Grenal       | 12          | Denticulate Mousterian          | 12               | 14.1   |
| Combe-Grenal       | 13          | Denticulate Mousterian          | 12               | 7.0    |
| Combe-Grenal       | 14          | Denticulate Mousterian          | 21               | 3.9    |
| Combe-Grenal       | 15/16       | Denticulate Mousterian          | 6                | 6.5    |
| Combe-Grenal       | 17          | Quina Mousterian                | 47               | 31.8   |
| Combe-Grenal       | 18          | Quina Mousterian                | 8                | 16.3   |
| Combe-Grenal       | 19          | Quina Mousterian                | 17               | 16.3   |
| Combe-Grenal       | 20          | Denticulate Mousterian          | 46               | 24.1   |
| Combe-Grenal       | 21          | Quina Mousterian                | 54               | 20.0   |
| Combe-Grenal       | 22          | Quina Mousterian                | 29               | 3.0    |
| Combe-Grenal       | 23          | Quina Mousterian                | 58               | 5.3    |
| Combe-Grenal       | 24          | Quina Mousterian                | 40               | 14.0   |
| Combe-Grenal       | 25          | Quina Mousterian                | 65               | 22.9   |
| Combe-Grenal       | 26          | Quina Mousterian                | 15               | 14.3   |
| Combe-Grenal       | 27          | Ferrassie Mousterian            | 91               | 30.7   |
| Combe-Grenal       | 28          | Typical Mousterian              | 38               | 31.1   |
| Combe-Grenal       | 29          | Typical Mousterian              | 76               | 33.9   |
| Combe-Grenal       | 30          | Typical Mousterian              | 22               | 28.6   |
| Combe-Grenal       | 31          | Typical or Ferrassie Mousterian | 6                | 7.1    |
| Combe-Grenal       | 32          | Ferrassie Mousterian            | 37               | 24.2   |
| Combe-Grenal       | 33          | Ferrassie Mousterian            | 11               | 20.4   |
| Combe-Grenal       | 34          | Ferrassie Mousterian            | 8                | 40.0   |
| Combe-Grenal       | 35          | Ferrassie Mousterian            | 165              | 49.8   |
| Combe-Grenal       | 36          | Typical Mousterian?             | 43 <sup>a</sup>  | 55.1   |
| Combe-Grenal       | 37          | Typical Mousterian              | 30 <sup>a</sup>  | 53.6   |
| Combe-Grenal       | 49          | Typical Mousterian?             | 31 <sup>a</sup>  | 51.7   |
| Combe-Grenal       | 50          | Typical Mousterian              | 680 <sup>a</sup> | 83.1   |
| Combe-Grenal       | 50a         | Typical Mousterian              | 262 <sup>a</sup> | 76.6   |
| Combe-Grenal       | 51          | ?                               | 47 <sup>a</sup>  | 64.4   |

| <i>site</i>   | <i>layer</i> | <i>tool industry</i>      | <i>NISP</i>      | <i>% NISP</i> |
|---------------|--------------|---------------------------|------------------|---------------|
| Combe-Grenal  | 52           | Typical Mousterian        | 655 <sup>a</sup> | 76.7          |
| Combe-Grenal  | 53           | ?                         | 29 <sup>a</sup>  | 70.7          |
| Combe-Grenal  | 54           | Typical Mousterian        | 209 <sup>a</sup> | 74.1          |
| Combe-Grenal  | 55           | ?                         |                  |               |
| Combe-Grenal  | 56           | Acheulean                 | 10 <sup>a</sup>  | 24.4          |
| Combe-Grenal  | 57           | Acheulean                 | 16 <sup>b</sup>  | 12.2          |
| Combe-Grenal  | 58           | Acheulean                 | 37 <sup>b</sup>  | 6.7           |
| Combe-Grenal  | 59           | Acheulean                 | 24 <sup>b</sup>  | 2.1           |
| Conty         | 27           | Federmesser               |                  |               |
| Ekain         | II           | Azilian                   | 13               | 32.5          |
| Ekain         | III          | Azilian                   | 62               | 68.9          |
| Ekain         | IV           | Final Magdalenian         | 128              | 72.3          |
| Ekain         | V            | Final Magdalenian         | 71               | 74.0          |
| Ekain         | VI           | Final Magdalenian         | 47               | 20.9          |
| Ekain         | VII          | Lower Magdalenian         | 650              | 85.2          |
| Ekain         | VIII         | ?Solutrean?               | 54               | 35.3          |
| Ekain         | IXb          | Aurignacian               | 76               | 19.1          |
| Ekain         | Xa           | Chatelperronian           | 87               | 46.8          |
| El Juyo       | 4            | Lower Magdalenian         | 3925             | 90.1          |
| El Juyo       | 6/7          | Lower Magdalenian         | 2627             | 93.1          |
| El Juyo       | 8/9          | Lower Magdalenian         | 1289             | 90.3          |
| Erralla       | III          | Final Magdalenian         | 48               | 18.4          |
| Erralla       | V            | Lower Magdalenian         | 198              | 8.8           |
| Forcas 1      | 9            | Final Mag./Azilian        |                  |               |
| Forcas 1      | 11           | Final Mag./Azilian        |                  |               |
| Forcas 1      | 13           | Final Magdalenian         |                  |               |
| Forcas 1      | 14           | Final Magdalenian         |                  |               |
| Forcas 2      | II-IV        | Epipaleolithic            | 154              | 81.9          |
| Forcas 2      | V            | Epipaleolithic            | 125              | 82.8          |
| Forcas 2      | VI           | Epipaleolithic            | 38               | 71.7          |
| Fossellone    | 21           | Aurignacian               | 1171             | 36.8          |
| Fossellone    | 41-23        | Mousterian                | 112              | 34.7          |
| Fumane        | Aurignacian  | Aurignacian               | 167              | 14.4          |
| Fumane        | Mousterian   | Mousterian                | 258              | 40.9          |
| Gabasa        | a+c          | Typical Mousterian        | 66               | 10.9          |
| Gabasa        | d            | Typical Mousterian        | 75               | 11.9          |
| Gabasa        | e            | Typical Mousterian        | 348              | 27.1          |
| Gabasa        | f            | Typical Mousterian        | 359              | 32.8          |
| Gabasa        | g            | Typical Mousterian        | 511              | 31.2          |
| Gabasa        | h            | Typical Mousterian        | 159              | 22.0          |
| Gough's Cave  |              | Creswellian               |                  |               |
| Grays         |              | probable Clactonian       | 145              | 9.2           |
| Hortus        |              | Mousterian                |                  |               |
| Hoxne         |              | Acheulean                 | 51               | 10%           |
| Hummerich     |              | Middle Paleolithic        | 524 <sup>c</sup> | 42.2          |
| Ilford        |              | unknown                   | 106              | 6.4           |
| Kärlich       |              | mix                       | 18               | 11.7          |
| Kebara        | B            | Lower Natufian            |                  |               |
| Kebara        | C            | Kebaran Upper Paleolithic |                  |               |
| Kebara        | E            | Middle Paleolithic        |                  |               |
| Kent's Cavern |              | mix                       |                  |               |
| Kettig        |              | Federmesser               |                  |               |
| I'Abri Pataud | 2            | Perigordian               | 51               | 1.4           |
| I'Abri Pataud | 3            | Perigordian               | 100              | 1.0           |
| I'Abri Pataud | 4            | Perigordian               | 480              | 1.1           |
| I'Abri Pataud | 7            | Aurignacian               | 39               |               |
| I'Abri Pataud | e. 3/4       | Perigordian               | 63               | 1.2           |
| I'Abri Pataud | e. 4/5       | Aurignacian               | 50               |               |
| I'Abri Pataud | e. 7/8       | Aurignacian               | 0!               |               |
| I'Abri Pataud | e. 8/9       | Aurignacian               | 1                |               |
| I'Arago       |              | Acheulean                 |                  |               |

| <i>site</i>     | <i>layer</i>  | <i>tool industry</i>    | <i>NISP</i>      | <i>% NISP</i> |
|-----------------|---------------|-------------------------|------------------|---------------|
| La Crouzade     |               | Mousterian              | 39               | 5.4           |
| La Riera        | 1             | Aurignacian?            | 161              | 44.3          |
| La Riera        | 2-3           | Solutrean               | 44               | 17.4          |
| La Riera        | 4+6           | Solutrean               | 199              | 35.1          |
| La Riera        | 5             | Solutrean               | 512              | 43.5          |
| La Riera        | 7             | Solutrean               | 1557             | 71.2          |
| La Riera        | 8             | Solutrean               | 1268             | 70.2          |
| La Riera        | 9             | Solutrean               | 1783             | 80.7          |
| La Riera        | 11            | Solutrean               | 830              | 90.4          |
| La Riera        | 14            | Solutrean               | 2494             | 77.4          |
| La Riera        | 15            | Solutrean               | 1160             | 80.0          |
| La Riera        | 16            | Solutrean               | 1797             | 79.1          |
| La Riera        | 20            | Magdalenian             | 706              | 81.1          |
| La Riera        | 21-23         | Magdalenian             | 983              | 84.3          |
| Labeko Koba     | VII           | Proto-Aurignacian       | 79               | 18.5          |
| Labeko Koba     | IX sup.       | likely hyena            | 367              | 36.3          |
| Labeko Koba     | IX inf.       | Châtelperronian         | 792              | 68.4          |
| Lazaret         | A             | Mousterian of Acheulean | 1385             | 75.9          |
| Lazaret         | B             | Mousterian of Acheulean | 1081             | 77.4          |
| Lazaret         | C             | Mousterian of Acheulean | 1183             | 76.9          |
| Lazaret         | D             | Mousterian of Acheulean | 1228             | 81.4          |
| Lazaret         | E             | Mousterian of Acheulean | 725              | 85.6          |
| Le Portel       | B             | Upper Paleolithic       | 101              | 18.7          |
| Le Portel       | C             | Charentian Mousterian   | 20               | 26.3          |
| Le Portel       | D             | Charentian Mousterian   | 37               | 6.7           |
| Le Portel       | F             | Charentian Mousterian   | 35               | 6.7           |
| Le Portel       | F1            | Charentian Mousterian   | 74               | 10.7          |
| Le Portel       | F2            | Charentian Mousterian   | 605              | 8.8           |
| Le Portel       | F3            | Charentian Mousterian   | 85               | 3.0           |
| Le Portel       | G             | Charentian Mousterian   | 9                | 4.2           |
| Le Portel       | K             | not archaeological      | 2                | 2.9           |
| les Conques     | C3            | Middle Magdalenian      | 114              | 26.8          |
| Majolicas       |               | Epipaleolithic          |                  |               |
| Marizulo        | I             | Bronze                  | 145              | 50.9          |
| Marizulo        | II            | Neolithic               | 230              | 58.2          |
| Marizulo        | III           | Mesolithic              | 21               | 59.8          |
| Miesenheim I    |               | Acheulean/mix           | 317 <sup>c</sup> | 29.3          |
| Miesenheim II   |               | Federmesser             | 1                |               |
| Niederbieber    |               | Federmesser             | 17               |               |
| Ornac           | 1             | Pre-Mousterian          | 45               | 14.9          |
| Ornac           | 2             | Acheulean Superior III  | 135              | 21.1          |
| Ornac           | 3             | Acheulean Superior III  | 87               | 33.6          |
| Ornac           | 4             | Acheulean Superior II   | 234              | 31.2          |
| Ornac           | 5             | Acheulean Superior I    | 552              | 39.6          |
| Ornac           | 6             | Acheulean Superior I    | 564              | 30.8          |
| Ornac           | 7             | none                    | 251              | 30.8          |
| Ornac           | 8             | none                    | 251              | 30.8          |
| Piégu           |               | Epi-Acheulean           | 62               | 67.4          |
| Ramandils       |               | Mousterian              | 145              | 29.7          |
| Romain la Roche |               | mix                     |                  |               |
| Romanelli       |               | Romanellian             | 5107             | 38.7          |
| Rouquette       |               | Mousterian              |                  |               |
| San Bernardino  |               | Mousterian              | 241              | 23.7          |
| Schweinskopf    |               | Middle Paleolithic      | 93               | 14.8          |
| Skhul           |               | Mousterian              |                  |               |
| Soman           | Bronze        | Bronze                  | 35               | 57.4          |
| Soman           | Epigravettian | Epigravettian           | 211              | 21.1          |
| Soman           | Mesolithic    | Mesolithic              | 69               | 24.1          |
| Star Carr       |               | Mesolithic              | 561              | 51.0          |

| <i>site</i>    | <i>layer</i> | <i>tool industry</i> | <i>NISP</i> | <i>% NISP</i> |
|----------------|--------------|----------------------|-------------|---------------|
| Swanscombe     |              | Acheulean            |             |               |
| Tabun          | C            | Mousterian           |             |               |
| Tabun          | D            | Mousterian           |             |               |
| Tabun          | Ea-d         | Acheulo-Yabrudian    |             |               |
| Tito Bustillo  | 1a           | Final Magdalenian    | 836         | 78.6          |
| Tito Bustillo  | 1b           | Final Magdalenian    | 1062        | 79.3          |
| Tito Bustillo  | 1c           | Final Magdalenian    | 1222        | 85.2          |
| Tito Bustillo  | 2            | unknown              | 418         | 94.8          |
| Tönchesberg    | To2B         | Middle Paleolithic   | 25          | 18.2          |
| Tournal à Bize | IIB          | Mousterian           | 40          | 4.4           |
| Urbar          |              | Federmesser          | 32          |               |
| Urtiaga        | C            | Azilian              | 335         | 63.2          |
| Urtiaga        | D            | Final Magdalenian    | 1002        | 47.0          |
| Urtiaga        | E            | Middle Magdalenian   | 106         | 50.2          |
| Urtiaga        | F            | Lower Magdalenian    | 557         | 67.5          |
| Vogelherd      | VII          | Mousterian           |             |               |
| West Renton    |              | mix                  |             |               |
| Wad            | D-E          | Aurignacian          |             |               |
| Wad            | G            | Mousterian           |             |               |
| Wannen         | 1            | Middle Paleolithic   | 1           | 3.7           |
| Wannen         | 2            | Middle Paleolithic   | 3           | 7.5           |
| Wannen         | 2/3          | Middle Paleolithic   | 42          | 7.7           |
| Wannen         | 4            | Middle Paleolithic   | 31          | 11.0          |
| Wannen         | 5            | Middle Paleolithic   | 61          | 20.4          |
| Wannen         | 6            | mix                  | 165         | 41.5          |
| Zuttiyeh       | Mous.        | Mousterian           | < 26        |               |

<sup>a</sup> *C. simplicidens*

<sup>b</sup> Both *C. elaphus* and *C. simplicidens*

<sup>c</sup> includes antler fragments

| <i>site</i>        | <i>layer</i> | <i>climate</i> | <i>OIS</i> | <i>date with method</i>                            |
|--------------------|--------------|----------------|------------|--|
| Altamira           | Mag.         |                | 2          | 15,910±230; 15,500±700; 13,900±700 <sup>14</sup> C |
| Altamira           | Sol.         |                | 2          |  |
| Andernach          | 2            |                | Allerød    | 12,000-11,300 <sup>14</sup> C                      |
| Biache-Saint-Vaast |              |                | 7          |  |
| Bockstein          | h III a+b    |                | 3          |  |
| Cagny-l'EpINETTE   |              | temperate      | 9          | 296±53 kya ESR                                     |
| Castillo           | Mag β        | cold           | 2          | 16,850±220 AMS <sup>14</sup> C                     |
| Chaves             | 2            |                | 2          | 12,950±70, 12,660±70, 12,020±350 <sup>14</sup> C   |
| Clacton            |              |                | 11         |  |
| Combe-Grenal       | 4            |                | 3          |  |
| Combe-Grenal       | 5            |                | 3          |  |
| Combe-Grenal       | 6            |                | 3          |  |
| Combe-Grenal       | 7            |                | 3          |  |
| Combe-Grenal       | 8            |                | 3          |  |
| Combe-Grenal       | 9            |                | 3          |  |
| Combe-Grenal       | 10           |                | 3          |  |
| Combe-Grenal       | 11           | mild, wet      | 3          |  |
| Combe-Grenal       | 12           | mild, wet      | 3          |  |
| Combe-Grenal       | 13           | mild, wet      | 3          |  |
| Combe-Grenal       | 14           | mild, wet      | 3          |  |
| Combe-Grenal       | 15/16        | cold, dry      | 4          |  |
| Combe-Grenal       | 17           | cold, dry      | 4          |  |
| Combe-Grenal       | 18           | cold, dry      | 4          |  |
| Combe-Grenal       | 19           | cold, dry      | 4          |  |
| Combe-Grenal       | 20           | mild, wet      | 4          |  |
| Combe-Grenal       | 21           | mild, wet      | 4          |  |
| Combe-Grenal       | 22           | mild, wet      | 4          |  |
| Combe-Grenal       | 23           | cold, dry      | 4          |  |
| Combe-Grenal       | 24           | cold, dry      | 4          |  |
| Combe-Grenal       | 25           | cold, dry      | 4          |  |
| Combe-Grenal       | 26           | cold, wet      | 4          |  |
| Combe-Grenal       | 27           | cold, wet      | 4          |  |
| Combe-Grenal       | 28           | cold, wet      | 4          |  |
| Combe-Grenal       | 29           | cold, wet      | 4          |  |
| Combe-Grenal       | 30           | cold, wet      | 4          |  |
| Combe-Grenal       | 31           | cold, wet      | 4          |  |
| Combe-Grenal       | 32           | cold, wet      | 4          |  |
| Combe-Grenal       | 33           | cold, wet      | 4          |  |
| Combe-Grenal       | 34           | cold, wet      | 4          |  |
| Combe-Grenal       | 35           | cold, wet      | 4          |  |
| Combe-Grenal       | 36           | transition     | 5          |  |
| Combe-Grenal       | 37           | transition     | 5          |  |
| Combe-Grenal       | 49           | temperate, wet | 5          |  |
| Combe-Grenal       | 50           | temperate, wet | 5          |  |
| Combe-Grenal       | 50a          | temperate, wet | 5          |  |
| Combe-Grenal       | 51           | temperate, wet | 5          |  |
| Combe-Grenal       | 52           | temperate, wet | 5          |  |
| Combe-Grenal       | 53           | temperate, wet | 5          |  |
| Combe-Grenal       | 54           | temperate, wet | 5          |  |
| Combe-Grenal       | 55           |                | 6->5       |  |
| Combe-Grenal       | 56           | cold, dry      | 6          |  |
| Combe-Grenal       | 57           | cold, dry      | 6          |  |
| Combe-Grenal       | 58           | cold, dry      | 6          |  |
| Combe-Grenal       | 59           | cold, dry      | 6          |  |
| Conty              | 27           |                | Allerød    | 11,800±90 to 11,410±80 <sup>14</sup> C             |
| Ekain              | II           | more temperate | 1          |  |
| Ekain              | III          | more temperate | 1          | 12,750±250 <sup>14</sup> C charcoal                |
| Ekain              | IV           |                | 2          |  |

| <i>site</i>   | <i>layer</i> | <i>climate</i>                           | <i>OIS</i>   | <i>date with method</i>  |
|---------------|--------------|--|--------------|--|
| Ekain         | V            |  | 2            | 13,350±250 <sup>14</sup> C charcoal                              |
| Ekain         | VI           | very cold                                | 2 (Dryas II) | 12,050±190 <sup>14</sup> C                                       |
| Ekain         | VII          | humid, early<br>temperate, later<br>cold | 2 (Dryas I)  | 15,400±240 to 16,510±270 <sup>14</sup> C                         |
| Ekain         | VIII         | temperate                                | 2            | 20,900±450 <sup>14</sup> C                                       |
| Ekain         | IXb          |  | 3            | >30,600 <sup>14</sup> C  |
| Ekain         | Xa           |  | 3            |  |
| El Juyo       | 4            |  | 2            | 13,920±240 <sup>14</sup> C charcoal                              |
| El Juyo       | 6            |  | 2            |  |
| El Juyo       | 8            |  | 2            |  |
| Erralla       | III          | temperate                                | 2            | 12,310±190 <sup>14</sup> C                                       |
| Erralla       | V            | cold, dry                                | 2 (Dryas I)  | 16,270±240, 16,200±240,<br>15,740±240 <sup>14</sup> C            |
| Forcas 1      | 9            |  | 1            | 9,715±75 <sup>14</sup> C   |
| Forcas 1      | 11           |  | 1            |  |
| Forcas 1      | 13           |  | 2            | 12,620+380/-360 <sup>14</sup> C                                  |
| Forcas 1      | 14           |  | 2            | 13,010+320/-310 <sup>14</sup> C                                  |
| Forcas 2      | II-IV        |  | 1            | 7,090±340 <sup>14</sup> C  |
| Forcas 2      | V            |  | 1            | 6,940±90 <sup>14</sup> C   |
| Forcas 2      | VI           |  | 1            | 6,090±180 <sup>14</sup> C  |
| Fossellone    | 21           | colder, drier than<br>the Mousterian     | 3            |  |
| Fossellone    | 41-23        | warmer, wetter<br>than Aurignacian       |              |  |
| Fumane        | Aurig.       |  | 3            | 31,600±400;<br>40,000+4,000/-3,000 <sup>14</sup> C               |
| Fumane        | Mous.        |  |              |  |
| Gabasa        | a+c          | a: cold wet<br>c: warm, dry              | 3            |  |
| Gabasa        | d            | warm, dry                                | 3            |  |
| Gabasa        | e            | cold, wet                                | 3            | 46,500+4,400/-2,800 <sup>14</sup> C charcoal                     |
| Gabasa        | f            | cool, wet                                | 3            |  |
| Gabasa        | g            | cool, wet                                | 3            |  |
| Gabasa        | h            | cold, dry                                | 3            |  |
| Gough's Cave  |              |  | 2            | 12,800±170 <sup>14</sup> C                                       |
| Grays         |              |  | 9            |  |
| Hortus        |              |  |              |  |
| Hoxne         |              |  | 11           | 404+33/-42 kya U-series/ESR                                      |
| Hummerich     |              |  | 5 (a)        | more recent than 134-135 kya TL                                  |
| Ilford        |              |  | 7            |  |
| Kärlich       |              | interglacial                             | 9 or 11      | 396±20 kya 40Ar/39Ar   |
| Kebara        | B            |  |              |  |
| Kebara        | C            |  |              |  |
| Kebara        | E            |  |              |  |
| Kent's Cavern |              |  | 2 and 3      |  |
| Kettig        |              |  | Allerød      | 11,300 <sup>14</sup> C   |
| I'Abri Pataud | 2            | cold, dry                                | 2            | 21,940±250, 22,000±600 <sup>14</sup> C                           |
| I'Abri Pataud | 3            | cold, dry                                | 2            | 24,250±750, 23,010±170,<br>24,500±600 <sup>14</sup> C            |
| I'Abri Pataud | 4            | cooler, humid                            | 3            | 26,300±900, 27,060±370,<br>26,900±100 <sup>14</sup> C            |
| I'Abri Pataud | 7            |  | 3            | 29,300±45, 30,350±733, 32,800±500,<br>32,900±700 <sup>14</sup> C |
| I'Abri Pataud | e. 3/4       | temperate                                | 2->3         | 25,500±700, 26,100±900 <sup>14</sup> C                           |
| I'Abri Pataud | e. 4/5       |  | 3            | ~27,350 <sup>14</sup> C  |
| I'Abri Pataud | e. 7/8       |  | 3            |  |
| I'Abri Pataud | e. 8/9       |  | 3            |  |
| I'Arago       |              |  | 7            |  |
| La Crouzade   |              |  | 4            |  |

| <i>site</i>     | <i>layer</i> | <i>climate</i>  | <i>OIS</i> | <i>date with method</i>   |
|-----------------|--------------|---|------------|---|
| La Riera        | 1            |   | 2          | 19,620±390; 20,360±450; 20,860±410 <sup>14</sup> C bone                         |
| La Riera        | 2-3          | temperate, humid  | 2          |   |
| La Riera        | 4+6          | cold, dry   | 2          |   |
| La Riera        | 5            | cold, dry   | 2          |   |
| La Riera        | 7            | cold, dry   | 2          |   |
| La Riera        | 8            | cold, dry   | 2          | 15,860±330; 20,690±810 <sup>14</sup> C charcoal                                 |
| La Riera        | 9            | temperate, humid  | 2          |   |
| La Riera        | 11           | temperate, humid  | 2          |   |
| La Riera        | 14           | temperate, humid  | 2          | 15,690±310 <sup>14</sup> C bone   |
| La Riera        | 15           | temperate, humid  | 2          | 17,225±350 <sup>14</sup> C bone, 15,600±570 <sup>14</sup> C charcoal            |
| La Riera        | 16           | temperate, humid  | 2          | 18,200±610 <sup>14</sup> C charcoal   |
| La Riera        | 20           | cooler, drier   | 2          | 9,090±570, 12,360±670 <sup>14</sup> C bone, 17,160±440 <sup>14</sup> C charcoal |
| La Riera        | 21-23        |   | 2          | 10,340±560, 12,620±300 <sup>14</sup> C bone                                     |
| Labeko Koba     | VII          | cold, dry then temperate, humid                               | 3          | 31,455±915 <sup>14</sup> C  |
| Labeko Koba     | IX sup.      | wooded, mild  | 3          | 29,750±740 <sup>14</sup> C  |
| Labeko Koba     | IX inf.      | temperate, humid  | 3          | 34,125±1265 <sup>14</sup> C   |
| Lazaret         | A            | cold, damp  | 6          | 130±15 kya U-Th/ESR   |
| Lazaret         | B            | cold, damp  | 6          | 130±15 kya U-Th/ESR   |
| Lazaret         | C            | cold, damp  | 6          | 130±15 kya U-Th/ESR   |
| Lazaret         | D            | cold, damp  | 6          | 130±15 kya U-Th/ESR   |
| Lazaret         | E            | warmer, more forested   | 6          | 170±20 kya U-Th/ESR   |
| Le Portel       | B            | cold  | 3          |   |
| Le Portel       | C            | cold, dry   | 3          |   |
| Le Portel       | D            | cold, dry   | 3          |   |
| Le Portel       | F            | cold, humid   | 3          |   |
| Le Portel       | F1           | cold, humid   | 3          |   |
| Le Portel       | F2           | cold, humid   | 3          |   |
| Le Portel       | F3           | cold, humid   | 3          |   |
| Le Portel       | G            | cold, dry   | 3 or 4     |   |
| Le Portel       | K            | cold, humid   | 5e         |   |
| les Conques     | C3           | cold, dry   | 2          |   |
| Majolicas       |              |   | 1          |   |
| Marizulo        | I            |   | 1          | 5,285±65 <sup>14</sup> C bone   |
| Marizulo        | II           |   | 1          |   |
| Marizulo        | III          |   | 1          |   |
| Miesenheim I    |              |   | 13         |   |
| Miesenheim II   |              |   | Allerød    | 10,986±46 <sup>14</sup> C   |
| Niederbieber    |              |   | Allerød    | 11,800-10,800 <sup>14</sup> C   |
| Orgnac          | 1            | cold, dry   | 7          |   |
| Orgnac          | 2            | cold, dry   | 7          |   |
| Orgnac          | 3            | cold, humid   | 9          |   |
| Orgnac          | 4            | cold, humid   | 9          |   |
| Orgnac          | 5            | cold, humid   | 9          |   |
| Orgnac          | 6            | temperate, humid  | 9          |   |
| Orgnac          | 7            | temperate, humid  | 11         |   |
| Orgnac          | 8            | temperate, humid  | 11         |   |
| Piégu           |              | temperate, humid  | 7->6       | 110±6, 132±9, 167±12, 163, 141 kya U-Th/ESR                                     |
| Ramandiis       |              | temperate, humid  | 4          |   |
| Romain la Roche |              |   | 5e         |   |
| Romanelli       |              | E: damp forest, end of Allerød<br>D-B: dry, cold<br>Dryas III | 1          | D: 11,930±520 & 10,640±100<br>A: 9,980±100 <sup>14</sup> C                      |

| <i>site</i>       | <i>layer</i> | <i>climate</i>                                      | <i>OIS</i> | <i>date with method</i>   |
|-------------------|--------------|---|------------|---|
| Rouquette         |              |   | 6 & 7      |   |
| San Bernardino    |              |   | 6          |   |
| Schweinskopf      |              | open, cold  | 6          |   |
| Skhul             |              |   | 5          | Ave. 119±18 TL<br>81±15 ESR/EU; 101±12.6 ESR/LU                                 |
| Soman             | Bronze       |   | 1          |   |
| Soman             | Epi.         | cold, dry   | 1          |   |
| Soman             | Meso.        | temperate, humid                                    | 1          |   |
| Star Carr         |              | temperate   | 1          | 9,600 <sup>14</sup> C   |
| Swanscombe        |              |   | 11         |   |
| Tabun             | C            |   | 5          | 171±17 TL<br>102±17 ESR/EU; 119±11 ESR/LU                                       |
| Tabun             | D            |   | 6          | 212±22, 244±28, 265±27 TL<br>122±20 ESR/EU; 166±20 ESR/LU                       |
| Tabun             | Ea-d         |   | 7 or 8     | 306±33, 350±33, 331±30 TL<br>151±21 to 215±22 ESR/EU<br>168±15 to 290±36 ESR/LU |
| Tito Bustillo     | 1a           |   | 2          | Sublevels of 1 not distinguished:   |
| Tito Bustillo     | 1b           |   | 2          | 14,220±300, 15,400±300, 13,250±300,<br>13,870±300 <sup>14</sup> C               |
| Tito Bustillo     | 1c           |   | 2          |   |
| Tito Bustillo     | 2            |   |            |   |
| Tönchesberg       | To2B         | warm  | 5e->d      | 115 kya from multiple methods   |
| Tournal<br>à Bize | IIB          | winter: cold, dry<br>summer: more<br>temperate, wet | 3          | 38±8 kya ESR, 33±4 kya Pa-231/U-235,<br>33±8 kya Th-230/U-234                   |
| Urbar             |              |   | Allerød    | 11,300 <sup>14</sup> C  |
| Urtiaga           | C            |   | 1          | 8,700±170 <sup>14</sup> C shell   |
| Urtiaga           | D            |   | 2          | 10,280±190 <sup>14</sup> C shell  |
| Urtiaga           | E            |   | 2          |   |
| Urtiaga           | F            |   | 2          | 17,050±140 <sup>14</sup> C bone   |
| Vogelherd         | VII          |   |            |   |
| West Renton       |              |   | 13         |   |
| Wad               | D-E          |   | 3          |   |
| Wad               | G            |   |            |   |
| Wannen            | 1            |   |            |   |
| Wannen            | 2            |   |            |   |
| Wannen            | 2/3          |   |            |   |
| Wannen            | 4            |   | 6          |   |
| Wannen            | 5            |   | 6          |   |
| Wannen            | 6            |   | 6          |   |
| Wannen            | 2/3          |   |            |   |
| Zuttiyeh          | Mous.        |   | 8          | 106±7, 157±13 Th/U  |

## Bibliography

- Adams, A. W. (1982). Migration. In (J. W. Thomas & D. E. Towell, Eds) *Elk of North America: Ecology and Management*. Stackpole Books: Harrisburg, PA, pp. 301-321.
- Alhaique, F., Bietti, A., Biondi, S., Cassoli, P. F., Tagliacozzo, A. & Vitagliano, S. (1995). Grotta del Fossellone (San Felice Circeo, Latina). In (A. Bietti & R. Grifoni Cremonesi, Eds) *Guide Archeologiche: Preistoria e Protostoria in Italia. Volume 10 - Lazio e Abruzzo*. A.B.A.C.O. srl: Forlì, pp. 115-121.
- Alhaique, F., Biondi, S., Cassoli, P. F., Recchi, A. & Tagliacozzo, A. (1996). Modification in the exploitation of animal resources between the Middle Paleolithic and the Aurignacian at Grotta del Fossellone (Monte Circeo, Italy). *Proceedings of the XIII U.I.S.P.P. Congress* **2**, 571-576.
- Altuna, J. (1972). Fauna de mamíferos de los yacimientos prehistóricos de Guipuzcoa. *Munibe* **24**, 1-464.
- Altuna, J. (1976). *Los Mamíferos del Yacimiento Prehistorico de Tito Bustillo (Asturias)*. Oviedo: Instituto de Estudios Asturianos.
- Altuna, J. (1986). The mammalian faunas from the prehistoric site of La Riera. In (L. G. Straus & G. A. Clark, Eds) *La Riera Cave: Stone Age Hunter-Gatherer Adaptations in Northern Spain*. Anthropological Research Papers: Arizona State University, pp. 327-274, 421-477.
- Altuna, J., Baldeon, A. & Mariezkurrena, K. (1985). Cazadores magdalenenses en Erralla (Cestona, País Vasco). *Munibe* **37**, 1-206.
- Altuna, J. & Mariezkurrena, K. (1993). Faunes de mammifères des gisements Magdaléniens du Pays Basque et zones limitrophes. *Congrès National des sociétés historiques et scientifiques* **118 PAU**, 149-162.
- Altuna, J. & Mariezkurrena, K. (2000). Macromamíferos del yacimiento de Labeko Koba (Arrasate, País Vasco). *Munibe* **52**, 107-181.
- Altuna, J. & Merino, J. M. (1980). *El Yacimiento Prehistorico de la Cueva de Ekain (Deba, Guipúzcoa)*. San Sebastian: Eusko Ikaskuntza. Sociedad de Estudios Vascos.
- Ambrose, S. H. (1998). Chronology of the Later Stone Age and food production in East Africa. *Journal of Archaeological Science* **25**, 377-392.

- Amorosi, T. (1989). *A Postcranial Guide to Domestic Neo-Natal and Juvenile Mammals*. (Vol. 533). Oxford: BAR International Series.
- Aouraghe, H. (1992). *Les Faunes des Grands Mammifères du Site Pléistocène Moyen d'Orgnac 3 (Ardèche, France). Etude paléontologique et palethnographique. Implications paléoécologiques et biostratigraphiques*. Ph.D. Thesis, Muséum National d'Histoire Naturelle, Paris.
- Aouraghe, H. (1999). Nouvelle reconstitution de paléoenvironnement par les grands mammifères: les faunes du Pléistocène Moyen d'Orgnac 3 (Ardèche, France). *L'Anthropologie* **103**, 177-184.
- Arrizabalaga, A. (2000). El yacimiento arqueológico de Labeko Koba (Arrasate, País Vasco). Entorno. Crónica de las investigaciones. Estratigrafía y estructuras. Cronología absoluta. *Munibe* **52**, 15-72.
- Ashton, K. G., Tracy, M. C. & de Queiroz, A. (2000). Is Bergmann's rule valid for mammals? *The American Naturalist* **156**, 390-415.
- Auguste, P. (1995a). *Cadres Biostratigraphiques et Paléoécologiques du Peuplement Humain dans la France Septentrionale durant le Pléistocène. Apports de l'Étude Paléontologique des Grands Mammifères du Gisement de Biache-Saint-Vaast (Pas-de-Calais)*. Ph.D. Thesis, Museum National d'Histoire Naturelle, Paris.
- Auguste, P. (1995b). Chasse et charognage au Paléolithique Moyen: L'apport du gisement de Biache-Saint-Vaast (Pas-de-Calais). *Bulletin de la Société préhistorique française* **92**, 155-167.
- Auguste, P. (1995c). Révision préliminaire des grands mammifères des gisement du Paléolithique Inférieur et Moyen de la Vallée de la Somme. *Bulletin de la Société préhistorique française* **92**, 143-154.
- Banes, L. (1998). *La Faune Mousterienne de la Grotte des Ramandils (La Nouvelle, Aude)*. Memoire de D.E.A. Thesis, Université de Perpignan, Perpignan.
- Bar-Yosef, O. (1998). The chronology of the Middle Paleolithic of the Levant. In (T. Akazawa, K. Aoki & O. Bar-Yosef, Eds) *Neandertals and Modern Humans in Western Asia*. Plenum Press: New York, pp. 39-56.
- Bar-Yosef, O. (2000). A Mediterranean perspective on the Middle/Upper Palaeolithic revolution. In (C. B. Stringer, R. N. E. Barton & J. C. Finlayson, Eds) *Neanderthals on the Edge*. Oxbow Books: Oxford, pp. 9-18.
- Bartolomei, G., Broglio, A., Cassoli, P. F., Castelletti, L., Cattani, L., Cremaschi, M., Giacobini, G., Malerba, G., Maspero, A., Peresani, M., Sartorelli, A. & Tagliacozzo, A. (1994). La Grotte de Fumane. Un site aurignacien au pied des Alpes. *Preistoria Alpina - Museo Tridentino di Scienze Naturali* **28**, 131-179.

- Bartram, L. E. (1993). Perspectives on skeletal part profiles and utility curves from eastern Kalahari ethnoarchaeology. In (J. Hudson, Ed.) *From Bones to Behavior: Ethnoarchaeological and Experimental Contributions to the Interpretation of Faunal Remains*. Center for Archaeological Investigations, Southern Illinois University: Carbondale, IL, pp. 115-137.
- Binford, L. R. (1985). Human ancestors: Changing views of their behavior. *Journal of Anthropological Archaeology* **4**, 292-327.
- Binford, L. R. (1988). Etude taphonomique des restes fauniques de la grotte Vaufrey. In (J.-P. Rigaud, Ed.) *La Grotte Vaufrey à Cénac et Saint-Julien (Dordogne): Paléoenvironnements, Chronologie et Activités Humaines*. Mémoires de la Société Préhistorique Française **19**, pp. 535-564.
- Binford, L. R. & Bertram, J. B. (1977). Bone frequencies and attritional processes. In (L. R. Binford, Ed.) *For Theory Building in Archaeology*. Academic Press: New York, pp. 77-153.
- Blasco, M. F. (1997). In the pursuit of game: The Mousterian cave site of Gabasa I in the Spanish Pyrennes. *Journal of Anthropological Research* **53**, 177-217.
- Blasco Sancho, M. F. (1995). Hombres, Fieras y Presas: Estudio arqueozoológico y tafonómico del yacimiento del Paleolítico Medio de las Cueva de Gabasa I (Huesca). *Dpto. Ciencias de la Antigüedad (Area de Prehistoria), Universidad de Zaragoza: Monografías Arqueológicas* **38**, 1-205.
- Blumenschine, R. J. (1987). Characteristics of an Early Hominid Scavenging Niche. *Current Anthropology* **28**, 383-407.
- Bocquet-Appel, J.-P. & Demars, P.-Y. (2000a). Neanderthal contraction and modern human colonization of Europe. *Antiquity* **74**, 544-552.
- Bocquet-Appel, J.-P. & Demars, P.-Y. (2000b). Population kinetics in the Upper Palaeolithic in western Europe. *Journal of Archaeological Science* **27**, 551-570.
- Boëda, E., Connan, J., Dessort, D., Muhsen, S., Mercier, N., Valladas, H. & Tisnérat, N. (1996). Bitumen as a hafting material on Middle Palaeolithic artefacts. *Nature* **380**, 336-338.
- Bordes, F. & Prat, F. (1965). Observations sur les faunes du Riss et du Würm I en Dordogne. *L'Anthropologie* **69**, 31-46.
- Boyd, D. K., Ream, R. R., Pletscher, D. H. & Fairchild, M. W. (1994). Prey taken by colonizing wolves and hunters in the Glacier National Park area. *Journal of Wildlife Management* **58**, 289-295.
- Boyle, K. (1990). *Upper Palaeolithic Faunas from South-West France*. (Vol. 557). Oxford: BAR International Series.

- Boyle, K. (1998). *The Middle Palaeolithic Geography of Southern France: Resources and Site Location*. (Vol. 723). Oxford: Archaeopress.
- Bradley, R. S. (1999). *Paleoclimatology: Reconstructing Climates of the Quaternary*. San Diego: Academic Press.
- Bräuer, G. (1989). The evolution of modern humans: a comparison of the African and non-African evidence. In (P. Mellars & C. B. Stringer, Eds) *The Human Revolution: Behavioural and Biological Perspectives on the Origins of Modern Humans*. Edinburgh University Press: Edinburgh, pp. 123-154.
- Brown, W. A. B. & Chapman, N. G. (1991a). Age assessment of red deer (*Cervus elaphus*): from a scoring scheme based on radiographs of developing permanent molariform teeth. *Journal of Zoology, London* **225**, 85-97.
- Brown, W. A. B. & Chapman, N. G. (1991b). The dentition of red deer (*Cervus elaphus*): a scoring scheme to assess age from wear of the permanent molariform teeth. *Journal of Zoology, London* **224**, 519-536.
- Brugal, J.-P. & David, F. (1993). Usure dentaire, courbe de mortalité et "saisonnalité": les gisements du Paléolithique moyen à bovidés. In *Exploitation des Animaux Sauvages a Travers le Temps*. APDCA: Juan-les-Pins, France, pp. 63-77.
- Bryant, L. D. & Maser, C. (1982). Classification and distribution. In (J. W. Thomas & D. E. Towell, Eds) *Elk of North America: Ecology and Management*. Stackpole Books: Harrisburg, PA, pp. 1-59.
- Bunn, H. T. (1993). Bone assemblage at base camps: A further consideration of carcass transport and bone destruction by the Hadza. In (J. Hudson, Ed.) *From Bones to Behavior: Ethnoarchaeological and Experimental Contributions to the Interpretation of Faunal Remains*. Center for Archaeological Investigations, Southern Illinois University: Carbondale, IL, pp. 156-168.
- Burke, A. (1995). *Prey Movements and settlement patterns during the Upper Palaeolithic in Southwestern France*. (Vol. 619). Oxford: BAR International Series.
- Cabrera, V., Pike-Tay, A., Lloret, M. & Bernaldo de Quirós, F. (2000). Continuity patterns in the Middle-Upper Palaeolithic transition in Cantabrian Spain. In (C. B. Stringer, R. N. E. Barton & J. C. Finlayson, Eds) *Neanderthals on the Edge*. Oxbow Books: Oxford, pp. 85-93.
- Campbell, J. B. (1977). *The Upper Paleolithic of Britain: A Study of Man and Nature in the Late Ice Age*. (Vol. 1). Oxford: Clarendon Press.
- Cann, R. L., Stoneking, M. & Wilson, A. C. (1987). Mitochondrial DNA and human evolution. *Nature* **325**, 31-36.

- Carbyn, L. N. (1983). Wolf predation on elk in Riding Mountain National Park, Manitoba. *Journal of Wildlife Management* **47**, 963-976.
- Cassoli, P. F., Fiore, I. & Tagliacozzo, A. (1997). Butchery and exploitation of large mammals in the Epigravettian levels of Grotta Romanelli (Apulia, Italy). *Anthropozoologica* **25**, **26**, 309-318.
- Cassoli, P. F. & Tagliacozzo, A. (1994a). Considerazioni paleontologiche, paleoecologiche e archeozoologiche sui macromammiferi e gli uccelli dei livelli del Pleistocene Superiore del Riparo de Fumane (VR) (Scavi 1988-91). *Boll. Mus. civ. St. nat. Verona* **18**, 349-445.
- Cassoli, P. F. & Tagliacozzo, A. (1994b). I resti ossei di macromammiferi, uccelli e pesci della Grotta Maggiore di San Bernardino sui Colli Berici (VI): considerazioni paleoeconomiche, paleoecologiche e cronologiche. *Bullettino di Paleontologia Italiana (Roma)* **85**, 1-71.
- Castaños, P. (1993). Estudio de los macromamíferos de los niveles paleolíticos de Chaves. *Bolskan: Revista de Arqueología del Instituto de Estudios Altoaragoneses* **10**, 9-30.
- Caughley, G. (1966). Mortality patterns in mammals. *Ecology* **47**, 906-918.
- Caughley, G. (1977). *Analysis of Vertebrate Populations*. London: John Wiley & Sons.
- Chase, P. G. (1986). *The Hunters of Combe-Grenal: Approaches to Middle Paleolithic Subsistence in Europe*. (Vol. 286). Oxford: BAR International Series.
- Chase, P. G. (1989). How different was Middle Palaeolithic subsistence? A zooarchaeological perspective on the Middle to Upper Palaeolithic transition. In (P. Mellars & C. B. Stringer, Eds) *The Human Revolution: Behavioural and Biological Perspectives on the Origins of Modern Humans*. Edinburgh University Press: Edinburgh, pp. 321-337.
- Cho, T.-S. (1998). *Etude Archeozoologique de la Faune du Perigordien Superieur (couches 2, 3 et 4) de l'Abri Pataud (Les Eyzies, Dordogne): Paléoécologie, Taphonomie, Paleoeconomie*. Ph.D. Thesis, Museum National d'Histoire Naturelle, Paris.
- Churchill, S. E. & Smith, F. H. (2000). Makers of the Early Aurignacian of Europe. *Yearbook of Physical Anthropology* **43**, 61-115.
- Clark, G. A. & Straus, L. G. (1983). Late Pleistocene hunter-gatherer adaptations in Cantabrian Spain. In (G. Bailey, Ed.) *Hunter-Gatherer Economy in Prehistory*. Cambridge University Press: Cambridge, pp. 131-148.
- Clark, J. G. D. (1954). *Excavations at Star Carr*. Cambridge: Cambridge University Press.

- Clutton-Brock, T. H. & Albon, S. D. (1983). Climatic variation and body weight of red deer. *Journal of Wildlife Management* **47**, 1197-1201.
- Clutton-Brock, T. H. & Albon, S. D. (1989). *Red deer in the Highlands*. Oxford: BSP Professional.
- Clutton-Brock, T. H., Coulson, T. N., Milner-Gulland, E. J., Thomson, D. & Armstrong, H. M. (2002). Sex differences in emigration and mortality affect optimal management of deer populations. *Nature* **415**, 633-637.
- Clutton-Brock, T. H., Guinness, F. E. & Albon, S. D. (1982). *Red deer: behavior and ecology of two sexes*. Chicago: University of Chicago Press.
- Conard, N. J. (1992). Tönchesberg and its position in the Paleolithic prehistory of Northern Europe. *Monographien des Römisch-Germanischen Zentralmuseum* **20**.
- Cruz-Uribe, K. (1991). Distinguishing hyena from hominid bone accumulations. *Journal of Field Archaeology* **18**, 467-486.
- Currant, A. & Jacobi, R. (2001). A formal mammalian biostratigraphy for the Late Pleistocene of Britain. *Quaternary Science Reviews* **20**, 1707-1716.
- d'Errico, F., Henshilwood, C. S. & Soressi, M. (2002, March 22, 2002). *New evidence for symbolism and behavioural modernity in the MSA and Mousterian*. Paper presented at the Society for American Archaeology, Denver, CO.
- d'Errico, F. & Soressi, M. (2002). Systematic use of manganese pigment by Pech-de-l'Azé Neandertals: implications for the origin of behavioral modernity. *Journal of Human Evolution* **42**, A13.
- d'Errico, F., Zilhão, J., Julien, M., Baffier, D. & Pelegrin, J. (1998). Neanderthal acculturation in western Europe? A critical review of the evidence and its interpretation. *Current Anthropology* **39**, S1-S44.
- Dark, P. (2000). Revised 'absolute' dating of the early Mesolithic site of Star Carr, North Yorkshire, in the light of changes in the early Holocene tree-ring chronology. *Antiquity* **74**, 304-307.
- Davies, W., Stewart, J. & van Andel, T. H. (2000). Neanderthal landscapes - a preview. In (C. B. Stringer, R. N. E. Barton & J. C. Finlayson, Eds) *Neanderthals on the Edge*. Oxbow Books: Oxford, pp. 1-8.
- Dayan, T., Simberloff, D., Tchernov, E. & Yom-Tov, Y. (1991). Calibrating the paleothermometer: climate, communities, and the evolution of size. *Paleobiology* **17**, 189-199.

- Deacon, H. J. (1989). Late Pleistocene palaeoecology and archaeology in the Southern Cape, South Africa. In (P. Mellars & C. B. Stringer, Eds) *The Human Revolution: Behavioural and Biological Perspectives on the Origins of Modern Humans*. Edinburgh University Press: Edinburgh, pp. 547-564.
- Deevey, E. S. (1947). Life tables for natural populations of animals. *Quarterly Review of Biology* **22**, 283-314.
- Delpech, F. (1983). *Les Faunes du Paléolithique Supérieur dans le Sud-Ouest de la France*. Paris: CNRS.
- Delpech, F. (1996). L'environnement animal des Moustériens Quina du Périgord. *Paleo* **8**, 31-46.
- Delpech, F. & Prat, F. (1995). Nouvelles observations sur les faunes Acheuléennes de Combe Grenal (Domme, Dordogne). *Paleo* **7**, 123-137.
- Dixon, S. L. & Lyman, R. L. (1996). On the Holocene history of elk (*Cervus elaphus*) in eastern Washington. *Northwest Science* **70**, 262-272.
- Dolukhanov, P., Sokoloff, D. & Shukurov, A. (2001). Radiocarbon chronology of Upper Palaeolithic sites in eastern Europe at improved resolution. *Journal of Archaeological Science* **28**, 699-712.
- Driesch, v. d. (1976). A Guide to the Measurement of Animal Bones from Archaeological Sites. *Bulletin of the Peabody Museum of Archaeology and Ethnology (Harvard University)* **1**, 1-136.
- Duarte, C., Maurícia, J., Pettitt, P. B., Souto, R., Trinkaus, E., van der Plicht, H. & Zilhão, J. (1999). The early Upper Paleolithic human skeleton from the Abrigo do Lagar Velho (Portugal) and modern human emergence in Iberia. *Proceedings of the National Academy of Science* **96**, 7604-7609.
- Ducos, P. (2000). A new approach to the construction of age profiles. *ArchaeoZoologia* **11**, 135-144.
- Efron, B. & Tibshirani, R. J. (1993). *An Introduction to the Bootstrap*. (Vol. 57). New York: Chapman & Hall.
- El Mansouri, M., El Fouikar, A. & Saint-Martin, B. (1996). Correlation Between <sup>14</sup>C Ages and Aspartic Acid Racemization at the Upper Palaeolithic Site of the Abri Pataud (Dordogne, France). *Journal of Archaeological Science* **23**, 803-809.
- Enloe, J. G. (1993). Subsistence organization in the Early Upper Paleolithic: Reindeer hunters of the Abri du Flageolet, Couche V. In (H. Knecht, A. Pike-Tay & R. White, Eds) *Before Lascaux: The Complex Record of the Early Upper Paleolithic*. CRC Press: Boca Raton, pp. 101-115.

- Fagnart, J.-P. (1997). Le Gisement du Marais de Conty (Somme). *Mémoires de la Société Préhistorique Française* **24**, 108-119.
- Falgueres, C., Bahain, J., Yokoyama, Y., Arsuaga, J., de Castro, J., Carbonell, E., Bischoff, J. & Dolo, J. (1999). Earliest humans in Europe: the age of TD6 Gran Dolina, Atapuerca, Spain. *Journal of Human Evolution* **37**, 343-352.
- Farizy, C., David, J., Jaubert, J., Eisenmann, V., Girard, M., Grün, R., Krier, V., Leclerc, J., Miskovsky, J.-C. & Simonnet, R. (1994). *Hommes et bisons du Paléolithique moyen à Mauran (Haute-Garonne)*. Paris: CNRS Editions.
- Fellag, H. (1998). Apport de l'analyse pollinique à la connaissance du paléoenvironnement du Paléolithique supérieur de l'abri Pataud (Dordogne, France). *Bulletin de la Société préhistorique française* **95**, 171-181.
- Flook, D. R. (1970). Causes and implications of an observed sex differential in the survival of wapiti. *Canadian Wildlife Service Report Series* **11**, 1-71.
- Fruyer, D. W. (1992). The persistence of Neanderthal features in post-Neanderthal Europeans. In (G. Bräuer & F. H. Smith, Eds) *Continuity or Replacement: Controversies in Homo sapiens evolution*. A.A. Balkema: Rotterdam, pp. 179-189.
- Freeman, L. G., González Echegaray, J., Klein, R. G. & Crowe, W. T. (1988). Dimensions of research at El Juyo. In (H. L. Dibble & A. Montet-White, Eds) *Upper Pleistocene Prehistory of Western Eurasia*. The University Museum: Philadelphia, pp. 3-39.
- Frison, G. C. (1987). Prehistoric, plains-mountain, large-mammal, communal hunting strategies. In (M. H. Nitecki & D. V. Nitecki, Eds) *The Evolution of Human Hunting*. Plenum Press: New York, pp. 177-223.
- Frison, G. C. (1991a). Hunting strategies, prey behavior and mortality data. In (M. C. Stiner, Ed.) *Human Predators and Prey Mortality*. Westview Press: Boulder, CO, pp. 15-30.
- Frison, G. C. (1991b). *Prehistoric Hunters of the High Plains*. San Diego: Academic Press.
- Gambier, D. (1989). Fossil hominids from the early Upper Paleolithic (Aurignacian) of France. In (P. Mellars & C. B. Stringer, Eds) *The Human Revolution: Behavioural and Biological Perspectives on the Origins of Modern Humans*. Edinburgh University Press: Edinburgh, pp. 194-211.
- Gamble, C. (1999). *The Palaeolithic Societies of Europe*. Cambridge: Cambridge University Press.

- Gardeisen, A. (1997). *La grotte ouest du Portel, Ariège, France: Restes fauniques et stratégies de chasse dans le Pléistocène supérieur pyrénéen*. (Vol. 673). Oxford: BAR International Series.
- Gardeisen, A. (1999). Middle Palaeolithic subsistence in the West Cave if "Le Portel" (Pyénées, France). *Journal of Archaeological Science* **26**, 1145-1158.
- Garrod, D. A. E. & Bate, D. M. A. (1937). *The Stone Age of Mount Carmel: Excavations at the Wady El-Mughara*. (Vol. 1). Oxford: The Calendon Press.
- Gaudzinski, S. (1995). Wallertheim revisited: a Re-analysis of the fauna from the Middle Palaeolithic site of Wallertheim (Rheinhessen/Germany). *Journal of Archaeological Science* **22**, 51-66.
- Gaudzinski, S. (1996). On bovid assemblages and their consequences for the knowledge of subsistence patterns in the Middle Paleolithic. *Proceedings of the Prehistoric Society* **62**, 19-39.
- Gaudzinski, S. (1999). Considerations on the taphonomy of the faunal assemblage from the Middle Pleistocene Kärlich-Seeufer site (Central Rhineland, Germany). *Monographien des Römisch-Germanischen Zentralmuseum* **42**, 139-151.
- Gaudzinski, S., Bittmann, F., Boenigk, W., Frechen, M. & van Kolfschoten, T. (1996). Palaeoecology and archaeology of the Kärlich-Seeufer open-air site (Middle Pleistocene) in the Central Rhineland, Germany. *Quaternary Research* **46**, 319-334.
- Gaudzinski, S., Street, M. & Turner, E. (1995). Middle and Upper Pleistocene hominid occupation in the Neuwied Basin (Rhineland). In (W. Schirmer, Ed.) *Quaternary Field Trips in Central Europe*. Verlag Dr. Friedrich Pfeil: München, pp. 1449-1475.
- Geist, V. (1982). Adaptive behavioral strategies. In (J. W. Thomas & D. E. Toweill, Eds) *Elk of North America: Ecology and Management*. Stackpole Books: Harrisburg, PA, pp. 219-277.
- Geist, V. (1998). *Deer of the World: Their Evolution, Behavior, and Ecology*. Mechanicsburg, PA: Stackpole Books.
- Gifford-Gonzalez, D. (1991). Examining and refining the Quadratic Crown Height Method of Age Estimation. In (M. C. Stiner, Ed.) *Human Predators and Prey Mortality*. Westview Press: Boulder, CO, pp. 41-78.
- Grayson, D. K. & Delpech, F. (1994). The evidence for Middle Palaeolithic scavenging from Couche VIII, Grotte Vaufrey (Dordogne, France). *Journal of Archaeological Science* **21**, 359-375.

- Grayson, D. K. & Delpech, F. (1998). Changing diet breadth in the Early Upper Palaeolithic of Southwestern France. *Journal of Archaeological Science* **25**, 1119-1129.
- Grayson, D. K. & Delpech, F. (2002, March 21, 2002). *Specialized Early Upper Paleolithic hunters in Southwestern France?* Paper presented at the Society for American Archaeology, Denver, CO.
- Grayson, D. K., Delpech, F., Rigaud, J.-P. & Simek, J. F. (2001). Explaining the development of dietary dominance by a single ungulate taxon at Grotte XVI, Dordogne, France. *Journal of Archaeological Science* **28**, 115-125.
- Grün, R. & Schwarcz, H. P. (2000). Revised open system U-series/ESR age calculations for teeth from Stratum C at the Hoxnian Interglacial type locality, England. *Quaternary Science Reviews* **19**, 1151-1154.
- Guadelli, J.-L. (1996). Les cerfs du Würm ancien en Aquitaine. *Paleo* **8**, 99-108.
- Hadly, E. A. (1997). Evolutionary and ecological response of pocket gophers (*Thomomys talpoides*) to late-Holocene climatic change. *Biological Journal of the Linnean Society* **60**, 277-296.
- Hamlin, K. L., Pac, D. F., Sime, C. A., DeSimone, R. M. & Dusek, G. L. (2000). Evaluating the accuracy of ages obtained by two methods for Montana ungulates. *Journal of Wildlife Management* **64**, 441-449.
- Hardy, B. L., Kay, M., Marks, A. E. & Monigal, K. (2001). Stone tool function at the paleolithic sites of Starosele and Buran Kaya III, Crimea: Behavioral implications. *Proceedings of the National Academy of Science* **98**, 10972-10977.
- Harpole, J. L. & Lyman, R. L. (1999). The Holocene biogeographic history of elk (*Cervus elaphus*) in western Washington. *Northwest Science* **73**, 106-113.
- Harrold, F. B. (1989). Mousterian, Châtelperronian and Early Aurignacian in western Europe: Continuity or discontinuity? In (P. Mellars & C. B. Stringer, Eds) *The Human Revolution: Behavioural and Biological Perspectives on the Origins of Modern Humans*. Edinburgh University Press: Edinburgh, pp. 677-713.
- Henshilwood, C. S., d'Errico, F., Marean, C. W., Milo, R. G. & Yates, R. (2001). An early bone tool industry from the Middle Stone Age at Blombos Cave, South Africa: implications for the origins of modern human behavior, symbolism and language. *Journal of Human Evolution* **41**, 631-678.
- Henshilwood, C. S., d'Errico, F., Yates, R., Jacobs, Z., Tribolo, C., Duller, G. A. T., Mercier, N., Sealy, J., Valladas, H., Watts, I. & Wintle, A. G. (2002). Emergence of modern human behavior: Middle Stone Age engravings from South Africa. *Science* **295**, 1278-1280.

- Hillson, S. (1986). *Teeth*. Cambridge: Cambridge University Press.
- Hoffecker, J. F. (1999). Neanderthals and modern humans in Eastern Europe. *Evolutionary Anthropology* **7**, 129-141.
- Hoffecker, J. F., Baryshnikov, G. & Potapova, O. (1991). Vertebrate remains from the Mousterian site of Il'skaya I (Northern Caucasus, U.S.S.R.): New analysis and interpretation. *Journal of Archaeological Science* **18**, 113-147.
- Holliday, T. W. (1997). Body proportions in Late Pleistocene Europe and modern human origins. *Journal of Human Evolution* **32**, 423-447.
- Houston, D. B. (1982). *The Northern Yellowstone Elk: Ecology and Management*. New York: Macmillan Publishing Co., Inc.
- Howell, F. C. & Fritz, M. C. (1975). Israel. In (K. P. Oakley, B. G. Campbell & T. I. Molleson, Eds) *Catalogue of Fossil Hominids. Part III: Americas, Asia, Australia*. Trustees of the British Museum (Natural History): London, pp. 125-154.
- Hublin, J.-J. (1998). Climatic changes, paleogeography, and the evolution of the Neandertals. In (T. Akazawa, K. Aoki & O. Bar-Yosef, Eds) *Neandertals and Modern Humans in Western Asia*. Plenum Press: New York, pp. 295-310.
- Hublin, J.-J., Spoor, F., Braun, M., Zonneveld, F. & Condemi, S. (1996). A late Neanderthal associated with Upper Paleolithic artefacts. *Nature* **381**, 224-226.
- Hulbert. (1982). Population dynamics of the three-toed horse *Neohipparion* from the late Miocene of Florida. *Paleobiology* **8**, 159-167.
- Iacumin, P., Bocherens, H., Delgado Huertas, A., Mariotti, A. & Longinelli, A. (1997). A stable isotope study of fossil mammal remains from the Paglicci cave, Southern Italy. N and C as palaeoenvironmental indicators. *Earth and Planetary Science Letters* **148**, 349-357.
- Ingman, M., Kaessmann, H., Pääbo, S. & Gyllensten, U. (2000). Mitochondrial genome variation and the origin of modern humans. *Nature* **408**, 708-713.
- Janis, C. M. (1990). Correlations of cranial and dental variables with body size in ungulates and macropods. In (J. Damuth & B. J. MacFadden, Eds) *Body Size in Mammalian Paleobiology: Estimation and Biological Implications*. Cambridge University Press: Cambridge, pp. 255-299.
- Janis, C. M. & Lister, A. M. (1985). The morphology of the lower fourth premolar as a taxonomic character in the Ruminantia (Mammalia; Artiodactyla), and the systematic position of *Triceromeryx*. *Journal of Paleontology* **59**, 405-410.

- Jaubert, J. & Brugal, J.-P. (1990). Contribution à l'étude du mode de vie au Paléolithique moyen: les chasseurs d'aurochs de la Borde. In (J. Jaubert, M. Lorblanchet, H. Laville, R. Slott-Moller, A. Turq & J.-P. Brugal, Eds) *Les Chasseurs d'Aurochs de La Borde: un site du Paléolithique moyen (Livernon, Lot)*. Maison des Sciences de l'Homme (Documents d'Archéologie Française 27): Paris, pp. 128-145.
- Justus, A. (1992). *Der Mittelpaläolithische Fundplatz "In den Wannan" (Östlicher Wanner-Vulkan-Komplex)*. Ph.D. Thesis, Universität zu Köln, Köln.
- Kaplan, H. & Hill, K. (1992). The evolutionary ecology of food acquisition. In (E. A. Smith & B. Winterhalder, Eds) *Evolutionary Ecology and Human Behavior*. Aldine de Gruyter: New York, pp. 167-201.
- Karavanic, I. & Smith, F. H. (1998). The Middle/Upper Paleolithic interface and the relationship of Neanderthals and early modern humans in the Hrvatsko Zagorje, Croatia. *Journal of Human Evolution* **34**, 223-248.
- Ke, Y., Su, B., Song, X., Lu, D., Chen, L., Li, H., Qi, C., Marzuki, S., Deka, R., Underhill, P. A., Xiao, C., Shriver, M., Lell, J., Wallace, D., Wells, R. S., Seielstad, M. T., Oefner, P. J., Zhu, D., Jin, J., Huang, W., Chakraborty, R., Chen, Z. & Jin, L. (2001). African origin of modern humans in East Asia: A tale of 12,000 Y chromosomes. *Science* **292**, 1151-1153.
- Keiss, R. E. (1969). Comparison of eruption-wear patterns and cementum annuli as age criteria in elk. *Journal of Wildlife Management* **33**, 175-180.
- Kierdorf, U. & Becher, J. (1997). Mineralization and wear of mandibular first molars in red deer (*Cervus elaphus*) of known age. *Journal of Zoology, London* **241**, 135-143.
- Klein, R. G. (1978). Stone Age predation on large African bovids. *Journal of Archaeological Science* **5**, 195-217.
- Klein, R. G. (1982a). Age (mortality) profiles as a means of distinguishing hunted species from scavenged ones in Stone Age archeological sites. *Paleobiology* **8**, 151-158.
- Klein, R. G. (1982b). Patterns of ungulate mortality and ungulate mortality profiles from Langebaanweg (Early Pliocene) and Elandsfontein (Middle Pleistocene), South-western Cape Province, South Africa. *Annals of the South African Museum* **20**, 49-94.
- Klein, R. G. (1986). Carnivore size and Quaternary climatic change in Southern Africa. *Quaternary Research* **26**, 153-170.
- Klein, R. G. (1992). The archeology of modern human origins. *Evolutionary Anthropology* **1**, 5-14.

- Klein, R. G. (1994). Southern Africa before the Iron Age. In (R. S. Corruccini & R. L. Ciochon, Eds) *Integrative Paths to the Past: Paleoanthropological Advances in Honor of F. Clark Howell*. Prentice Hall: Englewood Cliffs, NJ, pp. 471-519.
- Klein, R. G. (1995). Anatomy, behavior, and modern human origins. *Journal of World Prehistory* **9**, 167-198.
- Klein, R. G. (1998). Why anatomically modern people did not disperse from Africa 100,000 years ago. In (T. Akazawa, K. Aoki & O. Bar-Yosef, Eds) *Neandertals and Modern Humans in Western Asia*. Plenum Press: New York, pp. 509-521.
- Klein, R. G. (1999). *The Human Career: Human Biological and Cultural Origins*. (Second ed.). Chicago: The University of Chicago Press.
- Klein, R. G. (2000a). Archaeology and the evolution of human behavior. *Evolutionary Anthropology* **9**, 17-36.
- Klein, R. G. (2000b). The Earlier Stone Age of Southern Africa. *South African Archaeological Journal* **55**, 1-16.
- Klein, R. G., Allwarden, K. & Wolf, C. (1983). The calculation and interpretation of ungulate age profiles from dental crown heights. In (G. Bailey, Ed.) *Hunter-Gatherer Economy in Prehistory: A European Perspective*. Cambridge University Press: Cambridge, pp. 47-57.
- Klein, R. G., Avery, G., Cruz-Uribe, K., Halkett, D., Hart, T., Milo, R. G. & Volman, T. P. (1999). Duinefontein 2: an Acheulean site in the Western Cape Province of South Africa. *Journal of Human Evolution* **37**, 153-190.
- Klein, R. G. & Cruz-Uribe, K. (1983). The computation of ungulate age (mortality) profiles from dental crown heights. *Paleobiology* **9**, 70-78.
- Klein, R. G. & Cruz-Uribe, K. (1984). *The Analysis of Animal Bones from Archeological Sites*. Chicago: The University of Chicago Press.
- Klein, R. G. & Cruz-Uribe, K. (1994). The Paleolithic mammalian fauna from the 1.910-14 excavations at El Castillo Cave (Cantabria). *Museo y Centro de Investigación de Altamira* **17**, 141-158.
- Klein, R. G. & Cruz-Uribe, K. (1996a). Exploitation of large bovids and seals at Middle and Later Stone Age sites in South Africa. *Journal of Human Evolution* **31**, 315-334.
- Klein, R. G. & Cruz-Uribe, K. (1996b). Size variation in the rock hyrax (*Procapra capensis*) and Late Quaternary climatic change in South Africa. *Quaternary Research* **46**, 193-207.

- Klein, R. G., Wolf, C., Freeman, L. G. & Allwarden, K. (1981). The use of dental crown heights for constructing age profiles of red deer and similar species in archaeological samples. *Journal of Archaeological Science* **8**, 1-31.
- Knight, A., Batzer, M. A., Stoneking, M., Tiwari, H., Scheer, W. D., Herrera, R. J. & Deininger, P. L. (1996). DNA sequences of *Alu* elements indicate a recent replacement of the human autosomal genetic complement. *Proceedings of the National Academy of Science* **93**, 4360-4364.
- Koike, H. & Ohtaishi, N. (1985). Prehistoric hunting pressure estimated by the age composition of excavated sika deer (*Cervus nippon*) using the annual layer of tooth cement. *Journal of Archaeological Science* **12**, 443-456.
- Kramer, A., Crummett, T. L. & Wolpoff, M. H. (2001). Out of Africa and into the Levant: replacement or admixture in western Asia? *Quaternary International* **75**, 51-63.
- Krings, M., Capelli, C., Tschentscher, F., Geisert, H., Meyer, S., von Haeseler, A., Grossschmidt, K., Possnert, G., Paunovic, M. & Pääbo, S. (2000). A view of Neandertal genetic diversity. *Nature genetics* **26**, 144-146.
- Krings, M., Geisert, H., Schmitz, R. W., Krainitzki, H. & Pääbo, S. (1999). DNA sequence of the mitochondrial hypervariable region II from the Neandertal type specimen. *Proceedings of the National Academy of Science* **96**, 5581-5585.
- Krings, M., Stone, A., Schmitz, R. W., Krainitzki, H., Stoneking, M. & Pääbo, S. (1997). Neandertal DNA sequences and the origins of modern humans. *Cell* **90**, 19-30.
- Kuhn, S. L., Stiner, M. C., Reese, D. S. & Güleç, E. (2001). Ornaments of the earliest Upper Paleolithic: New insights from the Levant. *Proceedings of the National Academy of Science* **98**, 7641-7646.
- Kunkel, K. E., Ruth, T. K., Pletscher, D. H. & Hornocker, M. G. (1999). Winter prey selection by wolves and cougars in and near Glacier National Park, Montana. *Journal of Wildlife Management* **63**, 901-910.
- Kurtén, B. (1953). On the variation and population dynamics of fossil and recent mammal populations. *Acta Zoologica Fennica* **76**, 1-122.
- Lahr, M. M. (1994). The Multiregional Model of modern human origins: a reassessment of its morphological basis. *Journal of Human Evolution* **26**, 23-56.
- Lahr, M. M. & Foley, R. A. (1998). Towards a theory of modern human origins: Geography, demography, and diversity in recent human evolution. *Yearbook of Physical Anthropology*, 137-176.
- Langvatn, R. & Albon, S. D. (1986). Geographic clines of body weight of Norwegian red deer: a novel explanation of Bergmann's rule? *Holarctic Ecology* **9**, 285-293.

- Lévêque, F. & Vandermeersch, B. (1980). Découverte de restes humains dans un niveau castelperronien à Saint-Césaire (Charente-Maritime). *Compte Rendu de l'Académie des Sciences de Paris* **291**, 187-189.
- Levine, M. A. (1983). Mortality models and the interpretation of horse population structure. In (G. Bailey, Ed.) *Hunter-Gatherer Economy in Prehistory: A European Perspective*. Cambridge University Press: Cambridge, pp. 23-46.
- Lieberman, D. E. (1993). Life history variables preserved in dental cementum microstructure. *Science* **261**, 1162-1164.
- Lieberman, D. E., Pearson, O. M. & Mowbray, K. M. (2000). Basicranial influence on overall cranial shape. *Journal of Human Evolution* **38**, 291-315.
- Lieberman, D. E. & Shea, J. J. (1994). Behavioral differences between archaic and modern humans in the Levantine Mousterian. *American Anthropologists* **96**, 300-332.
- Lindly, J. M. & Clark, G. A. (1990). Symbolism and modern human origins. *Current Anthropology* **31**, 233-261.
- Lister, A. M. (1981). *Evolutionary Studies on Pleistocene Deer*. Ph.D. Thesis, University of Cambridge, Cambridge.
- Lister, A. M. (1984). Evolutionary and ecological origins of British deer. *Proceedings of the Royal Society of Edinburgh* **82B**, 205-229.
- Lister, A. M. (1986). New results on deer from Swanscombe, and the stratigraphical significance of deer in the Middle and Upper Pleistocene of Europe. *Journal of Archaeological Science* **13**, 319-338.
- Lister, A. M. (1987). Giant deer and giant red deer from Kent's Cavern, and the status of *Strongyloceros spelaeus* Owen. *Transactions of the Proceedings of the Torquay Natural History Society* **19**, 189-198.
- Lister, A. M. (1989). Rapid dwarfing of red deer on Jersey in the Last Interglacial. *Nature* **342**, 539-542.
- Lister, A. M. (1993). Cervidae, deer. In (R. Singer, B. G. Gladfelter & J. J. Wymer, Eds) *The Lower Paleolithic Site at Hoxne, England*. The University of Chicago Press: Chicago, pp. 176-190.
- Lowe, V. P. W. (1967). Teeth as indicators of age with special reference to Red deer (*Cervus elaphus*) of known age from Rhum. *Journal of Zoology, London* **152**, 137-153.
- Lowe, V. P. W. (1969). Population dynamics of the red deer (*Cervus elaphus* L.) on Rhum. *Journal of Animal Ecology* **38**, 425-457.

- Lubinski, P. M. (1997). *Pronghorn Intensification in the Wyoming Basin*. Ph.D. Thesis, University of Wisconsin, Madison.
- Lubinski, P. M. (2000). A comparison of methods for evaluating ungulate mortality distributions. *ArchaeoZoologia* **11**, 121-134.
- Lyman, R. L. (1984). Bone density and differential survivorship of fossil classes. *Journal of Anthropological Archaeology* **3**, 259-299.
- Lyman, R. L. (1985). Bone frequencies: Differential transport, *in situ* destruction, and the MGUI. *Journal of Archaeological Science* **12**, 221-236.
- Lyman, R. L. (1987). On the analysis of vertebrate mortality profiles: Sample size, mortality type, and hunting pressure. *American Antiquity* **51**, 125-142.
- Lyman, R. L. (1994). *Vertebrate Taphonomy*. Cambridge: Cambridge University Press.
- Marean, C. W. (1995). Of taphonomy and zooarcheology. *Evolutionary Anthropology* **4**, 64-72.
- Marean, C. W. (1997). Hunter-gatherer foraging strategies in tropical grasslands: Model building and testing in the East African Middle and Later Stone Age. *Journal of Anthropological Archaeology* **16**, 189-225.
- Marean, C. W. (1998). A critique of the evidence for scavenging by Neandertals and early modern humans: new data from Kobeh Cave (Zagros Mountains, Iran) and Die Kelders Cave 1 Layer 10 (South Africa). *Journal of Human Evolution* **35**, 111-136.
- Marean, C. W. & Kim, S. Y. (1998). Mousterian large-mammal remains from Kobeh Cave. *Current Anthropology* **39**, S79-S113.
- Marean, C. W. & Spencer, L. M. (1991). Impact of carnivore ravaging on zooarchaeological measures of element abundance. *American Antiquity* **56**, 645-658.
- Mariezkurrena, K. & Altuna, J. (1983). Biometría y diformismo sexual en el esqueleto de *Cervus elaphus* wüirmiense, postwüirmiense y actual del Cantábrico. *Munibe* **35**, 203-256.
- Markova, A. K., Smirnov, N. G., Kozharinov, A. V., Kazantseva, N. E., Simakova, A. N. & Kitaev, L. M. (1995). Late Pleistocene distribution and diversity of mammals in Northern Eurasia (PALEOFAUNA Database). *Paleontologia/Evolució* **28-29**, 5-143.
- Mayr, E. (1956). Geographical character gradients and climatic adaptation. *Evolution* **10**, 105-108.

- Mayr, E. (1970). *Populations, Species, and Evolution*. Cambridge, MA: The Belknap Press of Harvard University Press.
- McBrearty, S. & Brooks, A. S. (2000). The revolution that wasn't: a new interpretation of the origins of modern human behavior. *Journal of Human Evolution* **39**, 453-563.
- McCabe, R. E. (1982). Elk and Indians: historical values and perspectives. In (J. W. Thomas & D. E. Towell, Eds) *Elk of North America: Ecology and Management*. Stackpole Books: Harrisburg, PA, pp. 61-123.
- McCullough, D. R. (1969). The Tule Elk: Its history, behavior, and ecology. *University of California Publications in Zoology* **88**, 1-209.
- McKinley, V. & Burke, A. (2000). A new control sample for season of death estimates for *Equus caballus* from dental thin-sections. *ArchaeoZoologia* **11**, 33-42.
- Mech, L. D. (1970). *The Wolf: The Ecology and Behavior of an Endangered Species*. New York, NY: Doubleday & Company, Inc.
- Mech, L. D., Adams, L. G., Meier, T. J., Burch, J. W. & Dale, B. W. (1998). *The Wolves of Denali*. Minneapolis: University of Minnesota.
- Mech, L. D., Smith, D. W., Murphy, K. M. & MacNulty, D. R. (2001). Winter severity and wolf predation on a formerly wolf-free elk herd. *Journal of Wildlife Management* **65**, 998-1003.
- Mellars, P. (1973). The character of the Middle-Upper Paleolithic transition in south-west France. In (C. Renfrew, Ed.) *The Explanation of Culture Change: Models in Prehistory*. Duckworth: London, pp. 255-276.
- Mellars, P. (1982). On the Middle/Upper Palaeolithic transition: A reply to White. *Current Anthropology* **23**, 238-240.
- Mellars, P. (1989). Technological changes across the Middle-Upper Palaeolithic transition: Economics, social and cognitive perspectives. In (P. Mellars & C. B. Stringer, Eds) *The Human Revolution: Behavioural and Biological Perspectives on the Origins of Modern Humans*. Edinburgh University Press: Edinburgh, pp. 338-365.
- Mellars, P. (1996). *The Neanderthal Legacy*. Princeton, NJ: Princeton University Press.
- Mellars, P. (1999). The Neanderthal problem continued. *Current Anthropology* **40**, 341-364.
- Mellars, P. (2000). Châtelperronian chronology and the case for Neanderthal/modern human 'acculturation' in western Europe. In (C. B. Stringer, R. N. E. Barton & J. C. Finlayson, Eds) *Neanderthals on the Edge*. Oxbow Books: Oxford, pp. 33-39.

- Mercier, N., Valladas, H., Joron, J.-L. & Reyss, J.-L. (1993). Thermoluminescence dating of the prehistoric site of La Roche à Pierrot, Saint-Césaire. In (F. Lévêque, A. M. Backer & M. Guilbaud, Eds) *Context of a Late Neandertal*. Prehistory Press: Madison, WI, pp. 15-21.
- Mitchell, B. (1967). Growth layers in dental cement for determining the age of red deer (*Cervus elaphus* L.). *Journal of Animal Ecology* **36**, 279-293.
- Moigne, A.-M., Bails, H. & Grégoire, S. (1998). Les magdaléniens de las grotte des Conques (Pyrénées-Orientales), caractérisation du site d'après les restes osseux et l'outillage. In (APDCA, Ed.) *Économie Préhistorique: Les Comportements de Subsistance au Paléolithique*. XVIII Rencontres Internationales d'Archéologie et d'Histoire d'Antibes: Sophia Antipolis, pp. 397-411.
- Monnier, J. L. (1985). Données nouvelles sur le gisement Paleolithique Moyen de Piegu (Pléneuf-Val-André, Côtes-du-Nord). *Revue archéologique Ouest* **2**, 7-21.
- Monnier, J. L. (1991). *La Préhistoire de Bretagne d'Armorique*.
- Mooney, C. Z. & Duval, R. D. (1993). *Bootstrapping: A Nonparametric Approach to Statistical Inference*. Newbury Park, CA: Sage Publications.
- Moran, A. J. & Chamberlain, A. T. (1997). The incidence of dorsal sulci of the scapula in a modern human population from Ensay, Scotland. *Journal of Human Evolution* **33**, 521-524.
- Morris, P. (1972). A review of mammalian age determination methods. *Mammal Review* **2**, 69-104.
- Morrison, D. & Whitridge, P. (1997). Estimating the age and sex of caribou from mandibular measurements. *Journal of Archaeological Science* **24**, 1093-1106.
- Movius, H. L., Jr. (1975). Excavation of the Abri Pataud, Les Eyzies (Dordogne). *American School of Prehistoric Research, Peabody Museum, Harvard University* **30**, 1-305.
- Müller-Beck, H. (1988). The ecosystem of the "Middle Paleolithic" (Late Lower Paleolithic) in the Upper Danube Region: A stepping-stone to the Upper Paleolithic. In (H. L. Dibble & A. Montet-White, Eds) *Upper Pleistocene Prehistory of Western Eurasia*. The University Museum: Philadelphia, pp. 233-254.
- Munson, P. J. (1991). Mortality profiles of white-tailed deer from archaeological sites in Eastern North America: Selective hunting or taphonomy? In (J. R. Purdue, W. E. Klippel & B. W. Styles, Eds) *Beamers, Bobwhites, and Blue-Points: Tributes to the Career of Paul W. Parmalee*. Illinois State Museum Scientific Papers: Springfield, IL, pp. 139-151.

- Munson, P. J. (2000). Age-correlated differential destruction of bones and its effect on archaeological mortality profiles of domestic sheep and goat. *Journal of Archaeological Science* **27**, 391-407.
- Murie, O. J. (1951). *The Elk of North America*. Harrisburg, PA: The Stackpole Company.
- Nordborg, M. (1998). On the probability of Neanderthal ancestry. *American Journal of Human Genetics* **63**, 1237-1240.
- Nowak, R. M. & Paradiso, J. L. (Eds.). (1983). *Walker's Mammals of the World, 4th Edition*. Baltimore, MD: The John Hopkins University Press.
- O'Connell, J. F., Hawkes, K. & Blurton Jones, N. (1988). Hadza scavenging: Implications for Plio/Pleistocene hominid subsistence. *Current Anthropology* **29**, 356-363.
- O'Connor, T. (2000). *The Archaeology of Animal Bones*. College Station, TX: Texas A&M University Press.
- Oakley, K. P. (1971). British Isles. In (K. P. Oakley, B. G. Campbell & T. I. Molleson, Eds) *Catalogue of Fossil Hominids. Part II: Europe*. Trustees of the British Museum (Natural History): London, pp. 15-43.
- Olf, H., Ritchie, M. E. & Prins, H. H. T. (2002). Global environmental controls of diversity in large herbivores. *Nature* **415**, 901-904.
- Ovchinnikov, I. V., Götherström, A., Romanova, G. P., Kharitonov, V. M., Lidén, K. & Goodwin, W. (2000). Molecular analysis of Neanderthal DNA from the Northern Caucasus. *Nature* **404**, 490-493.
- Patou-Mathis, M. (1994). Archéozoologie des niveaux Moustériens et Aurignaciens de las Grotte Tournal à Bize (Aude). *Gallia Préhistoire* **36**, 1-64.
- Patou-Mathis, M. (1996). Les comportements de subsistence à la fin du Paléolithique moyen et du début du Paléolithique supérieur d'après les données archéozoologiques de quelques sites languedociens. In (CNRS-DGICYT, Ed.) *La Survivance des Derniers Neandertaliens dans les Pyrenees Mediterraneennes*. Laboratoire de Préhistoire de Carcassonne - Area de Prehistoria Universitat de Girona: Girona, pp. 34-56.
- Paupé, P. (1985). Informations Archéologiques: Romain-la-Roche. *Gallia Préhistoire* **28**, 238-239.
- Paupé, P. (1995). L'aven de Romain-la-Roche: un site paléontologique et Préhistorique. *Archéologia* **312**, 60-66.
- Pavlov, P., Svendsen, J. I. & Indrelid, S. (2001). Human presence in the European Arctic nearly 40,000 years ago. *Nature* **413**, 64-67.

- Petit-Marie, N., Ferembach, D., Bouvier, J.-M. & Vandermeersch, B. (1971). France. In (K. P. Oakley, B. G. Campbell & T. I. Molleson, Eds) *Catalogue of Fossil Hominids. Part II: Europe*. Trustees of the British Museum (Natural History): London, pp. 69-187.
- Pike-Tay, A. (1991). *Red Deer Hunting in the Upper Paleolithic of South-West France: A Study in Seasonality*. (Vol. 569). Oxford: BAR International Series.
- Pike-Tay, A. (1995). Variability and synchrony of seasonal indicators in dental cementum microstructure of the Kaminuriak caribou population. *Archaeofauna* **4**, 273-285.
- Pike-Tay, A. (Ed.). (2000). *Innovations in assessing season of capture, age and sex of archaeofaunas*. (Vol. XI/1.2). Grenoble: ArchaeoZoologia.
- Pike-Tay, A., Cabrera Valdés, V. & Bernaldo de Quirós, F. (1999). Seasonal variations of the Middle-Upper Paleolithic transition at El Castillo, Cueva Morín and El Pendo (Cantabria, Spain). *Journal of Human Evolution* **36**, 283-317.
- Pike-Tay, A., Morcomb, C. A. & O'Farrell, M. (2000). Reconsidering the Quadratic Crown Height Method of age estimation for *Rangifer* from archaeological sites. *ArchaeoZoologia* **11**, 145-174.
- Prat, F. & Suire, C. (1971). Remarques sur les cerfs contemporains des deux stades würmiens. *Bulletin de la Société préhistorique française* **68**, 75-79.
- Quimby, D. C. & Gaab, J. E. (1957). Mandibular dentition as an age indicator in Rocky Mountain Elk. *Journal of Wildlife Management* **21**, 435-451.
- Quintana-Murci, L., Semina, O., Bandelt, H.-J., Passarino, G., McElreavey, K. & Santachiara-Benerecetti, A. S. (1999). Genetic evidence of an early exit of *Homo sapiens sapiens* from Africa through eastern Africa. *Nature genetics* **23**, 437-441.
- Reitz, E. J. & Wing, E. S. (1999). *Zooarchaeology*. Cambridge: Cambridge University Press.
- Rigaud, J.-P. (2000). Late Neandertals in the South West of France and the emergence of the Upper Palaeolithic. In (C. B. Stringer, R. N. E. Barton & J. C. Finlayson, Eds) *Neanderthals on the Edge*. Oxbow Books: Oxford, pp. 27-31.
- Rightmire, P. G. (1976). Relationships of Middle and Upper Pleistocene hominids from Sub-Saharan Africa. *Nature* **260**, 238-240.
- Rightmire, P. G. (1989). Middle Stone Age humans from Eastern and Southern Africa. In (P. Mellars & C. B. Stringer, Eds) *The Human Revolution: Behavioural and Biological Perspectives on the Origins of Modern Humans*. Edinburgh University Press: Edinburgh, pp. 109-122.

- Roebroeks, W. (2001). Hominid behaviour and the earliest occupation of Europe: an exploration. *Journal of Human Evolution* **41**, 437-461.
- Sall, J. & Lehman, A. (1996). *JMP Start Statistics*. Belmont, CA: Duxbury Press.
- Schreve, D. C. (1997). *Mammalian Biostratigraphy of the later Middle Pleistocene in Britain*. Ph.D. Thesis, University of London, London.
- Schreve, D. C. (2001). Differentiation of the British late Middle Pleistocene interglacials: the evidence from mammalian biostratigraphy. *Quaternary Science Reviews* **20**, 1693-1705.
- Scott, K. M. (1987). Allometry and habitat-related adaptations in the postcranial skeleton of Cervidae. In (C. M. Wemmer, Ed.) *Biology and Management of the Cervidae*. Smithsonian Institution Press: Washington, D.C., pp. 65-80.
- Scott, K. M. (1990). Postcranial dimensions of ungulates as predictors of body mass. In (J. Damuth & B. J. MacFadden, Eds) *Body Size in Mammalian Paleobiology: Estimation and Biological Implications*. Cambridge University Press: Cambridge, pp. 301-335.
- Sekhr, A. (1998). *Etude Archeozoologique des Niveaux Aurignaciens (couches 14 à 6) et de la base des Niveaux Gravettiens (Niveaux X à T4) de l'Abri Pataud (Las Eyzies, Dordogne): Paléoécologie, Taphonomie, Paleoethnographie*. Ph.D. Thesis, Museum National d'Histoire Naturelle, Paris.
- Severinghaus, C. W. (1949). Tooth development and wear as criteria of age in white-tailed deer. *Journal of Wildlife Management* **13**, 195-216.
- Shea, J. J. (1989). A functional study of the lithic industries associated with hominid fossils in the Kebara and Qafzeh Caves, Israel. In (P. Mellars & C. B. Stringer, Eds) *The Human Revolution: Behavioural and Biological Perspectives on the Origins of Modern Humans*. Edinburgh University Press: Edinburgh, pp. 611-625.
- Shea, J. J. (1998). Neandertal and early modern human behavioral variability. *Current Anthropology* **39**, S45-S78.
- Shea, J. J., Davis, Z. & Brown, K. (2001). Experimental Tests of Middle Palaeolithic Spear Points Using a Calibrated Crossbow. *Journal of Archaeological Science* **28**, 807-816.
- Shipman, P. (1981). *Life History of a Fossil: An Introduction to Taphonomy and Paleoecology*. Cambridge, MA: Harvard University Press.
- Silva, M. & Downing, J. A. (1995). *Mammalian Body Mass*. Boca Raton: CRC Press.
- Silverman, B. W. (1982). Algorithm AS 176. Kernel density estimation using the fast fourier transformation. *Applied Statistics* **31**, 93-99.

- Silverman, B. W. (1986). *Density Estimation for Statistics and Data Analysis*. New York: Chapman and Hall.
- Slott-Moller, R. (1990). La Faune. In (J. Jaubert, M. Lorblanchet, H. Laville, R. Slott-Moller, A. Turq & J.-P. Brugal, Eds) *Les Chasseurs d'Aurochs de La Borde: un site du Paléolithique moyen (Livernon, Lot)*. Maison des Sciences de l'Homme (Documents d'Archéologie Française 27): Paris, pp. 33-68.
- Smith, D. W., Mech, L. D., Meagher, M., Clark, W. E., Jaffe, R., Phillips, M. K. & Mack, J. A. (2000). Wolf-bison interactions in Yellowstone National Park. *Journal of Mammalogy* **81**, 1128-1135.
- Smith, E. A. & Winterhalder, B. (1992). Natural selection and decision-making: some fundamental principles. In (E. A. Smith & B. Winterhalder, Eds) *Evolutionary Ecology and Human Behavior*. Aldine de Gruyter: New York, pp. 25-60.
- Smith, R. J. (1996). Biology and body size in human evolution. *Current Anthropology* **37**, 451-481.
- Sokal, R. R. & Rohlf, F. J. (1995). *Biometry: The Principles and Practice of Statistics in Biological Research*. (Third ed.). New York: W. H. Freeman and Company.
- Speth, J. D. (1997). Communal bison hunting in western North America: Background for the study of Paleolithic bison hunting in Europe. In (M. Patou-Mathis & M. Otte, Eds) *L'Alimentation des Hommes du Paléolithique*. ERAUL: Liège, pp. 23-57.
- Speth, J. D. & Tchernov, E. (1998). The role of hunting and scavenging in Neandertal procurement strategies: New evidence from Kebara Cave (Israel). In (T. Akazawa, K. Aoki & O. Bar-Yosef, Eds) *Neandertals and Modern Humans in Western Asia*. Plenum Press: New York, pp. 223-239.
- Speth, J. D. & Tchernov, E. (2002). Middle Paleolithic tortoise use at Kebara Cave (Israel). *Journal of Archaeological Science* **29**, 471-483.
- Spinage, C. A. (1971). Geratodontology and horn growth of the impala (*Aepyceros melampus*). *Journal of Zoology, London* **164**, 209-225.
- Spinage, C. A. (1972). Age estimation of zebra. *East African Wildlife Journal* **10**, 273-277.
- Spinage, C. A. (1973). A review of age determination of mammals by means of teeth, with special reference to Africa. *East African Wildlife Journal* **11**, 165-187.
- Spinage, C. A. & Brown, W. A. B. (1988). Age determination of the West African buffalo (*Syncerus caffer brachyceros*) and the constancy of tooth wear. *African Journal of Ecology* **26**, 221-227.

- Steele, T. E. & Weaver, T. D. (2002). The modified triangular graph: A refined method for comparing mortality profiles in archaeological samples. *Journal of Archaeological Science* **29**, 317-322.
- Stephens, D. W. & Krebs, J. R. (1986). *Foraging Theory*. Princeton, NJ: Princeton University Press.
- Stiner, M. C. (1990). The use of mortality patterns in archaeological studies of hominid predatory adaptations. *Journal of Anthropological Archaeology* **9**, 305-351.
- Stiner, M. C. (1991a). Food procurement and transport by human and non-human predators. *Journal of Archaeological Science* **18**, 455-482.
- Stiner, M. C. (1991b). An interspecific perspective on the emergence of the modern human predatory niche. In (M. C. Stiner, Ed.) *Human Predators and Prey Mortality*. Westview Press: Boulder, CO, pp. 149-185.
- Stiner, M. C. (1994). *Honor Among Thieves: A Zooarchaeological Study of Neandertal Ecology*. Princeton, NJ: Princeton University Press.
- Stiner, M. C. (1998). Mortality analysis of Pleistocene bears and its paleoanthropological relevance. *Journal of Human Evolution* **34**, 303-326.
- Stiner, M. C., Munro, N. D. & Surovell, T. A. (2000). The tortoise and the hare. *Current Anthropology* **41**, 39-73.
- Stiner, M. C., Munro, N. D., Surovell, T. A., Tchernov, E. & Bar-Yosef, O. (1999). Paleolithic population growth pulses evidenced by small animal exploitation. *Science* **283**, 190-194.
- Stiner, M. C. & Tchernov, E. (1998). Pleistocene species trends at Hayonim Cave. In (T. Akazawa, K. Aoki & O. Bar-Yosef, Eds) *Neandertals and Modern Humans in Western Asia*. Plenum Press: New York, pp. 241-262.
- Straus, L. G. (1977). Of deerslayers and mountain men: Paleolithic faunal exploitation in Cantabrian Spain. In (L. R. Binford, Ed.) *For Theory Building in Archaeology*. Academic Press: New York, pp. 41-76.
- Straus, L. G. (1981). On the habitat and diet of *Cervus elaphus*. *Munibe* **33**, 175-182.
- Straus, L. G. (1986). An overview of the La Riera Chronology. In (L. G. Straus & G. A. Clark, Eds) *La Riera Cave: Stone Age Hunter-Gatherer Adaptations in Northern Spain*. Anthropological Research Papers: Arizona State University, pp. 19-23.
- Straus, L. G. (1992). *Iberia Before the Iberians: The Stone Age Prehistory of Cantabrian Spain*. Albuquerque: University of New Mexico Press.

- Street, M. & Baales, M. (1999). Pleistocene/Holocene changes in the Rhineland fauna in a northwest European context. In (N. Benecke, Ed.) *The Holocene History of the European Vertebrate Fauna*. Verlag Marie Leidorf GmbH: Rahden, pp. 9-38.
- Stringer, C. B. & Andrews, P. (1988). Genetic and fossil evidence for the origin of modern humans. *Science* **239**, 1263-1239.
- Stringer, C. B. & Gamble, C. (1993). *In Search of the Neanderthals: Solving the Puzzle of Human Origins*. New York: Thames and Hudson Inc.
- Taber, R. D., Raedeke, K. & McCaughran, D. A. (1982). Population Characteristics. In (J. W. Thomas & D. E. Toweill, Eds) *Elk of North America: Ecology and Management*. Stackpole Books: Harrisburg, PA, pp. 279-298.
- Tagliacozzo, A. & Cassoli, P. F. (1994). La macrofaune de l'Abri Soman (Val d'Adige - Italie). *Preistoria Alpina - Museo Tridentino di Scienze Naturali* **28**, 181-192.
- Tattersal, I. (2001). How we came to be human. *Scientific American* **December**, 56-63.
- Tattersal, I. & Schwartz, J. H. (1999). Hominids and hybrids: The place of Neanderthals in human evolution. *Proceedings of the National Academy of Science* **96**, 7117-7119.
- Tavoso, A. (1987). Le remplissage de la grotte Tournal à Bize-Minervois (Aude). *Cypsela* **6**, 23-35.
- Taylor, R. D. (1988). Age determination of the African buffalo, *Syncerus caffer* (Sparman) in Zimbabwe. *African Journal of Ecology* **26**, 207-220.
- Tchernov, E. (1998). The faunal sequence of the southwest Asian Middle Paleolithic in relation to hominid dispersal events. In (T. Akazawa, K. Aoki & O. Bar-Yosef, Eds) *Neandertals and Modern Humans in Western Asia*. Plenum Press: New York, pp. 77-90.
- Thieme, H. (1997). Lower Palaeolithic hunting spears from Germany. *Nature* **385**, 807-810.
- Thomas, J. W. & Toweill, D. E. (Eds.). (1982). *Elk of North America: Ecology and Management*. Harrisburg, PA: Stackpole Books.
- Thomson, R., Pritchard, J. K., Shen, P., Oefner, P. J. & Feldman, M. W. (2000). Recent common ancestry of human Y chromosomes: Evidence from DNA sequence data. *Proceedings of the National Academy of Science* **97**, 7360-7365.

- Tishkoff, S. A., Dietzsch, E., Speed, W., Pakstis, A. J., Kidd, J. R., Cheung, K., Bonn -Tamir, B., Santachiara-Benerecetti, A. S., Moral, P., Krings, M., P  bo, S., Watson, E., Risch, N., Jenkins, T. & Kidd, K. K. (1996). Global patterns of linkage disequilibrium at the CD4 locus and modern human origins. *Science* **271**, 1380-1387.
- Tixier, J. (1967). Proc  d  s d'analyse et questions de terminologie concernant l'  tude des ensembles industriels du Pal  olithique r  cent et de l'Epipal  olithique dans l'Afrique de Nord-Ouest. In (W. W. Bishop & J. D. Clark, Eds) *Background to Evolution in Africa*. University of Chicago Press: Chicago, pp. 771-820.
- Trinkaus, E. (1981). Neanderthal limb proportions and cold adaptation. In (C. B. Stringer, Ed.) *Aspects of Human Evolution*. Taylor and Francis Ltd: London.
- Tuffreau, A., Antoine, P., Chase, P. G., Dibble, H. L., Ellwood, B. B., Kolfschoten, T. v., Lamotte, A., Laurent, M., McPherron, S. P., Moigne, A.-M. & Munaut, A. V. (1995). Le gisement Acheul  en de Cagny-l'EpINETTE (Somme). *Bulletin de la Soci  t   pr  historique fran  aise* **92**, 169-191.
- Turner, E. (1990). Middle and Late Pleistocene macrofaunas of the Neuwied Basin Region (Rhineland-Palatinate) of West Germany. *Jahrbuch des R  misch-Germanischen Zentralmuseums Mainz* **37**, 135-403.
- Turner, E. (1999). Lithic artefacts and animal bones in flood-plain deposits at Miesenheim I (Central Rhineland, Germany). *Monographien des R  misch-Germanischen Zentralmuseum* **42**, 103-119.
- Underhill, P. A., Passarino, G., Lin, A. A., Shen, P., Lahr, M. M., Foley, R. A., Oefner, P. J. & Cavalli-Sforza, L. L. (2001). The phylogeny of Y chromosome binary haplotypes and the origins of modern human populations. *Annals of Human Genetics* **65**, 43-62.
- Underhill, P. A., Shen, P., Lin, A. A., Jin, L., Passarino, G., Yang, W. H., Kauffman, E., Bonn -Tamir, B., Bertranpetit, J., Francalacci, P., Ibrahim, M., Jenkins, T., Kidd, J. R., Mehdi, S. Q., Seielstad, M. T., Wells, R. S., Piazza, A., Davis, R. W., Feldman, M. W., Cavalli-Sforza, L. L. & Oefner, P. J. (2000). Y chromosome sequence variation and the history of human populations. *Nature genetics* **26**, 358-361.
- Utrilla, P. & Mazo, C. (1997). La transici  n del Tardiglacial al Holoceno en el Alto Arag  n: Los abrigos de las Forcas (Graus, Huesca). In (R. de Balb  n Berhmann & P. Bueno Ram  rez, Eds) *Il Congreso de Arqueolog  a Peninsular: Paleol  tico y Epipaleol  tico*. Fundaci  n Rei Afonso Henriques: Zamora, pp. 349-365.
- Valensi, P. (1996). Taphonomie des grands mammif  res et palethnologies    la Grotte du Lazaret (Nice, France). *Anthropozoologica* **23**, 13-28.

- Valensi, P. (2000). The archaeozoology of Lazaret Cave (Nice, France). *International Journal of Osteoarchaeology* **10**, 357-367.
- Valensi, P. & Abbassi, M. (1998). Reconstitution de paléoenvironnements Quaternaires par l'utilisation de diverses méthodes sur une communauté de mammifères - application à la Grotte du Lazaret. *Quaternaire* **9**, 291-302.
- van Andel, T. H. (1998). Middle and Upper Palaeolithic environments and the calibration of  $^{14}\text{C}$  dates beyond 10,000 BP. *Antiquity* **72**, 26-33.
- van Andel, T. H. & Tzedakis, P. C. (1996). Palaeolithic landscapes of Europe and environs, 150,000-25,000 years ago: An overview. *Quaternary Research* **15**, 481-500.
- Van Deelen, T. R., Hollis, K. M., Anchor, C. & Etter, D. R. (2000). Sex affects age determination and wear of molariform teeth in white-tailed deer. *Journal of Wildlife Management* **64**, 1076-1083.
- Velleman, P. F. (1997). *DataDesk (version 6.0): Statistics Guide*. (Vol. 3). Ithaca, NY: Data Description.
- Velleman, P. F. & Hoaglin, D. C. (1981). *Applications, Basics, and Computing of Exploratory Data Analysis*. Boston, MA: Duxbury Press.
- Vigilant, L., Stoneking, M., Harpending, H., Hawkes, K. & Wilson, A. C. (1991). African populations and the evolution of human mitochondrial DNA. *Science* **253**, 1503-1507.
- Voorhies, M. R. (1969). *Taphonomy and Population Dynamics of an Early Pliocene Vertebrate Fauna, Know County, Nebraska*. (Vol. 1). Laramie, WY: University of Wyoming.
- Walker, R. B. (2000). White-tailed deer (*Odocoileus virginianus*) mortality profiles: examples from the southeastern United States. *ArchaeoZoologia* **11**, 175-186.
- Walvius, M. R. (1961). A discussion of the size of recent red deer (*Cervus elaphus* L.) compared with prehistoric specimens. *Beaufortia* **9**, 75-82.
- Weinstock, J. (1997). The relationship between body size and environment: The case of Late Pleistocene reindeer (*Rangifer tarandus*). *Archaeofauna* **6**, 123-135.
- White, R. (1982). Rethinking the Middle/Upper Paleolithic transition. *Current Anthropology* **23**, 169-192.
- White, T. D. & Folkens, P. (1991). *Human Osteology*. San Diego, CA: Academic Press.

- Willmott, C. J. & Matsuura, K. (2001). *Terrestrial Air Temperature and Precipitation: Monthly and Annual Climatologies (Version 3.02)*. Newark, DE: Center for Climatic Research, Department of Geography, University of Delaware.
- Wilson, B., Grigson, C. & Payne, S. (Eds.). (1982). *Ageing and Sexing Animal Bones from Archaeological Sites*. (Vol. 109). Oxford: BAR British Series.
- Wilson, D. E. & Reeder, D. M. (Eds.). (1993). *Mammal species of the World*. Washington, DC: Smithsonian Institution Press.
- Wolpoff, M. H. (1989). Multiregional Evolution: The fossil alternative to Eden. In (P. Mellars & C. B. Stringer, Eds) *The Human Revolution: Behavioural and Biological Perspectives on the Origins of Modern Humans*. Edinburgh University Press: Edinburgh, pp. 62-108.
- Wolpoff, M. H., Hawks, J. & Caspari, R. (2000). Multiregional, not multiple origins. *American Journal of Physical Anthropology* **112**, 129-136.
- Wolpoff, M. H., Hawks, J., Frayer, D. W. & Hunley, K. (2001). Modern human ancestry at the peripheries: A test of the replacement theory. *Science* **291**, 293-297.
- Wolpoff, M. H., Wu, X. & Thorne, A. G. (1984). Modern *Homo sapiens* origins: a general theory of hominid evolution involving the fossil evidence from East Asia. In (F. H. Smith & F. Spencer, Eds) *The Origins of Modern Humans: a World Survey of the Fossil Evidence*. Alan R. Liss: New York, pp. 411-483.
- Wymer, J. J. & Singer, R. (1993). Introduction. In (R. Singer, B. G. Gladfelter & J. J. Wymer, Eds) *The Lower Paleolithic Site at Hoxne, England*. The University of Chicago Press: Chicago, pp. 1-22.
- Zilhão, J. & d'Errico, F. (1999). The chronology and taphonomy of the earliest Aurignacian and its implications for the understanding of Neandertal extinction. *Journal of World Prehistory* **13**, 1-68.