Chapter 6
Bone's Intrinsic Traits: Inferring Species, Sex, and Age

All physical traits zooarchaeologists use to infer taxon, age, and sex in vertebrates emerge in life through the interaction of animals' genetics with their environment. Such traits are amenable to actualistic study and relational analogies, because most are linked to fundamental functional complexes of feeding, locomotion, and reproduction, and because they develop and function in predictable ways. Chapter 3 outlined how and why paleontologists or zooarchaeologists assign fossil bone specimens to species or other taxonomic classifications, based on their morphology. Likewise, certain physical attributes of vertebrate skeletons permit zooarchaeologists to identify or estimate body size, sex, and ages at death, given the generally uniform processes of growth and development. Some of these sexually specific features, such as antlers, grow in a seasonal pattern and can be used, with circumspection, to estimate the time of year they are acquired. Annular growth patterns in fish bone or mammal teeth can be used to estimate age at death, and season of death can sometimes also be inferred (see below).

The strong causal and functional linkages of such osteological traits make them sound building blocks for drawing more complex inferences about how people interacted with animals in the past. For example, did hunters focus mainly on reindeer, and why? Was more than one breed of horse present at this Roman frontier town? Did Neanderthals acquire adult animals in their prime as efficiently as did the anatomically modern human hunters who succeeded them in Europe? Did the herders at this encampment cull most immature males from their herds, but allow females to live and reproduce until a ripe old age? Was this site used only when the salmon ran in the nearby river or for a longer span of time during the year?

Despite strong causal relations between these traits and processes responsible for them, they still present interpretive problems. Animal populations encompass considerable inter-individual variability, often expressed in the time of development of individuals' sex- and age-related traits. In making such determinations, zooarchaeologists often benefit from research by zoologists and ecologists. Wildlife management studies of the relation of age to body size and methods of age estimation in modern populations can serve as actualistic datasets from which zooarchaeologists

D. Gifford-Gonzalez, *An Introduction to Zooarchaeology*,
https://doi.org/10.1007/978-3-319-65682-3_6

can base their inferences about ancient individuals from the same species. Often, however, zooarchaeologists find themselves working with species or body segments that have never been well-studied actualistically. In fact, zooarchaeologists have contributed to ecology and zoology by defining ages of tooth eruption and epiphyseal fusion in wild animal populations.

This chapter and Chap. 7 review the voluminous literature on determining species, size, sex, and age in mammals from their skeletal remains, highlighting major analytical tactics, classic and informative sources, and ongoing controversies. This chapter begins with species identification and then surveys size estimation and sex determination. Simply because the literature on age determination from teeth is so extensive, it is placed in a separate chapter, which will also address the question of precision and accuracy of all estimates in inherently variable biological populations. As other chapters, these two chapters do not attempt a comprehensive bibliography; rather, they refer readers to portals into that rich literature. Two key works in English that offer entry into this rich literature are Wilson, Grigson, and Payne's (1982) *Ageing and Sexing Animals from Archaeological Sites* and Ruscillo's (2006) *Recent Advances in Ageing and Sexing Animal Bones*.

6.1 Taxonomic Determination

Zooarchaeologists undertaking taxonomic identification from bone specimens can build on nearly four centuries of comparative anatomy and paleontology, including an illustrated literature on identification of various groups, as well as a methodology for initiating comparative research. Guides to osteology are part of that tradition, emphasizing morphological traits that set one taxon apart from closely related ones. From the 1930s, zoologists and paleontologists began supplementing purely qualitative prose descriptions and drawings with measurements to specify the small differences in proportion of closely related species' bodies and bones.

Like zooarchaeologists, paleontologists lack the skins and soft anatomy that zoologists use to distinguish extant animal species. As a consequence, their research has focused on preserved hard parts. They have developed systematic methods to approach the comparison and taxonomic identification that can guide zooarchaeological analysis, including threshold criteria for taxonomic identification to the generic or higher level rather than the species, and for documenting novel or difficult species identifications in initial site or monographic reports. Informative discussions of how these methods apply to zooarchaeology have been offered by Lawrence (1951), Driver (2011), and Lyman (2011, 2005), and excellent examples of osteometric comparisons in zooarchaeological research exist (Peters 1986a, b; Grayson 1988). However, as Driver and Lyman stress, this time-honored, systematic approach is not as pervasive in zooarchaeology as it should be. These procedures are especially important to review now that most prospective zooarchaeologists are trained in stand-alone courses in many departments of anthropology or archaeology, rather than studying directly with zoologists or paleontologists, as did most of the first cohort, where exposure to that literature was part of their training. A good example of such paleontological methods can be found in Barnosky (2004).

Today, DNA analysis is an increasingly affordable tool for tracing biogeographic and evolutionary histories in zoology, paleontology, and zooarchaeology. Zoologists regularly have used DNA analysis to sort out relationships of living taxa. For example skunks and their relatives have been placed their own zoological family, the Mephitidae, separate from the Mustelidae, in which they were formerly grouped with weasels, otters, wolverines, and ratels (Dragoo and Honeycutt 1997; Flynn et al. 2005). Given that these changes are ongoing, zooarchaeologists should stay current with the literature for geographic areas and taxa with which they work (Bovy 2011). Not all archaeofaunal specimens preserve sufficient ancient DNA (aDNA) for analysis, nor can zooarchaeologists afford to employ this as a standard identification tool. However, aDNA analysis has been used to distinguish species when neither morphology or measurements could do so, as in the case of fragmentary whale bones from sites on the northern Oregon coast of North America (Wellman et al. 2016). It was also used to check size-based identifications of cottontail (*Sylvilagus*) versus jackrabbit (*Lepus*) specimens in U.S. Southwestern archaeofaunal samples, with interesting results (Yang et al. 2005). Analyses of modern domestic animals' genomic variation, combined archaeofaunal specimens' aDNA, have revolutionized animal domestication research (see Chap. 23). As these examples imply, time-honored species identification methods are nonetheless the bedrock upon which samples for such analyses rest.

Another recently applied molecular biological method of taxonomic characterization currently less expensive than aDNA analysis is protein mass-fingerprinting from collagen (PMF), see Thiede et al. (2005). Originally developed and applied in biomedical studies, the technique's standardization, automation, and computer-based analysis permit swift analysis of taxonomically distinctive peptides in collagen. Its application to has been called Zooarchaeology by Mass Spectrometry or ZooMS (Richter et al. 2011). The method can differentiate samples at the familial level, as it did in Richter et al.'s study of fish peptides, and sometimes at the generic level, as it did in Buckley et al.'s (2010) analysis of sheep vs. goat peptides. One of its most interesting applications to date was to hair combs fashioned from deer antler in three Viking workshops around the far eastern North Sea and western Baltic (Ashby et al. 2015). Manufacturing processes in the workshops had substantially reduced chances of visually identifying most specimens' taxon. Peptide analysis revealed presence of local deer, undifferentiated by this method between red deer (*Cervus elaphus*) and elk/moose (*Alces alces*), and of reindeer (*Rangifer tarandus*), which were not native to the terrestrial hinterlands around these Viking settlements. From these results, as well as "traditional" zooarchaeological identification of reindeer antler in another such settlement to the south, the authors develop an argument that Viking settlements possessed overseas "hinterlands," mediated by extensive commercial seafaring, for which some documentary evidence exists.

6.1.1 Illustrations Versus Comparative Specimens

Nearly every guide to species identification of skeletal elements presents photographs or drawings of the elements. The best such guides offer multiple views of an element and indicate its species-specific, distinctive features. Some may also present measurements of elements previously shown to exhibit key metrical differences between two or more species (Lyman 2005). Many zooarchaeologists working in the field carry binders or digital tablets with images of skeletal elements from the species that we might have trouble distinguishing. My personal identification notes include illustrations from classic sources, my own drawings and photos, tables of suture and epiphyseal fusion ages for various species, photos of bone modifications from other researcher's and my own work, weathering stage criteria, and other useful references.

As implied above, zooarchaeologists are not only consumers but also producers of specimen illustrations. I urge my students to sit and draw bones as a way of learning morphological detail of different species, even if they consider themselves to be terrible artists who produce ugly little sketches and would rather photograph with their smart phone. Drawing requires a person to look long and hard at a specimen, and that is the real benefit. Once the image is committed to one's visual cortex, the drawing and notes on it may be more mnemonic devices than the actual means of identification.

However, drawings of bones are no substitute for actual comparative specimens. One zooarchaeological corollary of Murphy's Law is that the fragment of an element being examined is from the only part not illustrated in the identification guide. At the end of a particularly long day, I have actually caught myself trying to rotate a drawing, to see if that part of the bone would come into view. Three-dimensional scanning technology actually *does* permit a researcher to "rotate the illustration," although those currently available do not yet encompass the inter-individual variability with a species, by sex, age, or geographic region. Such aids are much better than nothing, but comparative collections in natural history museums or other collections are nonetheless essential when working with some cases of species identification (Lyman 2010).

6.1.2 Bone Measurements

To use size and morphology to determine species, to estimate body size (see next section), and to describe precisely the morphological differences between male and female (see **Sex Determination**), bone elements are measured. Morphometrics have been used not only to describe the shape of skeletal elements but also to infer from these animals' locomotor patterns and, by extension, foraging adaptations (e.g. Plummer and Bishop 1994).

The basic requirement of metrical data collection is that it be accurate, replicable, and made at commonly agreed-upon locations on an element. The classic guide

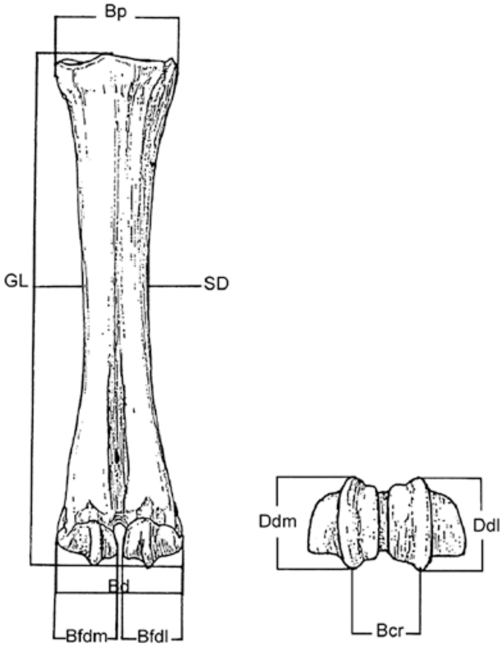

Fig. 6.1 Template for measurements taken on domestic cattle metapodials, from Telldahl et al. (2012:123, Fig. 2). (Drawing by the senior author with Bp, GL, SD and Bd measurements after von den Driesch (1976) and the BFdm, BFdl, Ddm, Ddl and Bcr after Duerst (1926), used with permission of senior author and Elsevier)

for measurements that fulfills these criteria for mammals is Angela von den Driesch's (1976) *A Guide to the measurement of animal bones from archaeological sites*, in which illustrations show the placement points for measurement of axial and appendicular skeletal elements in a wide variety of mammal species (Fig. 6.1). Each measurement is named by an abbreviation of its anatomical placement and type. Others have emulated this template for species not included in von den Driesch's volume (e.g. Etnier 2002).

Measuring is normally accomplished with vernier calipers, either manual or electronic, and the latter can be linked directly to a digital database. Other devices include the bone-measuring box, standard in human osteology. For very large specimens, one may resort to spreading calipers or to a large measuring tool known in physical anthropology as an anthropometer, as my colleague Josh Snodgrass did in our study of pinniped osteology, in which case it was, briefly, a pinnedometer. To measure micromammal elements, Donald Grayson (personal communication, 1978) used machinists' micrometers, usually employed on very small mechanical parts.

Publications often combine osteometrics with illustrations, as in Peters' (1986a) work on distinguishing the appendicular bones of cattle from those of the closely related African buffalo. Some differences can be conveyed reliably by measurements or ratios of measurements, while others are best conveyed in a visual representation of the bones in question. My own opinion is that, with the possible exception of features in very small animals, one should employ metrical distinctions to describe more precisely features first discernable by visual inspection.

Taphonomic history can affect frequencies of measurable bones in an archaeofauna. I have worked extensively with prehistoric assemblages from East African localities that osteological and other archaeological evidence indicates were pastoralist encampments (Gifford-Gonzalez 1998). Bones were broken to fit into cooking pots (Marshall 1990), possibly for bone grease manufacture, after their discard trampled by herds and flocks, and after burial sometimes split open by soil action. At one such site, (Gifford et al. 1980), identifiable specimens' modal maximum dimension was 3–6 cm (1.8–2.6 inches), and among about 600 carpal and tarsal specimens – usually among the most durable of elements – a student study found seven specimens, measurable with von den Driesch's system. Richard Meadow (personal communication, 2007) reports similar problems with prehistoric bovine samples from South Asian pastoralist settlements. Selective use of some elements for bone tool manufacture can also affect measureable specimens. British zooarchaeologist Sebastian Payne (personal communication, 1973) recounted his initial elation that simple measurements could reliably distinguish sheep from goat metacarpals (Payne 1969) and his subsequent disappointment upon realizing that metacarpals of both species had been popular materials for ancient bone tools, obliterating their measurable features. To deal with the fragmentary state of many archaeofaunal specimens, Meadows (1999) developed a method for comparing metrics from different skeletal elements, using logarithms of the measurements taken in relation to those from the same elements of a "standard animal" for the species. This Logarithmic Size Index (LSI) is widely used by zooarchaeologists in Eurasia monitoring body size changes in relation to domestication.

6.1.3 Osteological Guides to Wild and Domestic Animals

This listing here is not exhaustive but cites reference materials in North American zooarchaeology, with a few from Europe and Africa added. Some introductions to zooarchaeology, including Reitz and Wing's (2008) *Zooarchaeology*, contain good illustrations for the beginner. Classic sources include Lawrence's (1951) *Guide to postcranial characters of deer, pronghorn, and sheep-goat,* Schmid's *Atlas der Tierknochen/Atlas of animal bones* (1972), and Stanley Olsen's Peabody Museum publications (1960, 1972a, 1972b, 1968, 1973), which include mammal, bird, reptile, and amphibian reference drawings and photographs.

More recent publications with profuse photographic documentation and available in digital form, include France's (2009) *Human and nonhuman bone identification: A color atlas* and Adams and Crabtree's (2008) *Comparative skeletal anatomy: A photographic atlas for medical examiners, coroners, forensic anthropologists, and archaeologists* and (2012) *Comparative osteology: A laboratory and field guide of common North American animals.*

Additionally, textbooks of veterinary anatomy (Barone 1976; Sisson and Grossman 1975) provide valuable information on the relation of soft tissues to bone, as well as details of domestic animal osteology.

Other publications for North Americanists include B. Miles Gilbert's *Mammalian Osteology* (1990) and Brown and Gustafson's (1979) *Key to the postcranial skeletal remains of cattle/bison, elk and horse*. The latter is an excellent example of the multiple view approach to distinctive osteological features.

Classic articles with illustrations include those on distinguishing sheep from goat (Prummel and Frisch 1986; Boessneck 1969; Zeder and Lapham 2010; Zeder and Pilaar 2010), North American deer from sheep and goat (Hildebrand 1955), and different species of equid, with a focus on Africa (Klein and Cruz-Uribe 1996). Pacheco Torres et al. (1986) authored *The osteology of South American camelids*. Larger East African mammals are depicted in *A guide to post-cranial bones of East African animals: Mrs. Walker's bone book* (R. Walker 1985) and the Peters studies (1986; 1986a, 1986b; Peters and Brink 1992) mentioned earlier. Beisaw's (2013) *Identifying and interpreting animal bones: a manual* contributes a perspective on the process of analysis.

Veterinary and meat science literature has produced books of value to zooarchaeologists, among them, Sisson and Grossman's *Anatomy of domestic animals* (1975; Getty 1975). In addition to fine illustrations of bones of horse, cattle, pig, goat, dog, and chicken, it illustrates muscles, joints with ligaments, and other soft tissue features of interest to zooarchaeologists. In earlier editions – the book has been in print since before the internal combustion engine replaced horses – the illustrations are somewhat sharper. Another relevant veterinary anatomy book is *Muscles of the ox* (Butterfield and May 1966), with detailed descriptions and some illustrations of the origins and insertions of major muscles on elements of the appendicular skeleton, plus a short discussion of differences between cattle, buffalo, and bison. Recent English translations of König and Liebach's (2007) atlas, as well as Robert Barone's (1976) *Anatomie comparée des mammifères domestiques*, are other well-illustrated references that illustrate muscle origins and insertions on axial and appendicular elements.

Those working with rarer species should bear in mind that zoological research on vertebrates in the nineteenth and early twentieth centuries centered more on bones and morphology than in later years, with beautiful illustrative plates (e.g. Perrier 1893–1932). Vertebrate paleontological articles have dealt in detail with bones, and older works were often very well illustrated (e.g. Piveteau 1952–69; Pictet 1980 (1853–1857)). Zooarchaeological researchers should therefore consider searching this older literature for reference illustrations of the taxa with which they are working. Crania and mandibles of rodents are commonly illustrated in standard field guides to these taxa, even if skulls of larger animals are not.

6.2 Body Size Estimation

Zooarchaeologists may wish to estimate the size of the animal from which a skeletal element was derived for several reasons. These include diagnosing domestication, discerning the proportional representation of the sexes in a sample, monitoring environmental changes that affect achieved body size, inferring age in vertebrates of *indeterminate growth*, that is, those that continue growing over a long span of their lives, such as tortoises and some fishes, and by extension, assessing the intensity of human predation on them, and estimating the weights of prey animals acquired.

6.2.1 Diagnosing Domestication

For many years, size differences have been used to assign individual specimens to wild or domesticated forms of the same species. The assumption, based in part on comparing wild representatives of certain species with non-modern domestic breeds of the same taxon, is that domesticates are usually smaller. Zeder (2001) strongly cautioned against uncritically assuming that larger animals are wild and smaller ones domestic, especially when studying the earliest phases of domestication. Her metrical study of wild and domestic goats from Iran and Iraq demonstrated that a north-south cline in size exists in wild populations. This would be expected, according to Bergmann's Rule, which stipulates that members of a species living in higher latitudes will have larger body size than those farther south.

Zeder argues that zooarchaeologists have sometimes compared modern wild goats from the northern (and larger body size) end of their geographic range with archaeofaunal goat remains from the southern end, leading to inaccurate inferences about their domestic status. She contends that changes in (aggregate age-at-death) may be a more reliable indicator of early domestication. The same point regarding size as a poor diagnostic for domestication was made by Rossel et al. (2008) for early domesticated donkeys in Africa, and by Rowley-Conwy (1995) with regard to putative domestic cattle and pigs in different parts of Europe. In the case of pigs, ancient and modern DNA has added further complexity to using size to diagnose domestication. For many years, zooarchaeologists working in Europe assumed that the wide size range of pig molars and other elements observed in some Neolithic sites resulted from acquisition of the still abundant wild boar, combined with slaughter of domesticates. The range of sizes was thought to have been produced by combining two samples of sexually dimorphic pigs, large wild and smaller domesticates introduced from the Near East, into one culturally combined and deposited sample (Rowley-Conwy 1995). This may be the case in some European situations, but osteological and ancient DNA analysis revealed that some of the large, “wild” pigs in Neolithic sites displayed markers indicating domestication, including genes for the spotted coat color typical of domesticates and displayed haplogroups typical of later European domestic suids. In some earlier Neolithic sites, both domestic stocks of two different body sizes are represented in the mitochondrial DNA. The genetic evidence testifies to a relatively rapid process of replacement of domestic pigs introduced from Southwest Asia by newly domesticated swine derived from European wild boar (Larson et al. 2007).

6.2.2 *Size Differences Over Time and the Historical Ecology of Human Prey Species*

Size differences in a long-term chronological sample of one species may reflect both ecological factors and, in cases of domestication, human selectivity. Klein (1986, 1991) asserted that changes in sizes of South African carnivores and mole-rats during the Pleistocene reflected climatic change. Changes in the modal size of individuals of a species, especially the case with species of indeterminate growth, in a time series of archaeofaunas can also reflect changes in the intensities of human cropping on that species (Klein and Cruz-Uribe 1983; Stiner et al. 2000; Broughton 1997).

6.2.3 *Bone Size as an Estimator of Body Size*

Zooarchaeologists may wish to know the body size of an animal, quantified by body dimension (e.g. total length) or by weight, to estimate meat yields and thereby to assess handling costs and return rates or aspects of predation. Whatever their motivations for estimating the body size of vertebrates from archaeofaunal specimens, zooarchaeologists can turn to literature in theoretical evolutionary biology and applied wildlife management for guidance in developing formulae and, in some cases, for published information on a taxon.

Linear relations exist between the dimensions of certain skeletal elements and body size, especially length or height of the animal. Strong positive correlations between skeletal weight and total body weight exist, as well. Reitz and Wing (2008: 64–69) outline approaches to simple linear and allometric scaling. Even in circumstances in which size relations of skeletal elements to living body size are not known for a given species, zooarchaeologists can use established procedures for collecting samples, measuring bone, and fitting regressions that permit size estimation, either of body weight, skeletal weight, body length or, in the case of quadrupeds, height at shoulder (Chaplin 1971; Casteel 1976). Some authors have inserted a note of caution about taphonomic effects on ostensibly measurable elements, which would include both heat stress and, for elements of small prey, erosive effects of digestion (Tollit et al. 2004).

6.3 Sex Determination

Some traits of vertebrate skeletons vary with an individual's sex, as the result of one of several selective pressures. Physical competition for mates by one sex may produce size differences between the sexes. In species where male-male sparring for dominance allows winners greater access to reproducing females, as, for example, in deer and sea lions, males are larger than females due to an evolutionary "arms race" in body size. The same pressures may have selected for differentially developed body segments, as in larger neck muscles employed in clashes with other males. Specialized, sex-specific structures, such as the antlers or horns of many male artiodactyls, or canine teeth in pigs and primates, may evolve in this same selective context. Alternatively, certain physical traits may be selected for without such direct, same-sex competition, as when a potential mate of the opposite sex chooses to mate with an individual possessing an extreme expression of the trait. Such sexual selection directs development of secondary sexual characteristics in the sex being chosen, as in the case of the peacock's tail displayed to peahens.

Selective pressures other than competition for mates can also result in sexual dimorphism in size. Size differences between males and females may be the result of intraspecific niche partitioning, as Brown and Laziewski (1972) argued for the great sexual dimorphism in weasels. They contended that the much larger male weasels could not enter small burrows exploited by females living in overlapping foraging ranges, thereby guaranteeing the females access to prey without male interference. Erlinge (1979) proposed another explanation for weasel sexual dimorphism: female weasels rear their offspring without help from males, and their size better fits the energetic demands of foraging for a litter. Smith (1982) assesses explanations of the fact that, among raptorial birds that mate for life and share foraging ranges, females are larger than the males and dominant to them early in the breeding season. While niche-partitioning explanations have been proposed, Smith favors a behavioral explanation, in which female dominance dampens potentially lethal competition between the mates and ensures the female first choice at shared food, ultimately enhancing the reproductive success of both sexes.

Finally, the divergent demands of reproduction on females and males can produce physical differences between the sexes. Among the most common of these in placental mammals is differences in pelvic structures, related to accommodating birth of well-developed young. This contrast is well known in physical anthropology, and it holds for many other mammals as well. Measurable differences in the proportions of innominates, sacra, or femora may also distinguish female from male elements in an assemblage because these elements are associated in the pelvic girdle and articulating leg bones. Recent studies have shown that male and female primates display body-segment and bone-density differences that reflect the divergent selective pressures operating on females during pregnancy and while carrying their young, despite their living in the same groups and engaging in overall similar modes of locomotion as males (Morbeck et al. 1997).

In this connection, Greenfield (2006) noted a metrically distinguishable difference in the height of the acetabulum (hip socket) rim in male versus female bovid innominate bones, which clearly stems from the functional differences in the pelvic structure in the sexes. Among birds, only females deposit bone in their medullary cavities as a prelude to producing eggs. Driver (1982) noted this trait as a possible means of diagnosing site seasonality with wild bird species; van Neer and Lentacker (1996) used medullary bone to diagnose the season of slaughter in Roman-period Egyptian domestic fowl. Presence of sex-specific anatomical features such as antlers in deer or canine teeth in horses may also be used to diagnose sex.

Whatever their ultimate causes, zooarchaeologists can use sex differences in osteology to infer the probable sex of individual archaeofaunal specimens. If a single archaeofaunal species sample displays a generally bimodal distribution in skeletal element size, zooarchaeologists have inferred sexual dimorphism in the sample. Given a sample of sufficient numbers of specimens, it may be possible to explore whether sex-specific predation (e.g. Lyman 2007) or management of domesticates existed.

Higham and Message (1969) were among the first to use osteometrics to discern prehistoric cattle herd composition by sex. While size–based sexual dimorphism is the case in many wild species, domestic taxa can present exceptions to the bimodal rule. In meat- and wool-oriented production systems, male cattle, sheep, and goats are kept alive past sexual maturity for their economic value. However, they are usually castrated before or as they reach full growth, because castrated males are more manageable when herded with females and young and more tractable with humans. Castrates grow differently from either females or intact males, building body mass more swiftly and developing longer limbs than bulls (Rogol 1996; Martin et al. 1979). Explaining greater growth in castrated males was once considered straightforward, as androgens (male sex hormones) were assumed to damp down on Growth Hormone, and in the absence of testes, androgen production would be slower and lower. However, more recent research shows that androgens enhance and stimulate growth hormone in males, and that estrogens, found in both females and males, are more directly linked to epiphyseal fusions at the end of growth in humans (1969).

A recent, innovative project by Swedish zooarchaeologists and geneticists used a single-nucleotide polymorphism (SNP) that indicates sex in DNA recovered from archaeological metacarpals and metatarsals of cattle to assess the accuracy of measurements zooarchaeologists had used earlier to assign the specimens to male and female sexes (Watson 1969). They found that, overall, the key measurements employed did quite well in distinguishing males from females, and that measurements of males appear to be able to discriminate between bulls and castrated males, which cannot be differentiated from their DNA (Teldahl et al. 2012).

Davis's (2000) study of skeletons from one flock of Shetland sheep presents actualistic data on maturation of ewes, rams, and wethers (castrated males), including tooth eruption, epiphyseal fusions, and achieved size. Wethers were found to have longer, more slender long bones than rams due to a longer period of growth before epiphyseal fusion (see also *Endochondral Bone Fusion*, below). Davis cautioned that only osteometric differences in pubis shaft thickness, long bone lengths, and long bone shaft widths reliably distinguished ewes, rams, and wethers.

6.4 Estimating Age at Death from Osteological Markers

Zooarchaeologists have for some time studied the aggregate pattern of ages at death of archaeofaunal mammals, with the goal of linking such patterns to human predation practices or herd management systems. Studies of domestic fauna have often been referred to as "kill-off patterns"(Payne 1973), while studies of human predation have referred to "mortality patterns," following terminology developed in demographic studies of living animal populations. Despite terminological differences, these approaches are the same. Each attempts to discern the effects of humans (or pre-modern hominins) on animal populations through studying the ages at death of animals recovered from an archaeological sample.

Those working with domestic animals have argued that age- and sex-specific slaughtering patterns, and hence goals of ancient animal exploitation, can be reconstructed from aggregate ages at death (Payne 1973). Documented dairy cattle herds are numerically dominated by cows and heifers and male young-of-the-year, with rare bulls or steers (castrated males). Beef herds generally have a more balanced sex ratio, but nearly all males are steers rather than bulls. Wool-producing sheep flocks are also more or less sex-balanced, but again, most males are castrated. In all cases, human intervention in the demographics of the species produces the pattern of survivorship (Payne 1973; Redding 1981). Davis (1987) argued that the shift from food-oriented sheep exploitation to that focused on secondary products such as milk or wool could be traced by examining modal ages of the dead domestic stock in sites. Problems and potentials of this approach will be explored further in Chap. 22. New, independent lines of evidence from pottery residue analysis can help contextualize purely zooarchaeological indicators of dairying (Chap. 23 (Chaplin 1971; Ruscillo 2006; Silver 1963)).

Studies of age-sex composition in archaeofaunal samples rely on two distinct areas of research and analysis:

1. Accurately determining the sex and age at death of specimens;
2. Assigning a meaning to the aggregate mortality pattern of archaeofaunal specimens.

This section examines aging methods, and Chap. 22 will consider mortality pattern analysis in more detail. No single, uniform method of determining age at death exists today. Several different methods, most developed in wildlife biology or physical anthropology, are currently being used to estimate age-at-death. Most have been checked against known-age samples of mammals and have benefited from methods and perspectives drawn from wildlife biology and ecology. However, O'Connor (2006) has stressed that much more actualistic research is needed to reduce ambiguities in the present reference data.

O'Connor (2006) also noted a rarely acknowledged problem in age estimation research: deciding the appropriate level of precision in one's age estimates in relation to the intrinsic variability in the features used to estimate age in animal populations. Examples of this are discussed in more detail below, as various ageing methods applied to mammals are reviewed.

6.5 Osteological Estimations of Age

Bones, as opposed to teeth, remodel throughout life, and they also go through a series of developmental phases. In some mammal species, these phases and their timing have been relatively well studied and can be used to estimate the age at death of a maturing animal.

6.5.1 Cranial Suture Fusion

The cranium is composed of numerous dermal bones, joined together by a special type of joint called *squamous sutures*. In mammals, these joints fuse over an individual's development, some so thoroughly that they are difficult to see in mature individuals (Fig. 6.2). Cranial sutures fuse during adulthood in humans, and as with epiphyses, have a long history of use in ageing human remains. Fusion ages for

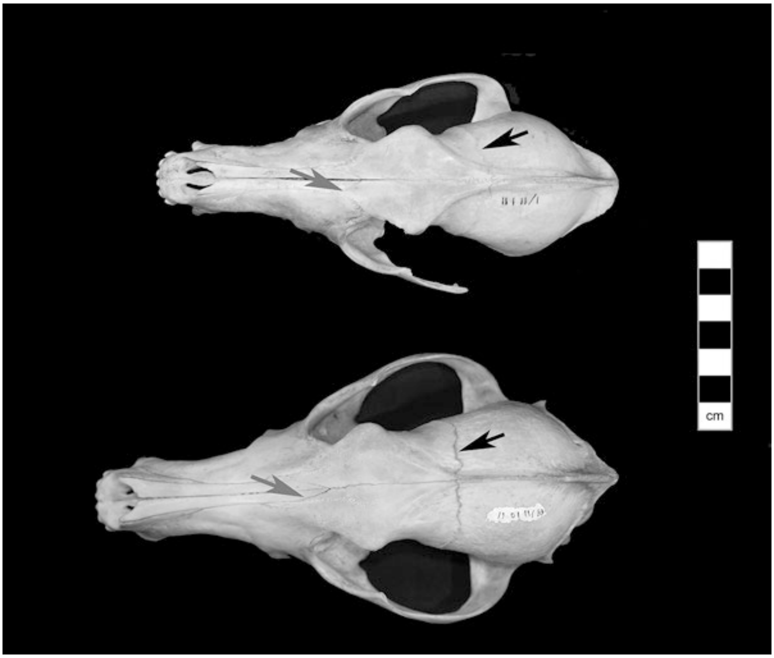

Fig. 6.2 Two adult coyote (*Canis latrans*) crania, showing an older adult (upper) and younger adult (lower). Note more fused nasal-frontal (gray arrows) and frontal-parietal (black arrows) regions in older individual. Larger (lower) individual was a road kill from the Rocky Mountain area, and the smaller (upper) was a depredation kill from the Santa Cruz Mountains (Photo by author of specimens from Anthropology Teaching Laboratories)

cranial sutures are known for domestic animals. They are much less well understood for most wild mammal species, largely because biologists have relied either upon tagging records of birth dates in managed wildlife areas or upon more easily observable dental eruption and wear, or they have made thin sections of dentine from incisors readily extracted from the jaws of dead mammals (Davis 1987:158–160).

In well-studied taxa such as humans, ages of specific cranial suture fusions vary from one individual to another, providing a range of ages rather than a precise number. Although much work is needed to use this trait in zooarchaeology, and some indicators suggest that it may not be so useful in some taxa as it is in humans (Robinette et al. 1957; Mitchell and Smith 1991), human skeletal biology nonetheless offers models for analyzing and quantifying these fusions.

6.5.2 Endochondral Bone Fusion

In mammals, epiphyses fuse to their adjacent diaphyses at more or less predictable times over the span of an animal's maturation (Fig. 6.3). Bones with unfused or fusing epiphyses can therefore be used to estimate age-at-death, a method employed for over a century with human remains. However, a good deal of individual variation exists in the calendrical age at which a specific epiphysis fuses, and fusion ages should be considered an age estimate rather than a precise determination.

Zooarchaeologists and biological anthropologists use these developmental features as indicators of age-at-death, at least into early adulthood. Ages of epiphyseal fusion are reasonably well known for domestic animals (see Chaplin 1971; Ruscillo 2006; Silver 1963 and references within; Wilson et al. 1982). However, they are poorly documented for many wild species for the same reasons that wildlife biologists have not extensively studied cranial suture fusions.

Some archaeologists have compared the age estimates based upon epiphyseal fusions against those derived from dental eruption and wear (Chap. 7). Zeder (1991) combined these approaches in ageing domestic sheep and goat samples from several sites in the Kur River Basin, Iran.

Zooarchaeologists, who deal mainly with isolated postcranial bones, are often more highly motivated than zoologists to document epiphyseal fusions and have contributed several major epiphyseal fusion studies of wild mammal species. Purdue (1983) linked age-at-death records for managed white-tailed deer, *Odocoileus virginianus*, to epiphyseal fusions, supplementing an earlier study by zoologists Lewall and Cowan (1963) on black-tailed (mule) deer, *Odocoileus hemionus*. Carden and Hayden's (2015) epiphyseal fusion study for European fallow deer *Dama dama* is another such example, as are Walker's (1987) study of Rocky Mountain bighorn sheep *Ovis canadensis* and Weinstock's (2009) study of brown bear *Ursus arctos* epiphyseal fusion.

It is often possible for zooarchaeologists to develop fusion tables using museum specimens. Storå (2001) used museum collections of modern ringed seal *Phoca groenlandica* and harp seal *Phoca hispida* for which environmental monitors had

Fig. 6.3 Tibia and fibula of a female northern fur seal (*Callorhinus ursinus*), showing recently fused proximal and fusing distal epiphyses with metaphyseal lines still clear (Photo by author of specimen from California Academy of Sciences)

estimated ages by dental cementum annulus analysis (see below). Storå correlated dental annuli-based ages (Chap. 7) with osteometrics and epiphyseal fusions in the associated skeletons. This strategy could be used on almost any species for which complete skeletons exist. Moreover, since many wildlife managers use sectioning of incisor cementum, it may be possible either to use existing data on the age of a specimen derived from this method or to make a case for such a time-honored study to collections managers.

Another actualistic approach to epiphyseal fusion involves studying natural mass deaths or mass wildlife culls. Haynes studied modern African elephant behavior and population dynamics as a modern analogue for late Pleistocene Eurasian and North American mammoth and mastodon ecology and for human predation on them. Most of his research was in Hwange National Park, western Zimbabwe (Weinstock 2009), where the overall numbers of elephants in the park rose above sustainable levels. Hwange Park officials shot entire elephant family groups and had the carcasses butchered for meat distribution to local people. Haynes was able to correlate long bone epiphyseal fusions with existing ages from dental development or from Park records. Such examples show that zooarchaeologists can exploit other situations to develop fusion tables without having to collect their own specimens.

6.5.3 Bone Durability and Missing Age Classes

Younger animals' bones do not resist destructive processes so well as do those of older animals of the same species, and archaeofaunal samples are thus highly likely to be biased against remains of younger age classes. This phenomenon has been known in human paleodemography for some time (Haynes 1987, 1991) and was recently shown to affect survival of children's bones on an historic scale. When burials in a California cemetery for which good burial records existed had to be relocated, physical anthropologists found that children's remains were substantially under-represented (Acsádi and Nemeskéri 1970; Buikstra 1981). They also found that skeletons of older people, whose bones were likely calcium-depleted at the time of death, were represented in lower frequencies than predicted by burial records. Parallel taphonomic problems have been documented for dentally based ageing approaches, as will be discussed below.

Paleodemographers have attempted to correct for preservation biases in human skeletal samples by interpolating a certain proportion of infants and members of very young age classes based on certain theoretical models of population structure (Walker et al. 1988). For zooarchaeologists, this problem of missing age classes is more vexing because we know that animals taken by humans seldom randomly sample the animal population from which they are drawn. Rather, we assume that they are a sample produced through age-specific choices of human predators or animal keepers. It is therefore not logically defensible for us to assume a given proportion of very young animals existed in our samples, because of the possibility that they may have been specifically excluded in human patterns of predation or management. This topic will be taken up again in Chap. 22 with regard to mortality profiles.

6.5.4 Osteohistological Age Indicators

As seen in Chap. 4, the nature, density, and architecture of bone cells and noncellular material change over the lifespan of a vertebrate. Dammers (2006) monitored changes during growth and development, which had prior applications in human skeletal biology, forensics, and paleontology, and its potential for application in zooarchaeology. Among the findings she reports are that secondary osteons and osteon fragments (by-products of remodeling) increase with age and that castration reduces bone tissue density in experimental animals (Dammers 2006:27–28). The latter could provide an independent check on the validity of the definition of castrates in an archaeofaunal sample by osteometrics.

References

Acsádi, G., & Nemeskéri, J. (1970). *History of human lifespan and mortality*. Budapest: Académiai Kiadó.

Adams, B. J., & Crabtree, P. J. (2008). *Comparative skeletal anatomy: A photographic atlas for medical examiners, coroners, forensic anthropologists, and archaeologists*. Totowa: Humana Press.

Adams, B. J., & Crabtree, P. J. (2012). *Comparative osteology: A laboratory and field guide of common North American animals*. Waltham: Academic Press.

Ashby, S. P., Coutu, A. N., & Sindbæk, S. M. (2015). Urban networks and Arctic outlands: Craft specialists and reindeer antler in Viking towns. *European Journal of Archaeology, 18*(4), 679–704.

Barnosky, A. D. (Ed.). (2004). *Biodiversity response to climate change in the middle Pleistocene: The Porcupine Cave fauna from Colorado*. Berkeley: University of California Press.

Barone, R. (1976). *Anatomie Comparée des Mammifères Domestiques* (2nd ed.). Paris: Vigot.

Beisaw, A. M. (2013). *Identifying and interpreting animal bones: A manual*. College Station: Texas A&M University Press.

Boessneck, J. (1969). Osteological differences between sheep (*Ovis aries* Linné) and goat (*Capra hircus* Linné). In D. R. Brothwell & E. S. Higgs (Eds.), *Science in archaeology* (pp. 331–358). London: Thames & Hudson.

Bovy, K. M. (2011). Comments on "identification, classification and zooarchaeology." *Ethnobiology Letters, 2*, 30.

Broughton, J. M. (1997). Widening diet breadth, declining foraging efficiency, and prehistoric harvest pressure: Ichthyofaunal evidence from the Emeryville Shellmound, California. *Antiquity, 71*(274), 845–862.

Brown, C. L., & Gustafson, C. E. (1979). *A key to postcranial skeletal remains of cattle/bison, elk, and horse* (Vol. 57, Laboratory of Anthropology Reports of Investigations, Washington State University). Pullman: Washington State University.

Brown, J. H., & Lasiewski, R. C. (1972). Metabolism of weasels: The cost of being long and thin. *Ecology, 53*(5), 939–943.

Buckley, M., Whitcher Kansa, S., Howard, S., Campbell, S., Thomas-Oates, J., & Collins, M. (2010). Distinguishing between archaeological sheep and goat bones using a single collagen peptide. *Journal of Archaeological Science, 37*(1), 13–20.

Buikstra, J. E. (1981). Mortuary practices, paleodemography, and paleopathology: A case study from the Koster site (Illinois). In R. Chapman, I. Kinnes, & K. Randsborg (Eds.), *The archeology of death* (pp. 123–132). Cambridge: Cambridge University Press.

Butterfield, R. M., & May, N. D. S. (1966). *Muscles of the ox*. Brisbane: University of Queensland Press.

Casteel, R. W. (1976). *Fish remains in archaeology and paleoenvironmental studies*. London: Academic Press.

Carden, R. F., & Hayden, T. J. (2015). 15. Epiphyseal fusion in the postcranial sleton as an indicator of age at death of European fallow deer (Dama dama dama, Linnaeus, 1758). In D. Ruscillo (Ed.), *Recent advances in ageing and sexing animal bones* (pp. 227–236). Oxford: Oxbow Books.

Chaplin, R. E. (1971). *The study of animal bones from archaeological sites*. New York: Seminar Press.

Dammers, K. (2006). Using osteohistology for ageing and sexing. In D. Ruscillo (Ed.), *Recent advances in ageing and sexing animal bones* (pp. 9–39, Proceedings of the 9th Conference of the International Council of Archaeozoology, Durham, August, 2002). Oxford: Oxbow Books.

Davis, S. J. M. (1987). *The archaeology of animals*. New Haven: Yale University Press.

Davis, S. J. M. (2000). The effect of castration and age on the development of the Shetland sheep skeleton and a metric comparison between bones of males, females and castrates. *Journal of Archaeological Science, 27*(5), 373–390.

Dragoo, J. W., & Honeycutt, R. L. (1997). Systematics of mustelid-like carnivores. *Journal of Mammalogy, 78*(2), 426–443.

Driver, J. C. (1982). Medullary bone as an indicator of sex in bird remains from archaeological sites. In B. Wilson, C. Grigson, & S. Payne (Eds.), *Ageing and sexing animal bones from archaeological sites* (Vol. 109, pp. 251–254). Oxford: British Archaeological Reports.

Driver, J. C. (2011). Identification, classification and zooarchaeology. *Ethnobiology Letters, 2*, 19–39.

Duerst, J. U. (1926). Vergleichende Untersuchungsmethoden am Skelett bei Säugern. In E. Abderhalden (Ed.), *Handbuch der biologischen Arbeitsmethoden* (Vol. 7, pp. 125–530). Berlin-Wien: Urban & Schwarzenberg.

Erlinge, S. (1979). Adaptive significance of sexual dimorphism in weasels. *Oikos, 33*(2), 233–245.

Etnier, M. A. (2002). *The effects of human hunting on northern fur seal (Callorhinus ursinus) migration and breeding distributions in the Late Holocene*. Doctoral dissertation, University of Washington, Seattle.

Flynn, J. J., Finarelli, J. A., Zehr, S., Hsu, J., & Nedbal, M. A. (2005). Molecular phylogeny of the Carnivora (Mammalia): Assessing the impact of increased sampling on resolving enigmatic relationships. *Systematic Biology, 54*(2), 317–337.

France, D. L. (2009). *Human and nonhuman bone identification: A color atlas*. Boca Raton: CRC Press.

Getty, R. (1975). *Sisson and Grossman's the anatomy of the domestic animals* (Vol. 2, 5th ed.). Philadelphia: W. B. Saunders Company.

Gifford, D. P., Isaac, G. L., & Nelson, C. M. (1980). Evidence for predation and pastoralism at prolonged drift, a pastoral Neolithic site in Kenya. *Azania, 15*, 57–108.

Gifford-Gonzalez, D. (1998). Early pastoralists in East Africa: Ecological and social dimensions. *Journal of Anthropological Archaeology, 17*(2), 166–200.

Gilbert, B. M. (1990). *Mammalian Osteology*. Columbia, MO: Missouri Archaeological Society.

Grayson, D. K. (1988). *Danger Cave, Last Supper Cave, and Hanging Rock Shelter: The faunas* (American Museum of Natural History Anthropological Papers, Vol. 66(1)). New York: American Museum of Natural History.

Greenfield, H. J. (2006). Sexing fragmentary ungulate acetabulae. In D. Ruscillo (Ed.), *Recent advances in ageing and sexing animal bones* (pp. 68–86). Oxford: Oxbow Books.

Haynes, G. (1987). Proboscidean die-offs and die-outs: Age profiles in fossil collections. *Journal of Archaeological Science, 14*(6), 659–668.

Haynes, G. (1991). *Mammoths, mastodons, and elephants. Biology, behavior, and the fossil record*. Cambridge: Cambridge University Press.

Higham, C., & Message, M. (1969). An assessment of a prehistoric technique of bovine husbandry. In D. R. Brothwell & E. S. Higgs (Eds.), *Science in archaeology* (pp. 315–330). London: Thames & Hudson.

Hildebrand, M. (1955). Skeletal differences between deer, sheep. and goats. *California Fish and Game, 41*(4), 327–346.

Klein, R. G. (1986). Carnivore size and Quaternary climatic change in southern Africa. *Quaternary Research, 26*(1), 153–170.

Klein, R. G. (1991). Size variation in the cape dune molerat (*Bathyrgus suillus*) and late Quaternary climatic change in the southwestern Cape Province, South Africa. *Quaternary Research, 36*(3), 243–256.

Klein, R. G., & Cruz-Uribe, K. (1983). Stone age population numbers and average tortoise size at Byneskranskop Cave 1 and Die Kelders cave 1, southern Cape Province, South Africa. *South African Archaeological Bulletin, 38*(137), 26–30.

Klein, R. G., & Cruz-Uribe, K. (1996). The identification of *Equus* skulls to species, with particular reference to the craniometric and systematic affinities of the extinct south African quagga. In K. M. Stewart & K. L. Seymour (Eds.), *Palaeoecology and palaeoenvironments of late Cenozoic mammals: Tributes to the career of C. S. (Rufus) Churcher* (pp. 598–629). Toronto: University of Toronto Press.

König, H. E., & Liebich, H.-G. (2007). *Veterinary anatomy of domestic mammals: Textbook and color atlas*. Stuttgart: Schattauer.

Larson, G., Albarella, U., Dobney, K., Rowley-Conwy, K., Schibler, J., Tresset, A., et al. (2007). Ancient DNA, pig domestication, and the spread of the Neolithic into Europe. *Proceedings of the National Academy of Science, 104*, 15276–15281.

Lawrence, B. (1951). Part II: Post-cranial skeletal characters of deer, pronghorn, and sheep-goat with notes on *Bos* and *Bison*. *Papers of the Peabody Museum of Archaeology and Ethnology, Harvard University, 35*(3), 3–43.

Lentacker, A., & Van Neer, W. (1996). Bird remains from two sites on the Red Sea coast and some observations on medullary bone. *International Journal of Osteoarchaeology, 6*(5), 488–496.

Lewall, E. F., & Cowan, I. M. (1963). Age determination in black-tail deer by degree of ossification of the epiphyseal plate in the long bones. *Canadian Journal of Zoology, 41*(4), 629–636.

Lyman, R. L. (2005). Zooarchaeology. In H. D. Maschner & C. Chippindale (Eds.), *Handbook of archaeological methods* (Vol. 1, pp. 835–870). Lanham, MD: Rowman Altamira.

Lyman, R. L. (2007). Prehistoric mink (*Mustela vison*) trapping on the Northwest Coast. *Journal of Field Archaeology, 32*(1), 91–95.

Lyman, R. L. (2010). Paleozoology's dependence on natural history collections. *Journal of Ethnobiology, 30*(1), 126–136.

Lyman, R. L. (2011). Comments on "Identification, classification and zooarchaeology." *Ethnobiology Letters, 2*, 33–34.

Marshall, F. B. (1990). Cattle herds and caprine flocks. In P. T. Robertshaw (Ed.), *Early pastoralists of south-western Kenya* (pp. 205–260). Nairobi: British Institute in Eastern Africa.

Martin, L. G., Grossman, M. S., Connor, T. B., Levitsky, L. L., Clark, J. W., & Camitta, F. D. (1979). Effect of androgen on growth hormone secretion and growth in boys with short stature. *Acta Endocrinologica, 91*(2), 201–212.

Meadow, R. H. (1999). The use of size index scaling techniques for research on archaeozoological collections from the Middle East. In J. Schibier (Ed.), *Historia animalium ex ossibus: Beitrage zür Palaoanatomie, Archäologie, Ägyptologie, Ethnologie, und Geschichte der Tiermedizin* (pp. 285–300). Rahden: Verlag Marie Leidorf.

Mitchell, C. J., & Smith, P. W. (1991). Reliability of techniques for determining age in southern white-tailed deer. *Journal of the Tennesse Academy of Science, 66*(3), 117–120.

Morbeck, M. E., Galloway, A., & Zihlman, A. L. (1997). *The evolving female: A life history perspective*. Princeton: Princeton University press.

Olsen, S. J. (1960). Post-cranial characters of *Bison* and *Bos*. *Papers of the Peabody Museum of Archaeology and Ethnology, Harvard University, 35*(4), 2–60.

Olsen, S. J. (1968). Fish, amphibian, and reptile remains from archaeological sites: Part I – Southeastern and Southwestern United States. *Papers of the Peabody Museum of Archaeology and Ethnology, Harvard University, 56*(2).

Olsen, S. J. (1972a). Osteology for the archaeologist: North American birds. *Papers of the Peabody Museum of Archaeology and Ethnology, Harvard University, 56*(4).

Olsen, S. J. (1972b). Osteology for the archaeologist: The American mastodon and the woolly mammoth. *Papers of the Peabody Museum of Archaeology and Ethnology, Harvard University, 56*(3).

Olsen, S. J. (1973). Mammal remains from archaeological sites: Part I – Southeastern and Southwestern United States. *Papers of the Peabody Museum of Archaeology and Ethnology, Harvard University, 56*(1).

Pacheco Torres, V. R., Enciso, A. A., & Porras, E. G. (1986). *The osteology of South American camelids* (trans: Sandefur, E., Vol. 30, Archaeological Research Tools). Los Angeles: Institute of Archaeology, University of California, Los Angeles.

Payne, S. (1969). A metrical distinction between sheep and goat metacarpals. In G. W. Dimbleby & P. J. Ucko (Eds.), *Domestication and exploitation of plants and animals* (pp. 295–305). Chicago: Aldine Publishing.

Payne, S. (1973). Kill-off patterns in sheep and goats: The mandibles from Aşvan kale. *Anatolian Studies, 23*, 281–303.

Perrier, E. (1893–1932). *Traité de Zoologie. Les Mammifères* (Vol. X). Paris: Masson.

Peters, J. (1986a). *Osteomorphology and osteometry of the appendicular skeleton of African Buffalo,* Syncerus caffer *(Spaarman, 1779) and cattle,* Bos primigenius *f.* taurus *(Bojanus, 1827)* (Vol. 1, Occasional Papers, Laboratory of Paleontology). Ghent: Rijksuniversiteit Gent.

Peters, J. (1986b). *Osteomorphology and osteometry of the appendicular skeleton of Grant's Gazelle,* Gazella granti *(Brooke, 1872), Bohor Reedbuck,* Redunca redunca *(Pallas, 1767), and Bushbuck Tragelaphus scriptus (Pallas, 1766)* (Vol. 2, Occasional Papers, Laboratory of Paleontology). Ghent: Rijksuniversiteit Gent.

Peters, J., & Brink, J. S. (1992). Comparative postcranial osteomorphology and osteometry of springbok, *Antidorcas marsupialis* (Zimmerman, 1780) and Grey rhebok, *Pelea capreolus* (Forster, 1790) (Mammalia: Bovidae). *Navorsinge van die Nasionale Museum: Researches of the National Museum, 8*(4), 189–201.

Pictet, F. J. (1980 (1853–1857)). *Traité élémentaire de paléontologie* (2nd ed.). New York: Arno Press.

Piveteau, J. (1952–69). *Traite de paleontologie*. Paris: Masson.

Plummer, T. W., & Bishop, L. C. (1994). Hominid paleoecology at Olduvai Gorge, Tanzania as indicated by antelope remains. *Journal of Human Evolution, 27*(1–3), 47–75.

Prummel, W., & Frisch, H.-J. (1986). A guide for the distinction of species, sex, and body side in bones of sheep and goat. *Journal of Archaeological Science, 13*(6), 567–577.

Purdue, J. R. (1983). Epiphyseal closure in white-tailed deer. *Journal of Wildlife Management, 47*(4), 1207–1213.

Redding, R. W. (1981). *Decision making in subsistence herding of sheep and goats in the Middle East*. Doctoral Dissertation, University of Michigan, Ann Arbor.

Reitz, E. J., & Wing, E. S. (2008). *Zooarchaeology* (2nd ed., Cambridge Manuals in Archaeology). Cambridge: Cambridge University Press.

Richter, K. K., Wilson, J., Jones, A. K. G., Buckley, M., van Doorn, N., & Collins, M. J. (2011). Fish 'n chips: ZooMS peptide mass fingerprinting in a 96 well plate format to identify fish bone fragments. *Journal of Archaeological Science, 38*(7), 1502–1510.

Robinette, W. L., Jones, D. A., Rogers, G., & Gashwiler, J. S. (1957). Notes on tooth development and wear for Rocky Mountain deer. *Journal of Wildlife Management, 21*(2), 134–153.

Rogol, A. D. (1996). Growth at puberty: The androgen connection. In S. Bhasin, H. L. Gabelnick, J. M. Spieler, R. S. Swerdloff, C. Wang, & C. Kelly (Eds.), *Pharmacology, biology, and clinical applications of androgens* (pp. 301–308). New York: Wiley-Liss.

Rossel, S., Marshall, F., Peters, J., Pilgram, T., Adams, M. D., & O'Connor, D. (2008). Domestication of the donkey: Timing, processes, and indicators. *Proceedings of the National Academy of Science, 105*(10), 3715–3720.

Rowley-Conwy, P. (1995). Wild or domestic? On the evidence for the earliest domestic cattle and pigs in south Scandinavia and Iberia. *International Journal of Osteoarchaeology, 5*(2), 115–126.

Ruscillo, D. (Ed.). (2006). *Recent advances in ageing and sexing animal bones*. Oxford: Oxbow Books.

Schmid, E. (1972). *Atlas of animal bones: For prehistorians, archaeologists and quaternary geologists*. Amsterdam: Elsevier Publishing Company.

Silver, I. A. (1963). The ageing of domestic animals. In D. R. Brothwell & E. Higgs (Eds.), *Science in archaeology: A comprehensive survey of the progress and research* (pp. 283–302). New York: Praeger.

Sisson, S., & Grossman, J. (1975). *The anatomy of the domestic animals* (5th ed.). Philadelphia: Saunders.

Smith, S. M. (1982). Raptor "reverse" dimorphism revisited: A new hypothesis. *Oikos, 39*(1), 118–122.

Stiner, M. C., Munro, N. D., & Surovell, T. A. (2000). The tortoise and the hare: small-game use, the Broad-Spectrum Revolution, and paleolithic demography. *Current Anthropology, 41*(1), 39–79.

Storå, J. (2001). *Reading bones: Stone age hunters and seals in the Baltic* (Stockholm studies in archaeology, Vol. 21). Stockholm: Stockholm University.

Teldahl, Y., Svensson, E. M., Götherström, A., & Storå, J. (2012). Osteometric and molecular sexing of cattle metapodia. *Journal of Archaeological Science, 39*(1), 121–127.

Thiede, B., Höhenwarter, W., Krah, A., Mattow, J., Schmid, M., Schmidt, F., et al. (2005). Peptide mass fingerprinting. *Methods, 35*(3), 237–247.

Tollit, D. J., Heaslip, S. G., Zeppelin, T. K., Joy, R., Call, K. A., & Trites, A. W. (2004). A method to improve size estimates of walleye pollock (*Theragra chalcogramma*) Atka mackerel (*Pleurogrammus monopterygius*) consumed by pinnipeds: Digestion correction factors applied to bones and otoliths recovered in scats. *Fishery Bulletin, 102*(3), 498–508.

von den Driesch, A. (1976). *A guide to the measurement of animal bones from archaeological sites*. Peabody Museum of Archaeology and Ethnology Bulletin, 1. Cambridge, MA: Harvard University, Peabody Museum.

Walker, R. (1985). *A guide to post-cranial bones of East African animals: Mrs. Walker's bone book*. Norwich: Hylochoerus Press.

Walker, D. N. (1987). Sequence of epiphyseal fusion in the Rocky Mountain bighorn sheep. *The Great Basin Naturalist, 47*(1), 7–12.

Walker, P. L., Johnson, J. R., & Lambert, P. M. (1988). Age and sex biases in the preservation of human skeletal remains. *American Journal of Physical Anthropology, 76*(2), 183–188.

Watson, M. J. (1969). The effects of castration on the growth and meat quality of grazing cattle. *Australian Journal of Experimental Agriculture and Animal Husbandry, 9*(37), 164–171.

Weinstock, J. (2009). Epiphyseal fusion in brown bears: A population study of grizzlies (*Ursus arctos horribilis*) from Montana and Wyoming. *International Journal of Osteoarchaeology, 19*(3), 416–423.

Wellman, H. P., Rick, T. C., Rodrigues, A. T., & Yang, D. Y. (2016). Evaluating ancient whale exploitation on the Northern Oregon Coast through ancient DNA and zooarchaeological analysis. *The Journal of Island and Coastal Archaeology, 12*(2), 255–275.

Wilson, B., Grigson, C., & Payne, S. (Eds.). (1982). *Ageing and sexing animal bones from archaeological sites* (Vol. 109). Oxford: British Archaeological Reports, British Series.

Yang, D. Y., Woiderski, J. R., & Driver, J. C. (2005). DNA analysis of archaeological rabbit remains from the American Southwest. *Journal of Archaeological Science, 32*(4), 567–578.

Zeder, M. A. (1991). *Feeding cities: Specialized animal economy in the Ancient Near East*. Washington, DC: Smithsonian Institution Press.

Zeder, M. A. (2001). A metrical analysis of a collection of modern goats (*Capra hircus aegagrus* and *C. h. hircus*) from Iran and Iraq: Implications for the study of caprine domestication. *Journal of Archaeological Science, 28*(1), 61–79.

Zeder, M. A., & Lapham, H. A. (2010). Assessing the reliability of criteria used to identify postcranial bones in sheep, *Ovis*, and goats, *Capra*. *Journal of Archaeological Science, 37*(11), 2887–2905.

Zeder, M. A., & Pilaar, S. E. (2010). Assessing the reliability of criteria used to identify mandibles and mandibular teeth in sheep, *Ovis*, and goats, *Capra*. *Journal of Archaeological Science, 37*(2), 225–242.