White-tailed deer harvest pressure & within-bone nutrient exploitation during the mid- to late Holocene in southeast Texas

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Abstract

Human population size and density increased in many areas of eastern North America after the mid-Holocene. As predators, human foragers relied heavily on ungulate prey for food in many areas of the world during prehistory. In southeast Texas, changes in foraging adaptations relate to broader subsistence and population trends. Analysis of a large, well-preserved archaeological faunal assemblage that spans much of the second half of the Holocene from the Eagle's Ridge site (41CH252) indicates that harvest pressure and carcass exploitation of white-tailed deer (*Odocoileus virginianus*) intensified through time following predictions framed under two theoretical models. The first model summarises effects of changes in harvest pressure and/or habitat productivity on prey population age structure and body size. Under harvest pressure age structures should become juvenile dominated expressing relatively steep survivorship, and ontogenetic growth rate of prey should increase. Habitat productivity affects ontogenetic growth rate but not proportional age structure in a prey population. The second model uses proxy measures of fragmentation to study exploitation of within-bone nutrients from white-tailed deer bones. Extent of fragmentation increases as marrow exploitation increases and intensity of fragmentation increases as grease exploitation intensifies. At Eagle's Ridge multiple lines of evidence related to the two models indicate that as human population density increased through time white-tailed deer were harvested at a higher rate.

1 Introduction

The mid-Holocene Altithermal/Hypsithermal episode along the margin between the Great Plains and the eastern woodlands in North America is associated temporally with changes in human foraging. In terms of hunting, there is a shift in focus from broader diets, focusing on a variety of small, medium, and large vertebrate prey during the mid-Holocene, to more specialised diets focusing primarily on white-tailed deer (*Odocoileus virginianus*), the remains of which dominate late Holocene faunal assemblages from several stratified sites in Missouri and Illinois, including Graham Cave, Rodgers Shelter, Arnold Research Cave, Pigeon Roost, and Koster (Bozell & Falk 1981; McMillan & Klippel 1981; Neusius 1982; Parmalee et al 1976; Wolverton 2005).

Even in less densely populated regions along the southern plains of north Texas there was an increasing focus on white-tailed deer during the late Holocene coming out of the Altithermal (Ferring & Yates 1997,

1998; Miller & Wolverton 2007). A similar late Holocene emphasis on deer is evident at Wilson-Leonard in central Texas where diet earlier in the Holocene incorporated a broad array of vertebrate taxa (Baker 1998; Collins 2004). Indeed a similar emphasis on white-tailed deer occurs along the southeast Texas coast at the Eagle's Ridge Site (41CH252), which we discuss in greater detail later in the paper.

Many late Holocene cultural adaptations have their roots in the mid-Holocene when climate forcing related to the Altithermal appears to have changed the distribution of faunal and floral resources and patterns of resource use by humans (Collins 2004; Ferring 1995; O'Brien & Wood 1995, 1998; O'Brien 2001; Ricklis 2004a,b). In particular, hunter-gatherers of the Midwest aggregated into river valleys where resources were concentrated during the mid-Holocene. It is this aggregation that promulgated major cultural changes to come during later periods. Similarly, on the upper coast of southeast Texas –

centring on the mid- to late Holocene establishment of coastal habitat at roughly 3000 BP (Ricklis 2004a,b)—it is recognised that human population density grew from 5000 years ago to the late prehistoric period developing into 'incipient socio-political complexity' over time (Ricklis 2004b). However, in contrast to the Midwest, where vertebrate taxonomic composition of diet appears to relate closely to other cultural changes, such as settlement location and site density (eg, McMillan & Klippel 1981; O'Brien 2001), no major change in subsistence has been identified for southeast Texas from the mid- to late Holocene (Reitz & Keck 1998; Ricklis 2004b). However, this lack of change is likely due to small sample sizes and a coarse analytical scale aimed at documenting vertebrate taxonomic composition in diet. Given that white-tailed deer were a very important terrestrial food resource throughout eastern North America during the Holocene, an increase in human population size and density should have produced harvest pressure effects on deer populations (eg, Davis 2003, 2005; Munro 2004; Stiner et al 1999, 2000).

The goal of this paper is to shift focus from documenting faunal composition of diet (eg, Reitz & Keck 1998) to a finer scale examination of if and how use of a single terrestrial resource, white-tailed deer, changed as a consequence of human population growth. Specifically, we use two models to make predictions about white-tailed deer use through time. The first model uses prey population structure and prey body size to document increasing harvest pressure resulting from larger human populations. The second model examines skeletal element fragmentation effects as indicative of changes in exploitation of within-bone nutrients (grease and marrow) from deer bones; however, our analysis using this model relies on preliminary data from an ongoing larger project. Analysing the white-tailed deer assemblage from the Eagle's Ridge site in southeast Texas, we examine if sustained harvest pressure on white-tailed deer occurred from the middle to the late Holocene and if deer populations declined enough to change how the hunter-gatherers occupying the upper southeast Texas coast exploited deer remains through time.

2 White-tailed deer: *the prey* in eastern North America

By the late Holocene, white-tailed deer come to dominate archaeological faunal assemblages in eastern North America. One explanation for hyperabundant deer

remains in sites dating to this period is that white-tailed deer populations irrupted after the mid-Holocene Altithermal/Hypsithermal interval as climate ameliorated, thus providing an abundantly available prey resource late in the Holocene. That is, there was a shift in prey availability related to habitat improvement through time. This explanation has been alluded to in press for several decades (McMillan & Klippel 1981; Purdue 1989; Purdue & Styles 1987; Wolverton 2005). However, the ultimate cause for the hyperabundance of deer during the Holocene may relate to the evolutionary biology of white-tailed deer (and mule deer) extending back into the late Pleistocene.

There are several ecological implications of the terminal Pleistocene extinctions relevant to the distribution and population size of white-tailed deer that have not been touched upon when considering hunting by humans during the Holocene. Among North American ungulates, members of the genus *Odocoileus* are considered paedomorphic and are consummate r-selected generalists (Geist 1987, 1998, 1999). Paedomorphy refers to phenotypes that require less growth of highly developed adult body forms, such as extensive horns and antlers, large body size, highly cursorial adaptations, as well as developed social behaviour in favour of reproductive maintenance and generalist adaptations. During the Late Pleistocene it appears that highly competitive ecological specialists within the ungulate guild (eg, mammoth, mastodon, various cervids, camel, horses) had a selective advantage, while the paedomorphic white-tailed deer was a scrappy generalist living on the fringe prior to the extinction event. Indeed, remains of white-tailed deer are rare in palaeozoological sites across eastern North America until the mid-Holocene (Ferring 2001; Geist 1998). As Valerius Geist (1999:84), a renowned wildlife biologist, puts it; 'megafaunal extinction swept away the ecological specialists, but left behind specialists in non-competition,' in particular, white-tailed deer.

What Geist (1999:84) is referring to when he describes white-tailed deer as 'specialists in non-competition' is that they are more sensitive to competition with other ungulates than harvest pressure for reducing their range and population size. As one of the most r-selected cervids (Geist 1998), white-tailed deer population growth can be limited by predation, but deer populations can recover from and support sustained harvest pressure much better than other cervids. Put in this ecological context, the Holocene is a period of *com-*

petitive release for white-tailed deer in eastern North America. These r-selected generalists, let loose from competition after the Pleistocene in a simplified Holocene ungulate guild, have thrived, and one should expect the palaeozoological abundance of their remains relative to those of other taxa to increase during the Holocene. Stated more strongly, white-tailed deer should become 'the prey' in eastern North America with increasing temporal distance from the Pleistocene. Harvest of white-tailed deer should be sustainable under low to moderate harvest pressure. But with heavy sustained harvest pressure resulting from larger human populations, we should see a decline in deer abundances and corresponding resource depression. In many areas of eastern North American, the adoption of farming in the middle to late Holocene should have insulated deer populations from population depression related to harvest pressure by humans because opening of land provides increased availability of favourable edge habitat and crops provide additional food for white-tailed deer (see discussion in Smith in press; Yerkes 2005; and see Hansen et al 1997; Nixon et al 1991; Seagle 2003 for wildlife biology references). Such was not the case in southeast Texas where people continued foraging after the adoption of pottery.

We examine these expectations about white-tailed deer populations and their relationship with late Holocene human foragers by looking at evidence for increasing harvest pressure on deer populations as well as indications of more intensive use of deer carcasses. Specifically we examine the ecological effects of harvest pressure via the analysis of deer body size and demography using the white-tailed deer assemblage from the Eagle's Ridge site located along the upper Texas coastal plain. In addition, we explore whether harvest pressure resulted in a significant decline in deer populations by analysing the use of within-bone nutrients to determine if deer were being used more intensively through time at the site.

3 Upper Texas Coastal Plain and Eagle's Ridge

The Upper Texas Coastal Plain (UTCP) is bound by the Sabine River to the east, the Brazos River to the west, and the Gulf of Mexico to the south (Aten 1983). The coastal area has low relief and as a result comprises a diversity of environments such as wetlands, lakes, estuaries, river deltas, bays, and barrier islands, as well as prairies, and pine, oak, and hardwood forests

(Ricklis 2004b). Prehistoric hunter-gatherers in the region exploited a wide variety of resources from these varied environments. Fish and shellfish from rivers, lakes, estuaries, and the coast were an important part of diet. Terrestrial mammals included deer, raccoons, and rabbits. Prickly pear, nuts such as hickory and pecan, as well as seed plants like amaranth and *Chenopodium* were some of the most productive edible wild plant resources available in the region (Tull 1987) and were most likely used by prehistoric people.

Human population density in the UTCP appears to have increased progressively from the Middle Archaic period (6000 to 3500 BP) through the Early Ceramic period (2000 to 1250 BP) burgeoning in the Late Prehistoric period (post 1250 BP) (Aten 1983; Ensor & Ricklis 1998; Patterson 1987, 1995; Ricklis 2004b). During this time, artefact density increases at archaeological sites suggesting more people were occupying these sites (Aten 1983; Ricklis 2004b). In addition, non-local lithic raw materials are common in Middle Archaic sites, while in Late Archaic sites lithic raw materials frequently consist of local pebbles, indicating that human populations were less mobile and may have had smaller territories due to more people across the landscape (Ensor & Ricklis 1998). Despite the inference that human population size grew progressively, Ricklis (2004b:189) in a recent regional synthesis states that there are 'no indications of major changes in lifeways', that 'fundamental continuities in settlement and subsistence patterns' exist, and that throughout the late Holocene 'sites [in the UTCP] continue to consist mostly of *Rangia* sp. [brackish water clam] shell middens along secondary bay margins or riverine estuaries' and that a mobile foraging lifestyle persisted through time.

While large-scale economic and settlement changes may not have occurred, one major change in UTCP prehistory was the appearance of pottery between 2500 and 2000 BP (Aten 1983; Ensor & Ricklis 1998). Early UTCP pottery is related to Tchefuncte and Mandeville wares of the Lower Mississippi Valley based on decoration and construction. Thus, archaeologists have speculated that pottery appeared on the UTCP as the result of westward movement of people and/or ideas from the Lower Mississippi Valley, and was possibly maintained as a technological tradition by small-scale interaction with cultures there (Ensor & Ricklis 1998; Moore 1995; Patterson 1993). While pottery is often associated with seed processing, storage, and often harkens the beginning of plant cultivation, in the UTCP

foraging remained the economic pattern throughout prehistory and it is unclear what role pottery played in subsistence.

We chose to analyse the deer assemblage from the Eagle's Ridge site (41CH252) because it has one of the longer occupation sequences in the region, spanning the middle to late Holocene from about 4500 to 1000 BP. The site is a multi-component shell-midden located near Galveston Bay, Texas (figure 1) with repeated long-term occupations (Ricklis 2004b). It is also one of the earliest sites in the UTCP with pottery. Eagle's Ridge (41CH252) was excavated in the mid-1990s as part of the Wallisville Lake project (Ensor & Ricklis 1998). The goal of the project was to identify, protect, and mitigate archaeological sites that might be adversely affected by the US Army Corps of Engineers' management plan in the region. The site is extensive, covering over 9000 square metres. It was initially sampled by several backhoe trenches and 58-50 x50 cm test units. Phase III recovery consisted of 65-1x1 m units excavated in four block excavations (A, B, C and D). This study focuses on the material recovered from these block excavations. Three stratigraphic layers were identified with excavation depths of up to 75 cm.

The faunal assemblage from the site is large and diverse. Approximately one-fourth of the Eagle's Ridge faunal assemblage was analysed as part of the Phase III excavations at the site (Reitz & Keck 1998). The sample from the ¼" mesh consisted of 17,367 bone specimens, of which 6834 NISP and 316 MNI were identified below the class level. This study found no significant differences in subsistence across time. However, the lack of change refers to the fact that the dominant taxa (eg, deer, rabbit, fish) remained constant over time. In terms of relative abundance based on number of identified specimens (NISP), deer remains represent roughly 90 percent of the mammal assemblage. It is clear that deer dominate the Eagle's Ridge fauna, but it is unclear whether or not an increase in harvest pres-
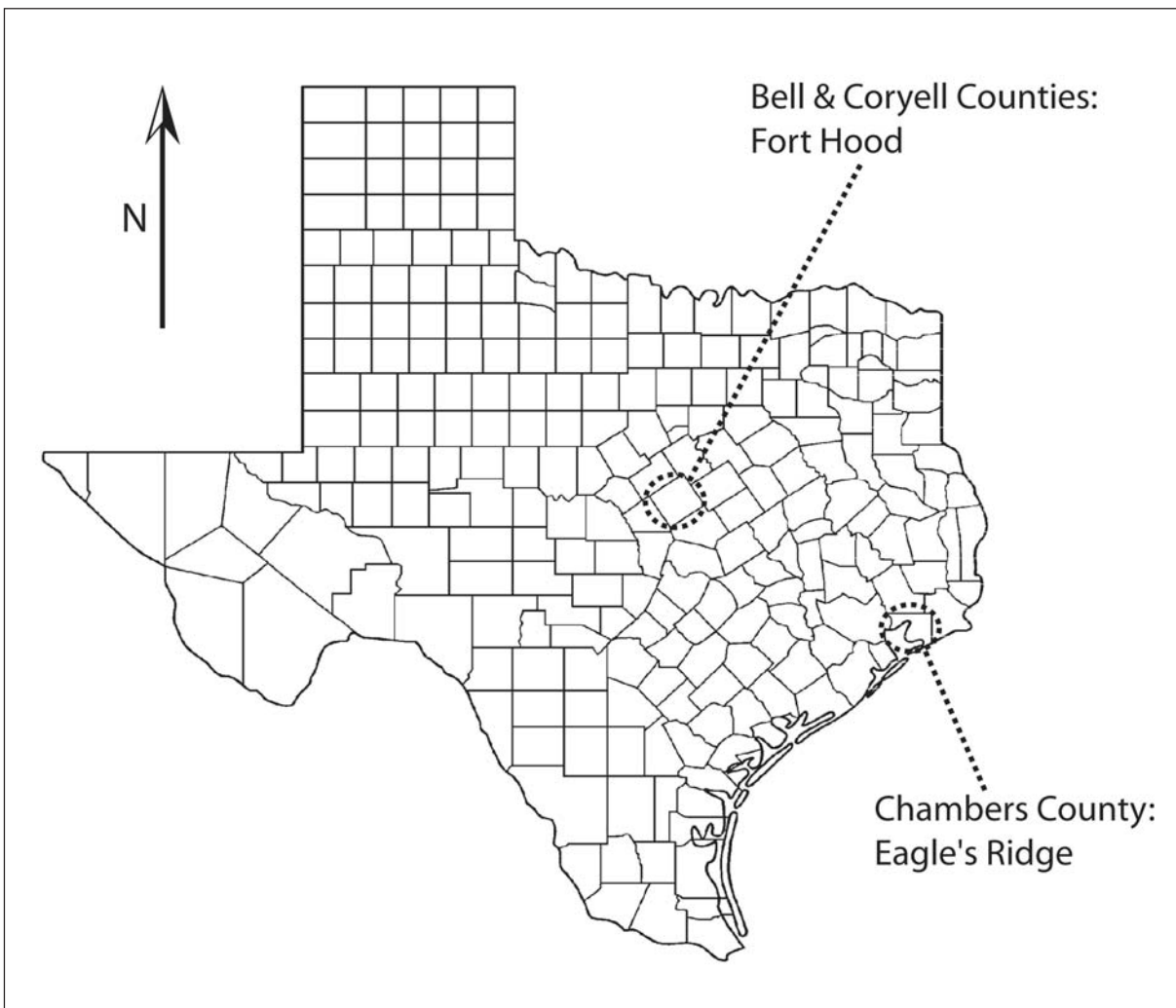

Figure 1 Map of Texas highlighting Chambers County near Galveston Bay where Eagle's Ridge (41CH252) is located and the location of Fort Hood

sure and resource intensification occurred as human populations grew in the region based on this small sub-sample from the site.

For this study, we examine deer remains from the remaining 75% of material not analysed by Reitz and Keck (1998). Remains from Eagle's Ridge are grouped into two assemblages, pre- and post-pottery. The first comprises remains from the late Middle Archaic and most of the Late Archaic (5000 to 2200 BP) deposits at the site and the second comprises the uppermost portion of the Late Archaic and the Clear Lake deposits (2200 to 1000 BP). Aggregation into these assemblages maximises sample size of white-tailed deer remains for analytical purposes and is relevant to models of culture change from the mid- to late Holocene with particular reference to increasing population density and the advent of pottery in the region (Aten 1983; Ensor & Ricklis 1998; Ricklis 2004b).

4 A model of harvest pressure and habitat productivity

Traditionally, harvest pressure has been examined by documenting changes in mortality profiles (Davis 1989, 2003, 2005; Elder 1965; Koike & Ohtaishi 1987; Lyman

1987; Smith 1974; Stiner 1990). With an increase in harvest pressure, mortality increases but fertility remains stable or slightly increases, and this produces shorter average lifespan and juvenile-dominated population age structures (Caughley 1977). A separate implication, however, is that as harvest pressure increases, intra-specific competition for food resources among prey decreases, resulting in an increase in body size (Kie et al 1983; Wolverton et al 2007). An improvement in habitat productivity can also create a similar increase in size (Geist 1998; Purdue 1989). To determine if habitat productivity has increased, archaeologists typically rely on palaeoenvironmental data such as pollen profiles. However, these data are often at a much coarser scale than faunal data, and may not be available for the area near a particular site. To remedy this situation, Wolverton (2008) developed a model that uses faunal data to distinguish harvest pressure from habitat productivity.

In this model (figure 2), body size is used in conjunction with mortality profiles to track changes in harvest pressure versus changes in habitat productivity (Wolverton 2008). A hallmark of an increase in harvest pressure on ungulates is a shift in direction toward
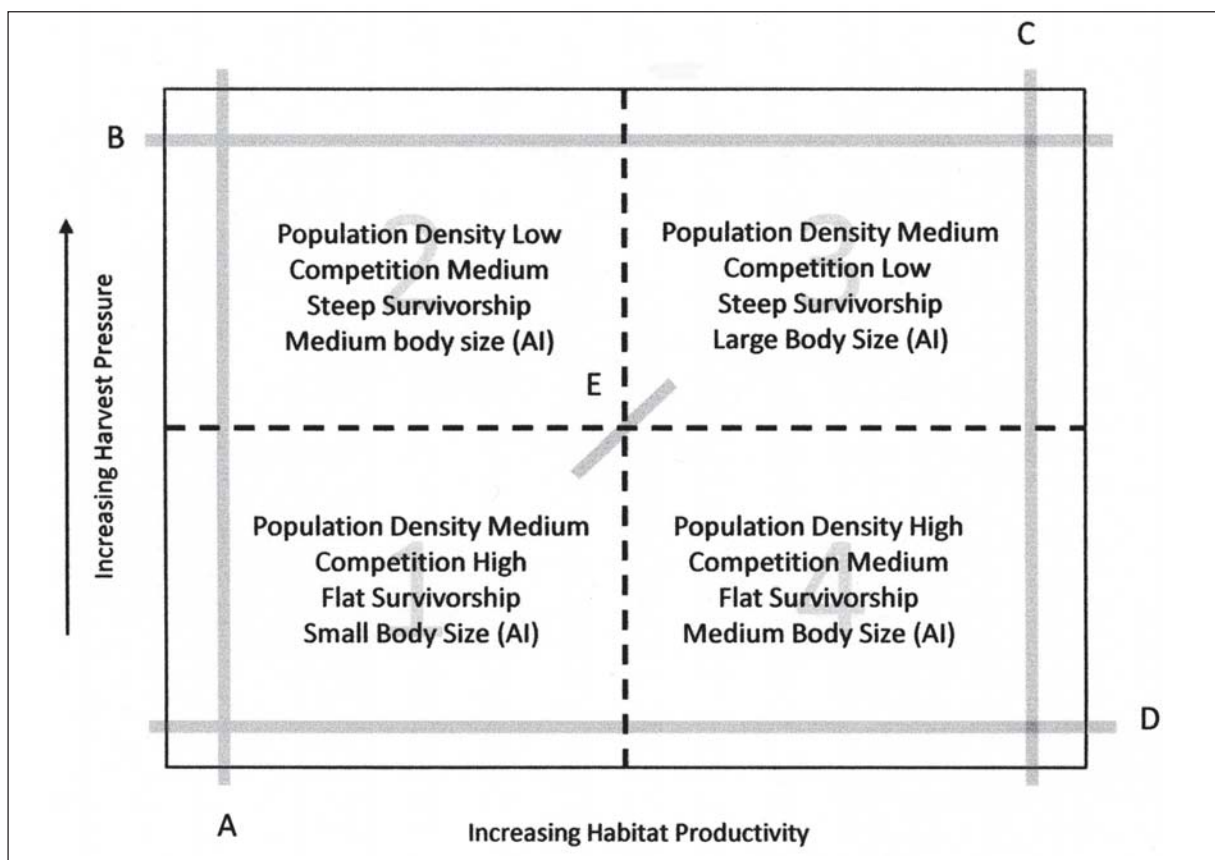

Figure 2 Bivariate model of the effects of fluctuations in habitat productivity and/or harvest pressure on several ecological and biological variables in white-tailed deer. Quadrants and labelled transects are explained in the text (after Wolverton 2008:183, figure 2). (AI) abbreviates 'age-independent' body size, which is explained in the text

more heavily juvenile dominated, old adult depleted populations (Caughley 1977; Koike & Ohtaishi 1987; Lyman 1987; Munro 2004; Stiner et al 1999, 2000; Taber et al 1982). Increased harvest pressure is clearly expressed in survivorship curves as relatively 'steep' (figure 3; Lyman 1987). Survivorship, or l_x, is defined as the distribution of the proportion of individuals that survive from one age class to the next, and it is estimated from age-structure mortality data when applied in zooarchaeological studies (eg, table 1; Lyman 1987). Unlike body size, survivorship, which directly reflects the age structure of a population, is not changed by fluctuations in habitat productivity because harvest pressure does not reduce fertility (Caughley 1977). Thus, the *combination* of these two techniques—analysis of biometry of size and analysis of mortality profiles and survivorship—can be used to distinguish between harvest pressure and habitat productivity (figure 2; Wolverton 2008).

For Eagle's Ridge, given the inferred increase in human population size and density, it is expected that harvest pressure on white-tailed deer should increase. With an increase in harvest pressure moving up transect A in figure 2, prey body size should increase because food (browse) availability per animal increases with predation-thinning of a prey population (Kie et al 1983; Wolverton et al 2007; Wolverton 2007, 2008). Further, habitat productivity (transect D), if anything, should have increased from the mid- to late Holocene along the prairie-forest margin after the Hypsithermal waned, also increasing food availability
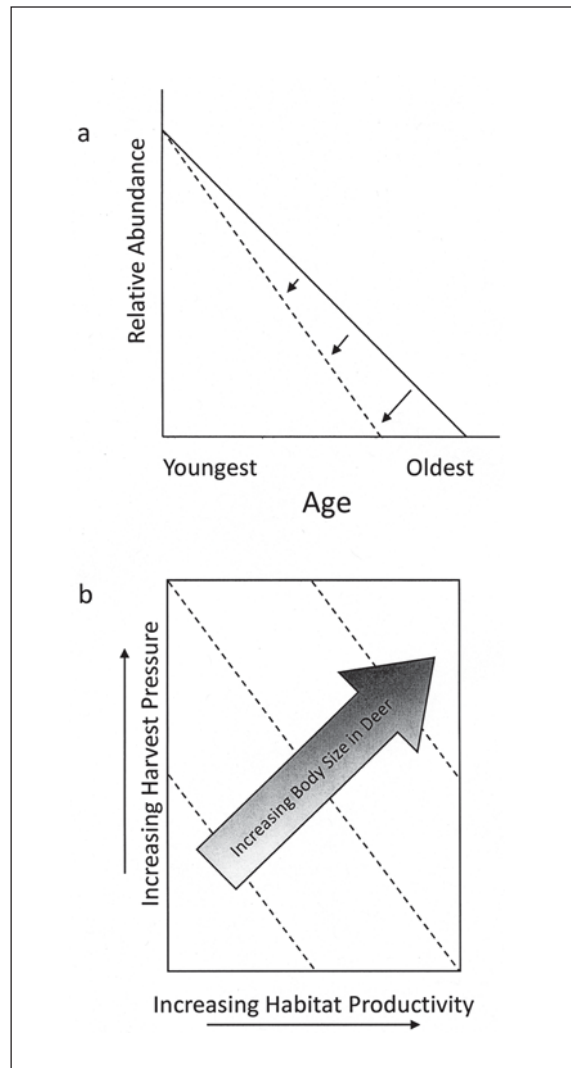

Figure 3 Theoretical graph depicting the ordinal-scale steepening of survivorship (a) and increase in body size (b) with an increase in harvest pressure on ungulate prey

Table 1 White tailed deer survivorship data for Eagle's Ridge

Age Class	MNI	Survivorship (MNI)	l_x
Pre-Pottery			
0	-	41	1.00
0.5/1.5	17	24	0.59
2.5	2	22	0.54
3.5	6	16	0.39
4.5	5	11	0.27
5.5	3	8	0.20
6.5	1	7	0.17
7.5	2	5	0.12
8.5	3	2	0.05
9.5	2	0	0.00
	Total MNI = 41		
Post-Pottery			
0	-	35	1.00
0.5/1.5	16	19	0.54
2.5	2	17	0.49
3.5	4	13	0.37
4.5	4	9	0.26
5.5	3	6	0.17
6.5	3	3	0.09
7.5	2	1	0.03
8.5	1	0	0
9.5	0	0	0
	Total MNI = 35		

per animal. But if harvest pressure is the dominating factor, then we should also expect a steepening of survivorship curves (transect A or C) and a shift toward juvenile dominated age structures.

To illustrate these expected outcomes, we use modern samples of white-tailed deer from Fort Hood in central Texas (figure 1). This population of deer has been managed by wildlife biologists from being unhunted and relatively crowded during the 1970s to one where sustained hunting has thinned the population. With continuous harvest pressure, the model predicts that the Fort Hood population should have an increase in body size and steeper survivorship over time. Body size in bucks and does increased significantly during the same period (figure 4), and this change is age-independent (eg, deer of a single age class [1.5 year old] increased in size through time compared to deer of the same age in an earlier decade). However, taken alone, this increase in body size could be tracking either increasing harvest pressure or increasing habitat productivity (see figure 2). We can differentiate between these two competing explanations by examining the mortality data. Survivorship curves for white-tailed deer at Fort Hood progressively steepen (figure

5), ie, fewer individuals are surviving to older age classes through time. Thus, as is expected for this known situation of continuous high-levels of hunting, harvest pressure rather than habitat productivity explains the changes seen in this white-tailed deer population at Fort Hood. We expect similar effects as human population density increased during the mid- to late Holocene at Eagle's Ridge.

To determine if harvest pressure at Eagle's Ridge was significant, we first examined changes in body size. Reitz and Keck's (1998) tracked body size changes across time using the astragalus (n=24) and the naviculo-cuboid (n=31). Even with small samples, their data show an increase through time in size of these elements. For our analysis, we measured astragali from the remaining 75% of the assemblage unanalysed by Reitz and Keck (1998). The astragalus was chosen because it matures by six months in whitetails (Purdue 1987; Wolverton 2008; figure 6), it is dense and preserves well, it is commonly represented in archaeological assemblages because it is tightly attached to the high-utility upper-hind limb portion, and it is easy to measure. Because the astragalus matures early in deer, it provides an age-independent measure of body
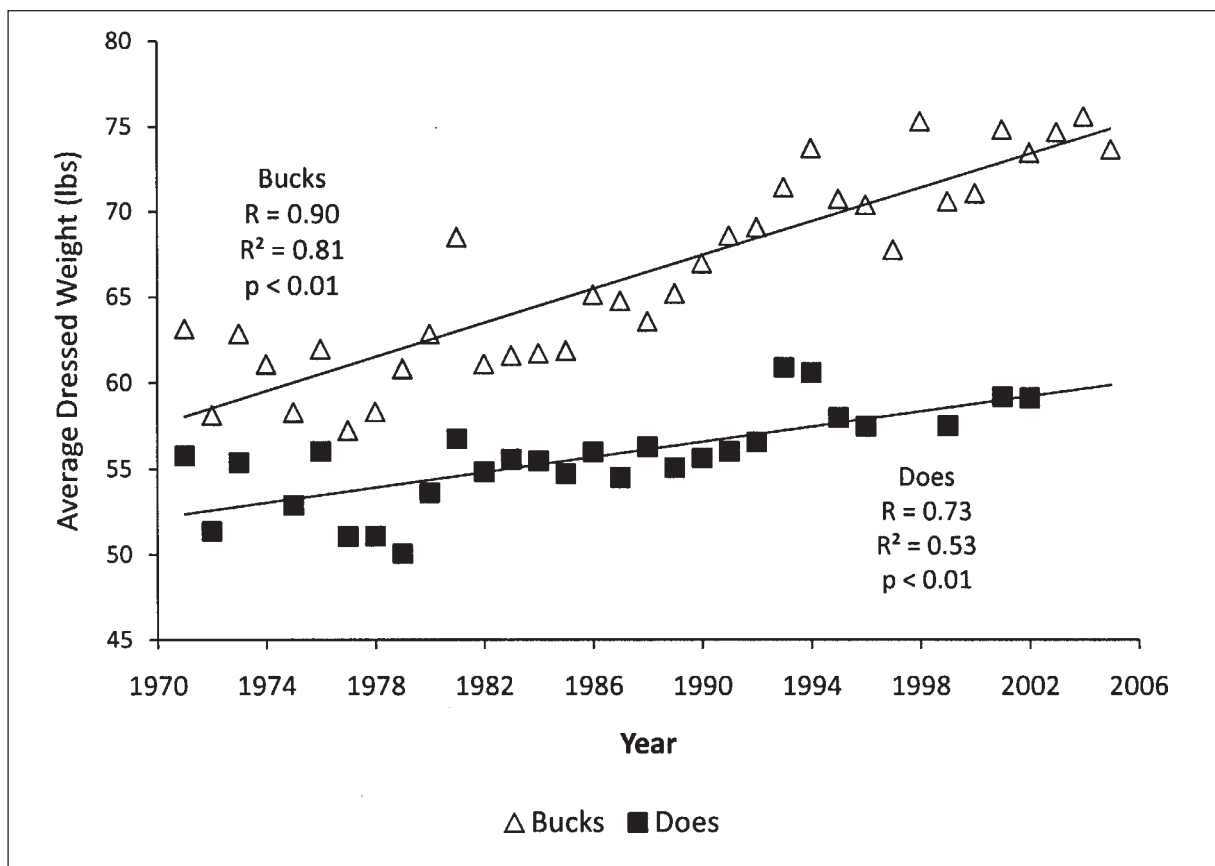

Figure 4 Average field-dressed weight of 1.5 year old deer harvested at Fort Hood from 1971 to 2005 (n = 8,416). Weight increased through time as sustained harvest pressure took place (after Wolverton 2008:189, figure 7)
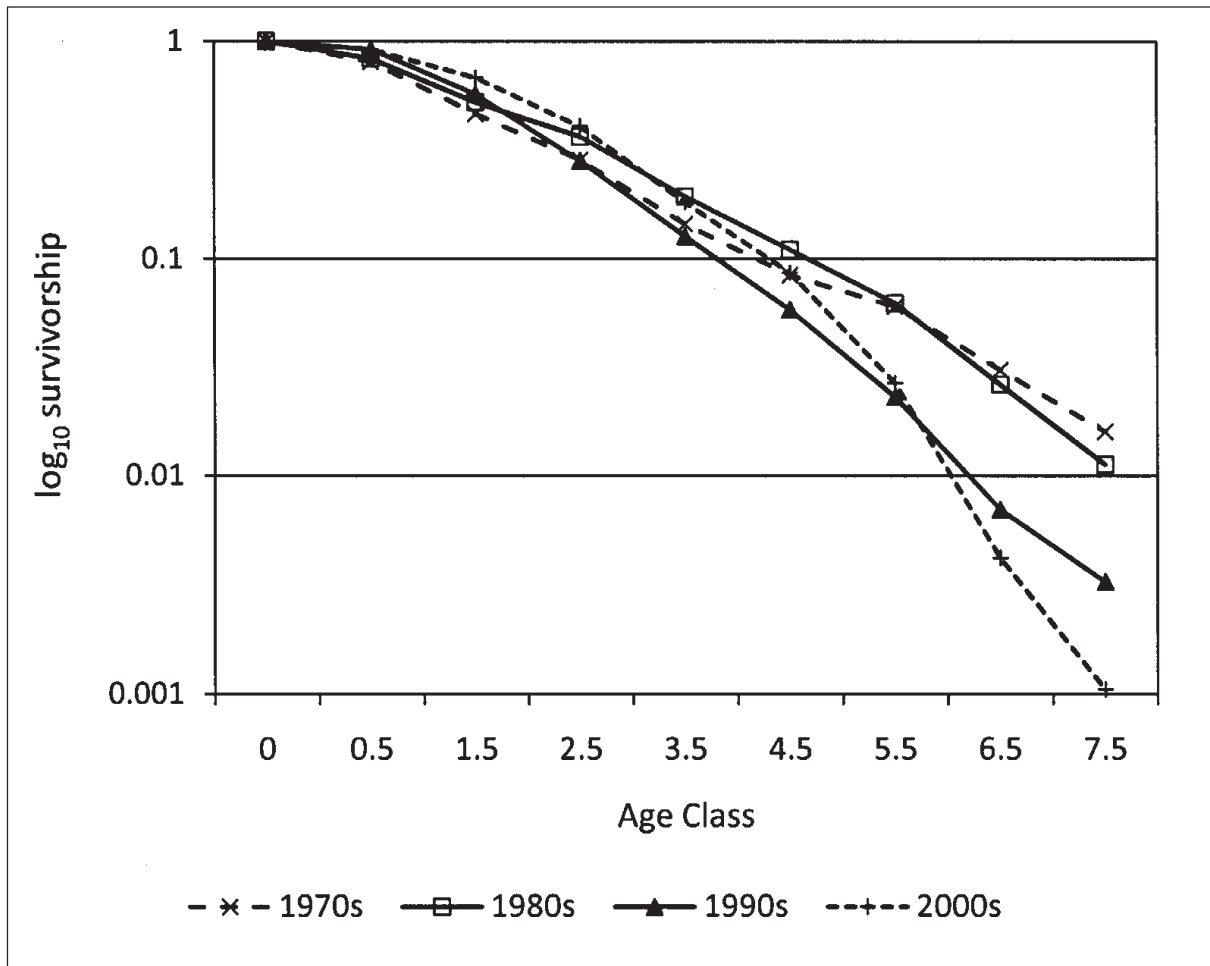
Figure 5 Survivorship curves at Fort Hood, Texas for four decades of sustained harvest pressure following a period of relaxed harvest pressure; survivorship steepens through time

size (Purdue 1987; Wolverton 2008). If size is not age-independent, then a change in age structure of the population will produce a corresponding shift in body size. Thus, a change in body size may reflect either smaller/bigger individuals or younger/older individuals. For our study, we use two measures of the astragalus that correlate well with body mass in modern individuals to examine astragalus size at Eagle's Ridge (figure 7).

The data from the Eagle's Ridge sample indicate that body size increased through time. Astragalus width and length are significantly larger in the post-pottery assemblage than the pre-pottery assemblage (table 2; Mann-Whitney: width, z = 2.97, p =0.003; length z = 2.81, p = 0.005). The box plots in figure 8 convey the ranges, interquartile ranges, and medians of the pre- and post-pottery astragalus assemblages for length and thickness. In particular, competitive release through population thinning should produce an increase in the upper range limit of size, and that is clearly the case in the post-pottery astragalus assemblage.

While it appears that astragalus size of white-tailed deer increases over time, the increase may reflect a shift in sex ratio rather than an increase in body size (Payne 1972; Zeder 2001). White-tailed deer are moderately sexually dimorphic in terms of body size (Geist 1998; Geist & Bayer 1988; Sauer 1984; Schmidly 1994). Thus, if more males than females were being harvested over time, this would cause an increase in astragalus size. To determine if sex ratios have changed significantly over time, we examined the shape of the size distribution graphs, focusing in particular on skewness. Figure 9a is a frequency graph of astragalus length (mm) from a sample of modern deer from central Texas with a roughly equivalent sex ratio. The distribution is slightly bimodal and symmetrical.

To assess whether or not astragali of bucks or does dominate a sample, Pearson's skewness is calculated:

$$\text{Pearson's skewness} = 3(\bar{x} - \text{Median}) / s$$

Pearson's skewness varies between -3 and 3, and skewness of 0 is perfectly symmetrical (McGrew & Monroe 2000). Skewness of greater than |0.6| is sub-
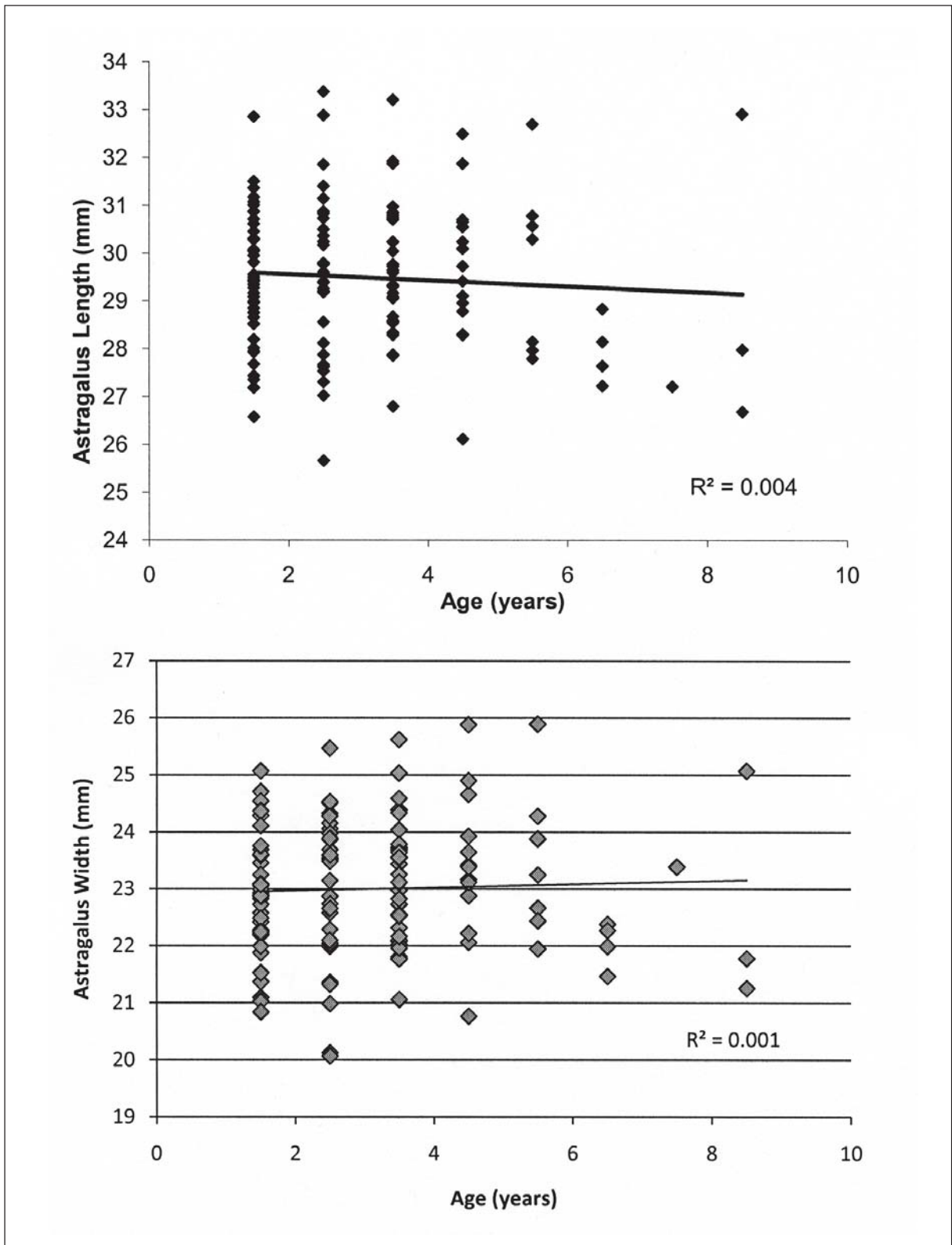
Figure 6 Astragalus length and width by age for modern deer from central Texas exhibiting no increase in size with age

stantially skewed and asymmetrical (Hildebrand 1986). If significantly more bucks than does are being taken through time, then we should expect skewness between -0.6 and -3.0. Astragalus thickness in the Eagle's Ridge deer sample becomes slightly positively skewed through time and length becomes slightly negatively skewed (table 3). Neither of the samples is significantly asymmetrical, indicating that the sex ratio did not change over time.
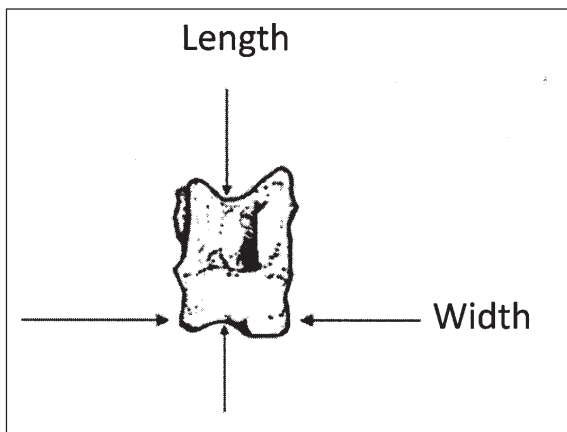
Equally important as Pearson's skewness, which

Figure 7 Measurements taken on the astragalus (mm) (after Purdue 1989:309, figure 1)

assesses the position of the mean relative to the median, are the position of the 25th and 75th percentiles relative to the median and the position of interquartile range relative to the range (Thorndike 1982). In boxplots, medians of symmetrical size distributions should fall in the middle of the interquartile range (the difference between the 25th and 75th percentiles hereafter referred to as IQR). In negatively skewed distributions the median should be positioned relatively close to the 75th percentile, in positively skewed distributions toward the 25th percentile. In addition, the position of the IQR relative to the range is important; in symmetrical distributions the IQR should lay in the middle of the range. In the modern sample (figure 9b) with a roughly balanced sex ratio; the median falls directly between the 25th and 75th percentiles and the IQR falls in the middle of the range. Regarding zooarchaeological astragalus assemblages, if no substantial difference in skewness from different samples is apparent, then it is unlikely that a significant size difference is the product of a shift in sex ratio between assemblages (Wolverton 2008). The positions of the medians and interquartile ranges in the boxplots indicate that astragalus size distributions in these assemblages are symmetrical (figure 8). Thus, the size increase does not appear to have been the result of a shift in sex ratio toward higher abundance of bucks in the later period.

While body size appears to have increased over time, we must examine mortality profiles to determine that the changes are due to harvest pressure. Reitz and Keck (1998) analysed mortality for white-tailed deer at Eagle's Ridge using epiphyseal fusion. However, few long bones were complete, thus their sample was too small (n=7) to reach any conclusions about changes in age structure. For our study, we were able to obtain a much larger sample of mortality data for white-tailed deer by examining all the teeth and mandibles from the 75% of the assemblage not analysed by Reitz and Keck (1998). To determine age, we used tooth wear patterns following Severinghaus (1949). We divided our sample into two time periods: pre- and post-pottery. Lyman (1987) established that roughly 30 individuals per assemblage is the requisite sample size to produce accurate mortality patterns across 10 age categories. Our sample of 35 individuals for the pre-pottery sample and 41 in the post-pottery sample meet this requirement.

It should be noted that tooth wear age classes are not interval scale even though they are reported in annual units. Age determination becomes more unreliable with progressively older individuals, thus the age class data should be considered ordinal data (Gee et al 2002). Ordinal scale changes in survivorship are able to reflect whether or not curves steepen through time with an increase in human population density in the region. Given concerns about using annual units, we also collapse the data into three ordinal categories: juveniles, prime adults, and old adults (Stiner 1990). We group all deciduous teeth, partially erupted teeth, and fully erupted but unworn teeth in the juvenile age class, those that fall in age categories above 2.5 years to 6.5 are combined as 'prime adults', and those that are older than 6.5 are 'old adults' (table 4; Schwartz & Schwartz 2001). Thus the division between juvenile and adult at the point that fully erupted teeth first exhibit wear is more discrete compared to our suite of wear/age classes used in survivorship curves (Stiner 1990), and the use of three ages categories allows a clearer ex-

Table 2 Morphometric data (mm) on white-tailed deer astragali from Eagle's Ridge

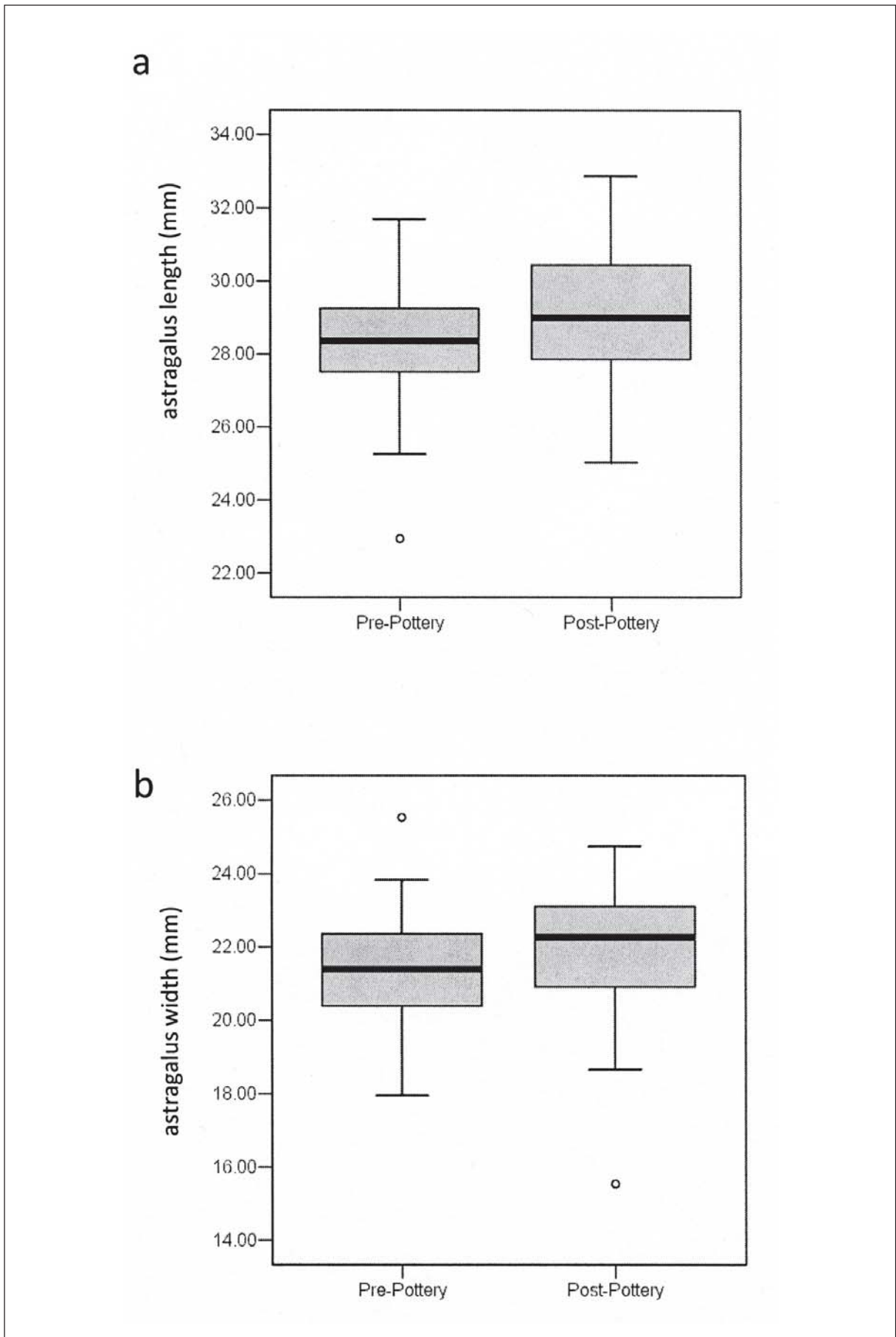| Assemblage/Measurement	Median	Mean	S	n
Pre-Pottery				
Width	21.40	21.38	1.36	77
Length	28.35	28.28	1.46	77
Post-Pottery				
Width	22.26	21.98	1.58	79
Length	28.99	29.01	1.84	79

Figure 8 Boxplot of astragalus length (a) and width (b) comparing pre- and post-pottery assemblages; astragali are significantly larger in the post-pottery assemblage. The circles indicate outliers greater than twice the interquartile-range distance from the interquartile-range box
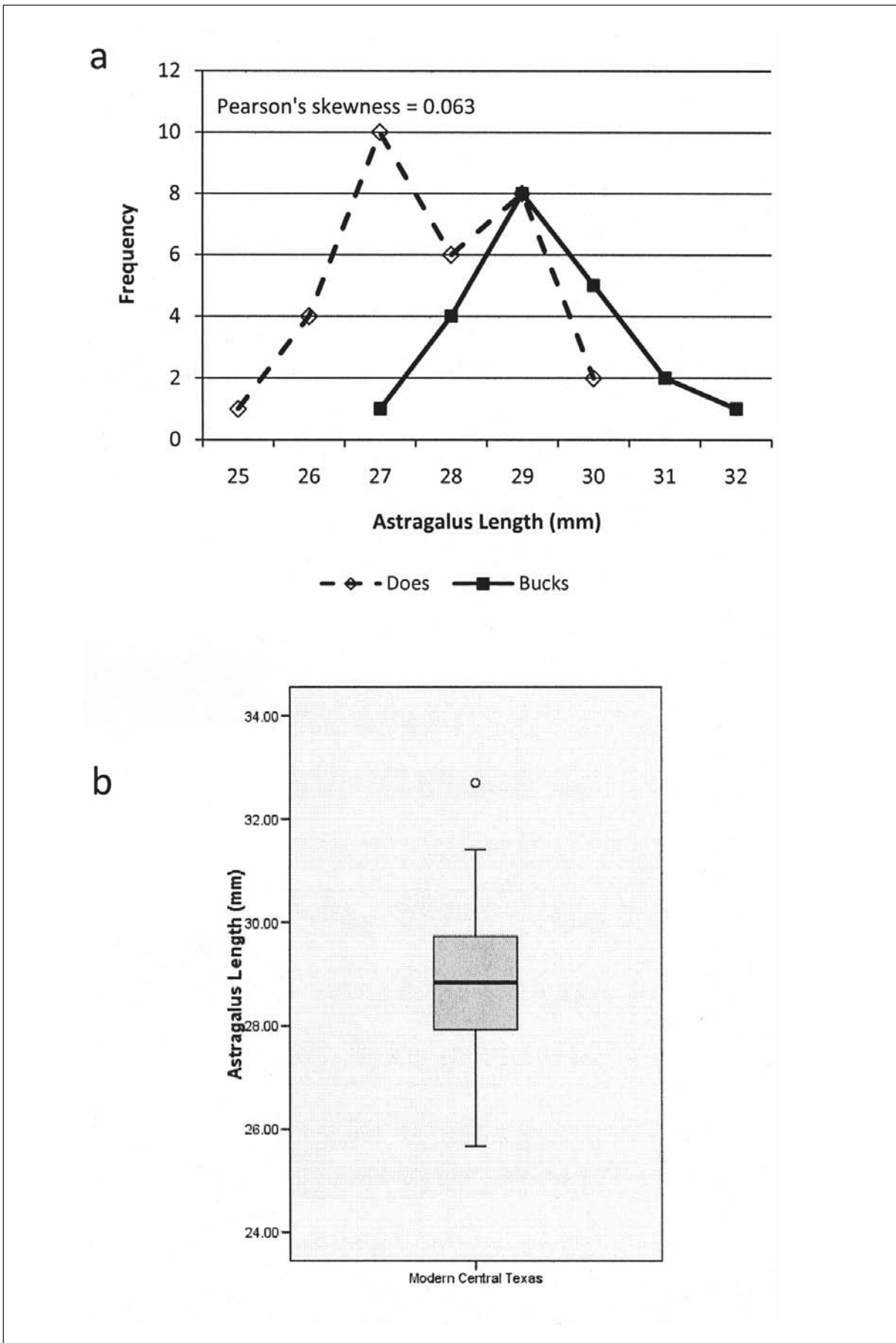
Figure 9 Sex distribution frequency graph (a) of bucks and does from an unmanaged deer population from central Texas with a roughly balanced sex ratio. Bucks and does are aggregated in the boxplot (b), which exhibits the characteristics of an unskewed distribution (Thorndike 1982)

Table 3 Pearson's skewness for astragalus length and width

	Length	Width
Pre-pottery	-0.14	-0.03
Post-pottery	0.03	-0.52

Table 4 White-tailed deer mortality data for Eagle's Ridge

	Juvenile (≤2.5 yrs)	Prime Adult (3.5-6.5 yrs)	Old Adult (≥7.5)	
Pre-Pottery	19	15	7	41
Post-Pottery	18	14	3	35
Pre-Pottery	46.3%	36.6%	17.1%	
Post-Pottery	51.4%	40.0%	8.6%	

amination of coarse changes in age structure, which are more reflective of ordinal-scale differences in age structure through time. Collapsing data into three age classes also reduces problems of fine-scale tooth-wear aging in old adults.

For the Eagle's Ridge deer, survivorship is relatively steep in the post-pottery assemblage compared to the pre-pottery sample (figure 10; Table 1). When the data are analysed by the three age categories, we can see that there are fewer individuals reaching old age and a higher proportion of individuals in the juvenile

and prime adult age categories (figure 11). Thus, over time, the population of white-tailed deer harvested by foragers at Eagle's Ridge appears to be shifting toward younger individuals. Thus, given this apparent demographic shift along with larger body size, harvest pressure on deer appears to have increased through time at the Eagle's Ridge site.

A limitation of our harvest pressure interpretation is that we have assumed that change in these archaeological assemblages represents change that occurred in the life assemblage (the wild population) of white-tailed deer through time. That is, we have presumed that selection of deer during harvest is representative of the death assemblage of animals killed by humans at Eagle's Ridge *and* of the living population that people hunted (*sensu* Klein & Cruz-Uribe 1984; Lyman 1994b). Given this assumption, the increase in deer body size, and the shift toward younger individuals in the deer population, it appears that harvest pressure increased across time at Eagle's Ridge. A second limitation of the harvest pressure, habitat productivity model is that it ignores seasonality of resource exploitation (Monks 1981).
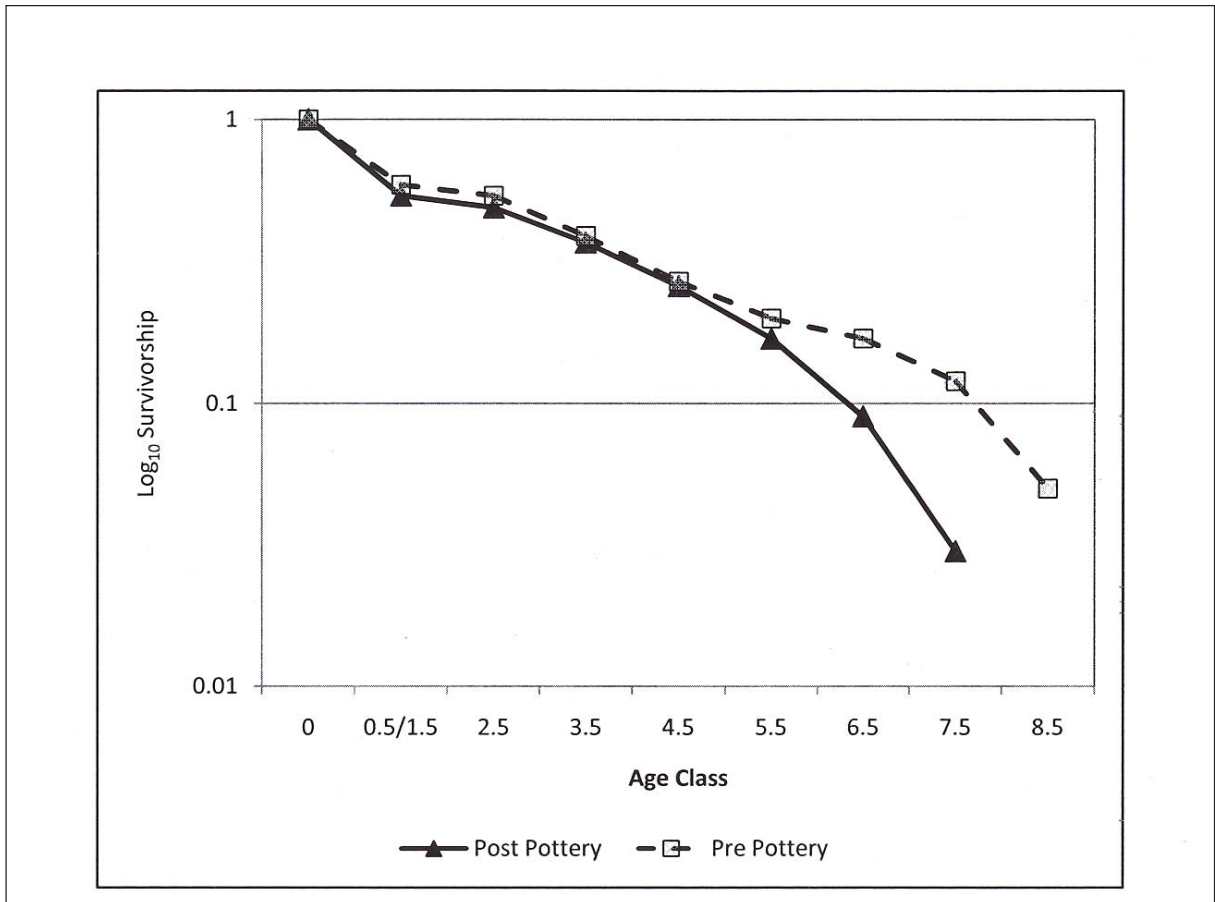

Figure 10 Survivorship for pre- and post-pottery white-tailed deer assemblages at Eagle's Ridge, which is relatively steep in the post-pottery assemblage
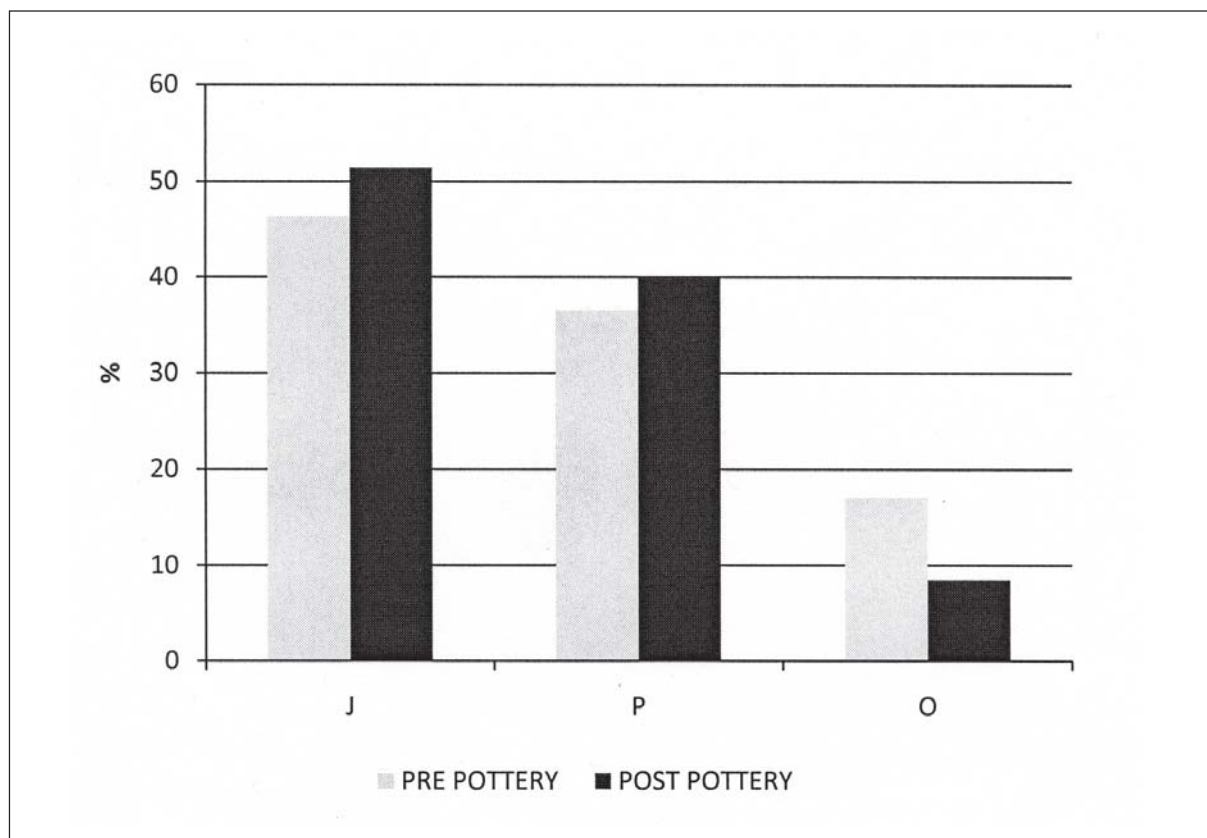
Figure 11 Histogram of pre- and post-pottery deer mortality profiles from Eagle's Ridge

This limitation can be accounted for here in two ways, however. First, seasonal use of resources occurs at a much finer temporal scale than the harvest pressure effects modelled and examined in assemblages studied in this paper, which are time-averaged agglomerations of multiple harvest events. Second, seasonal changes in body size reflect variability in muscle and fat tissue mass, which are highly phenotypically plastic (Kie et al 1983; Simard et al 2008) – so much so that body mass varies by season. It is important to note that we examine *bone size*, which is much less plastic and is more likely to reflect longer term changes in deer body size (Simard et al 2008). Further, the astragalus matures by six months and does not fluctuate in size after maturation, thus its size captures growth rate during early ontogeny, not seasonal variability in body mass. Given these limitations and assumptions, the increase in harvest pressure on white-tailed deer at Eagle's Ridge coincides with growth of human populations in the region from the mid-Holocene to the late Holocene. With an increase in harvest pressure, there may have been a significant decline in deer population size. If this occurred, then intensification of resources at a more localised scale, that of use of within-bone nutrients, may have occurred.

5 A model of fragmentation & within-bone nutrients exploitation

If the mid- to late Holocene white-tailed deer population experienced a significant increase in harvest pressure, deer should have been less commonly available as prey to humans. While in most studies, prey availability would have been measured using prey indices (eg, Bayham 1979; Broughton 1994a,b, 1997, 1999; Cannon 2000, 2003; Nagaoka 2002a,b; Szuter & Bayham 1989), our analysis has not yet generated a large enough sample of taxonomic abundances to use these measures. However, if deer populations are less available then human exploitation of within-bone nutrients may have intensified over time. That is, if deer carcasses (as a common large prey item) became less common, parts of those carcasses should become more valuable and processing should become more intensive. Our current sample of deer skeletal elements and specimens is large enough to conduct a preliminary analysis of this expectation.

A small industry of fragmentation studies focusing on exploitation of within-bone nutrients has been published for a variety of methodological and theoretical purposes in zooarchaeology (eg, Bar-Oz & Munro 2007; Brink 1997; Lyman 1994a; Morin 2007; Munro & Bar-Oz

2005; Nagaoka et al 2008; Outram 2001; Outram et al 2005; Stiner et al 1995; Wolverton 2002). We use two fragmentation classes in this study discussed by Lyman (1994a). Lyman (1994a,b) conceptualises zooarchaeological measures of fragmentation as either those of intensity or extent. Extent of fragmentation considers, of the bones in an assemblage, how many are broken? A convenient measure of extent of fragmentation is %whole, which simply reflects of the specimens of an element in an assemblage, what proportion is complete? Percent whole, as a measure of extent of fragmentation, is most relevant for consideration of marrow extraction. In order to extract marrow, it is only necessary to fracture the marrow cavity enough to provide access (Bar-Oz & Munro 2007; Munro & Bar-Oz 2005), and fragment size does not affect efficiency of extraction.

The same cannot be said for grease extraction. Although Church and Lyman (2003) report that after an hour fragment size does not change grease yields in boiling, it is important to note that contingencies of water boiling during prehistory (eg, fuel use) may have required short extraction times. As a result, intensity of fragmentation, or the degree to which specimens are fragmented, is relevant to efficiency of grease extrac-

tion as smaller fragments expose more surface area. Two measures are important for determining intensity of fragmentation. NISP:MNE answers: how many identifiable specimens are present in an assemblage per recognisable element for a particular species? Higher NISP:MNE reflects more intense fragmentation and smaller fragment size. For example if three fragments (NISP) of deer humerus are found per distinguishable element, the ratio is higher than if two fragments are found (Nagaoka et al 2008). At a coarser scale a similar ratio of NSP (number of unidentifiable and identifiable) specimens to NISP can be used in the same way. To illustrate this relationship we analysed a series of late Holocene zooarchaeological assemblages from Texas that were each analysed by the same analyst (SW). The single non-Texas sample is a very well preserved rockshelter fauna from central Missouri, Arnold Research Cave. The fauna from Eagle's Ridge is not highly fragmented and is closest in NSP:NISP and fragment size to Arnold Research Cave. In general, as NSP:NISP increases, fragments are smaller (figure 12; table 5), and are thus less identifiable (Grayson 1991). It is important to note that extent and/or intensity of fragmentation cannot be related to marrow or grease extraction unless other taphonomic processes that cause
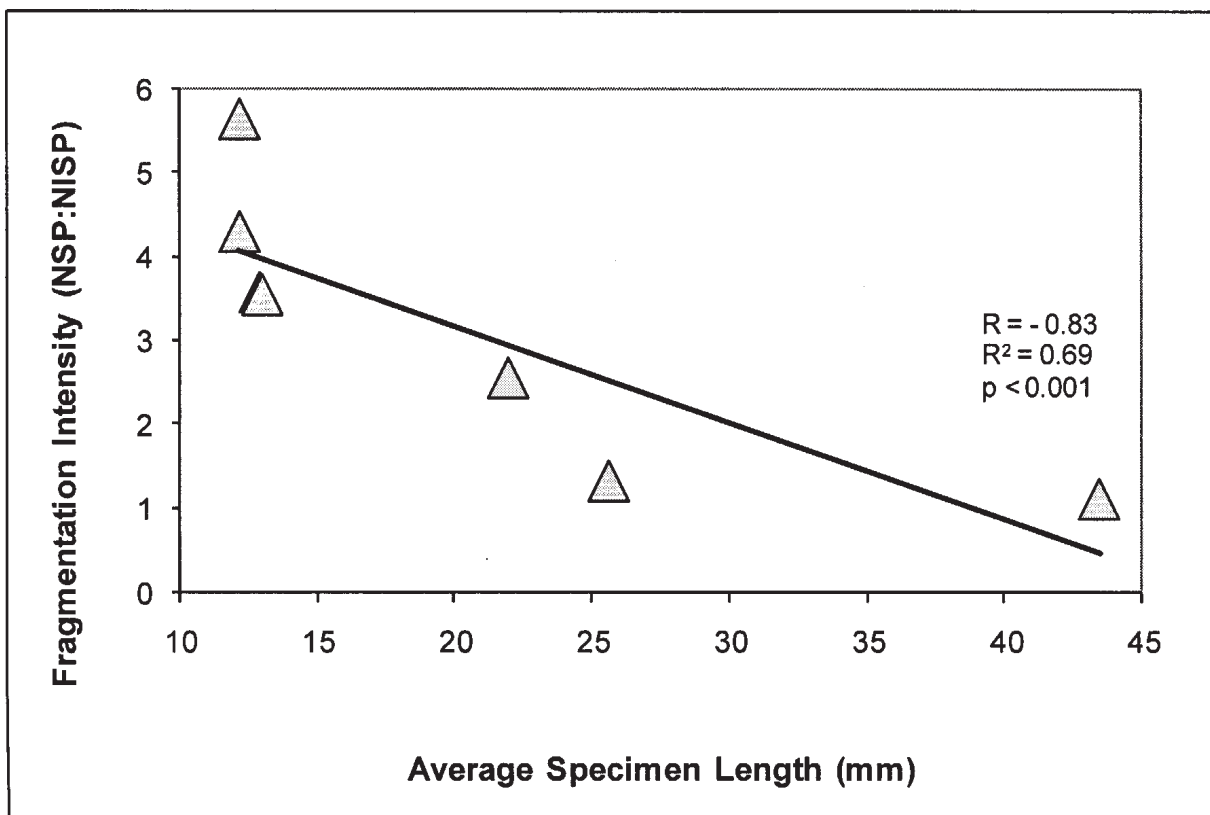

Figure 12 Bivariate plot illustrating the negative relationship between NSP:NISP and fragment size (mm). The data point to the farthest right is from Arnold Research Cave, Missouri. The rest of the data points represent zooarchaeological assemblages from Texas sites, of which the Eagle's Ridge fauna is closest to the Arnold Research Cave fauna in terms of fragment size and NSP:NISP

Table 5 NSP:NISP and fragment size for a sample of zooarchaeological assemblages

Assemblage	NSP	NISP	NSP:NISP	Avg Length (mm)
23CY64.1	75	67	1.12	43.46
41CH252	232	174	1.33	25.57
41TR170	174	68	2.56	21.92
41TR205.1	215	60	3.58	12.89
41TR205.2	198	56	3.54	13.00
41TR114.1	189	44	4.30	12.14
41TR114.2	220	39	5.64	12.17

fragmentation are rejected as important agents in an assemblage's accumulation and depositional history (Lyman 1994b; Wolverton 2002). Further, in terms of NISP:MNE, NISP can begin to decrease per MNE if fragmentation is so intense as to render fragments too small for identification (Marshall & Pilgram 1993). Such does not appear to be the case with the Eagle's Ridge fauna because fragments are large and relatively identifiable (figure 12), thus a change in NISP:MNE is more likely to reflect a shift in intensification of fragmentation than a shift in identifiability.

We conceive of three arbitrary fragmentation classes along a within-bone-nutrients exploitation continuum (figures 13 & 14). Class 1 is low intensity, low extent of fragmentation reflected in low NSP:NISP, low NISP:MNE, and high %whole. Class 2 is low intensity, high extent reflected in low NSP:NISP, low NISP:MNE, and low %whole. Class 3 represents the most intense within-bone nutrient exploitation with high extent and intensity reflected by low %whole, high NSP:NISP, and high NISP:MNE.

We examine grease exploitation at progressively decreasing analytical scales. NSP:NISP for pre- and post-pottery assemblages are examined to determine if fragmentation, in general, increases through time in vertebrate remains. NISP:MNE is then considered
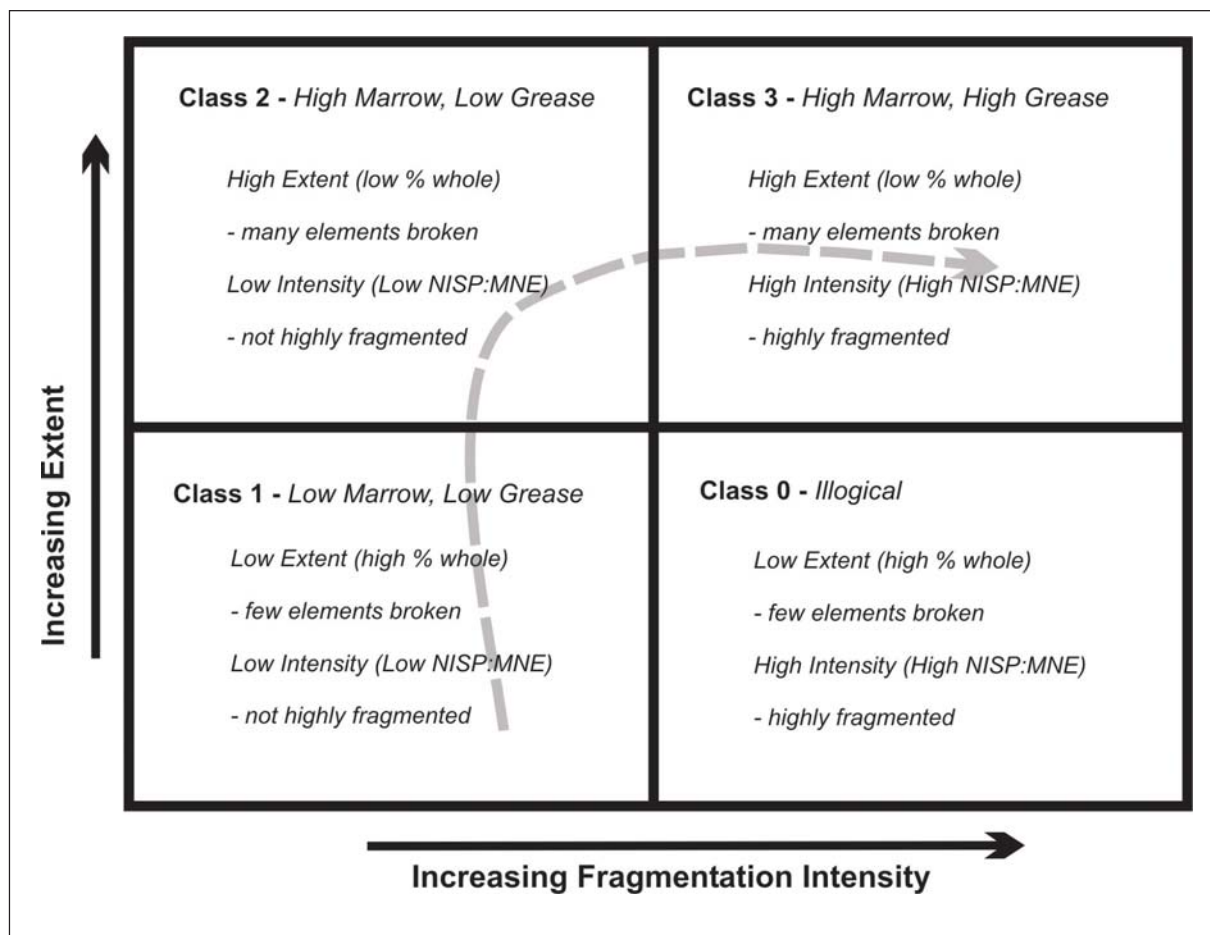

Figure 13 Chart describing fragmentation model that relates extent and intensity of fragmentation to %whole, NSP:NISP, and NISP:MNE (after Wolverton 2002:90, figure 2)
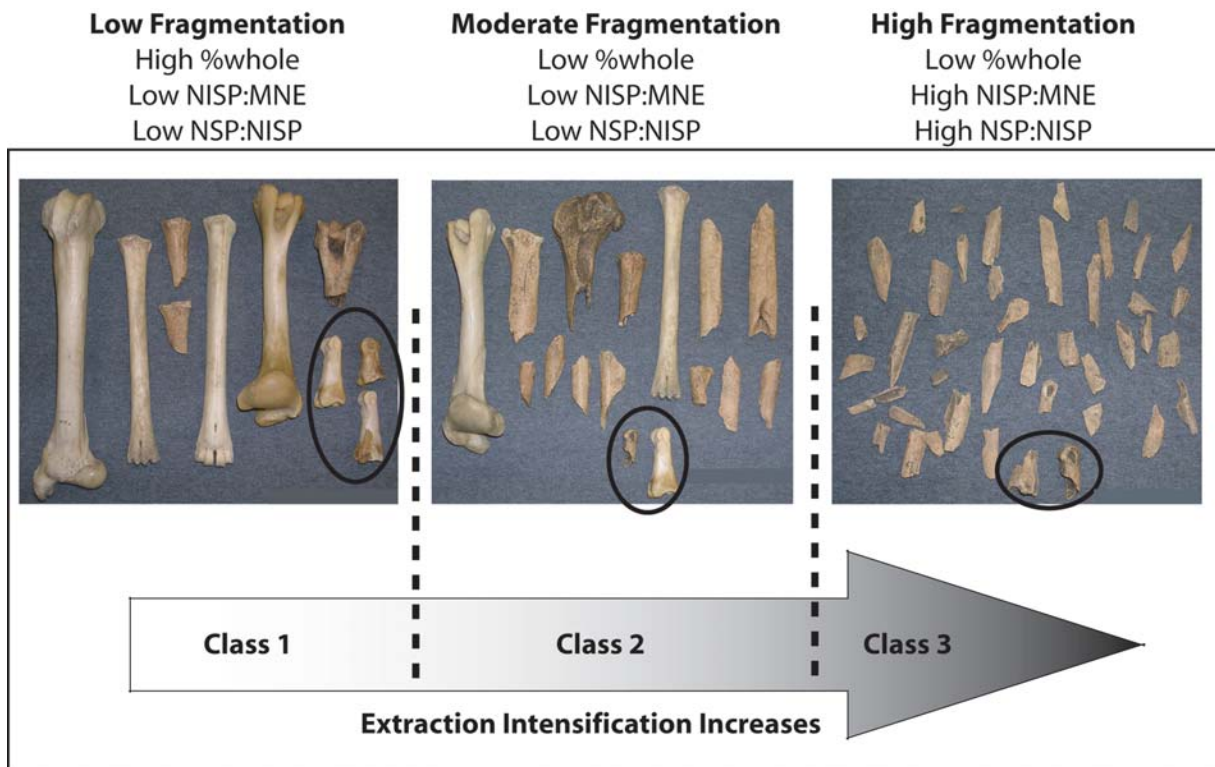
Figure 14 A visual example of the continuum represented by arbitrary classes in the fragmentation model

for fifteen white-tailed deer skeletal elements (table 6a) to determine if fragmentation of deer remains, in general, increases through time. The suite of elements is narrowed to six to determine if fragmentation of high-grease-value bones increases through time (table 6b). Finally, white-tailed deer elements are examined at a still finer scale to determine if high-grease-value portions are more intensely fragmented in the later assemblage by using relative abundance of high grease-utility ends for four elements—the humerus, radius, femur, and tibia (table 6c). If high-grease ends are more intensely fragmented in the post-pottery assemblage, they should be lower in proportional abundance compared to the pre-pottery assemblage because fragmentation renders portions less identifiable (Marean & Kim 1998; Marshal & Pilgram 1993). In addition, taphonomic variables related to fragmentation caused by non-human agents are examined to determine if the observed patterns are attributable to other causes.

Very few marrow-bearing elements are complete at Eagle's Ridge; thus, it appears that marrow extraction was common in both periods. However, phalanges represent one of the lowest-marrow utility elements, and % whole decreases through time for these elements (table 7). This suggests that relatively low-return elements were more frequently exploited later in time for marrow, which aligns with our prediction that intensification occurred.

In terms of intensity of fragmentation, NSP:NISP is substantially higher in the post-pottery assemblage indicating that fragmentation increased producing a higher proportion of unidentifiable, relatively small fragments (table 7). In addition, NISP:MNE in white-tailed deer remains increases slightly through time, a difference that increases in magnitude when high-grease utility elements are examined (table 7). High-grease utility ends for front and hind limbs are less abundant in the post-pottery assemblage indicating that they were more highly fragmented and thus less identifiable (table 6), ie, suggesting that intensification in grease extraction occurred.

To determine if other taphonomic factors may be influencing these patterns, we examined the percent NISP exhibiting presence of burning, weathering, carnivore damage, and green fracturing. Weathering, carnivore damage, and green fracturing decrease slightly through time (table 8). The proportion of specimens exhibiting evidence of burning slightly increases. In general, this pattern indicates that non-human agents that can affect fragmentation, such as weathering and carnivore damage, do not increase in im-

Table 6 White-tailed deer elements incorporated in grease extraction analysis; relative grease utility values follow are from sheep, *Ovis aries* (Binford 1978)

a. elements	grease value	b. high grease elements	c. element end portions
Mandible	11.75	Humerus	Front: Humerus &
Rib	9.30	Radius	Radius
Innominate	34.65	Femur	Hind: Femur & Tibia
Humerus	P, 56.67; D, 9.38	Tibia	
Radius	P, 32.54; D, 18.77	Calcaneus	
Ulna	na	All Metapodial	
Metacarpal	P, 13.24; D, 33.59	Specimens**	
Femur	P, 23.68; D, 100		
Tibia	P, 56.40; D, 26.84		
Astragalus	24.38		
Calcaneus	34.38		
Naviculo-cuboid	na		
Metatarsal	P, 12.37; D, 33.33		
1st phalanx	15.7		
2nd phalanx	13.33		
Metapodial*	na		

* Cannot not be distinguished to metacarpal or metatarsal.
** Includes metarsals, metacarpals, and metapodials.

Table 7 Extent and intensity of fragmentation at Eagle's Ridge

Variable	Pre-Pottery	Post-Pottery	NISP (NSP)
Extent			
%whole 1st & 2nd Phalanx	8.24	6.67	131
Intensity			
NSP:NISP	2.05	3.35	1594 (3873)
Median NISP:MNE WTD	1.76	2.00	689
Median NISP:MNE WTD-HG	1.99	2.13	461
% high grease ends			
Front (humerus & radius)	51%	33%	49
Hind (femur & tibia)	46%	36%	37

Table 8 Summary of presence of taphonomic signatures for pre- and post-pottery assemblages

Variable (% Total NISP)	Pre-Pottery	Post-Pottery
Burning	14.10	16.70
Weathering	4.64	2.97
Carnivore Damage	1.42	1.29
Green Fracture	21.40	17.30

portance through time. Carnivore damage, which is often a major factor in element destruction (Marean & Kim 1998; Marean & Cleghorn 2003), is rare in this assemblage. In general, the skeletal material is well-preserved with natural taphonomic processes appearing to have played a minor role in fragmentation. Thus, for the Eagle's Ridge sample, marrow extraction, as measured by fragmentation in phalanges, is more extensive in the post-pottery assemblage; for grease extraction, fragmentation is more intense suggesting that grease extraction increased during the post-pottery period.

6 Discussion and conclusions

Humans that practiced subsistence hunting as foragers were predators in the ecological communities they were part of. As a result, there are theoretical predictions that can be made regarding the relationship between humans as predators and the prey they hunted. With sufficient sample size, harvest pressure can be analysed through time to address predictions concerning human population growth and resource use in a region. Our study indicates that harvest pressure on white-tailed deer increased over time at the Eagle's Ridge site. In particular, the proportion of older

individuals in the population declined and that of juveniles increased. And with fewer individuals overall, deer population density should have decreased, freeing up resources for individual animals resulting in their larger body size.

In this paper, we also examined a relatively commonplace prediction (eg, Nagaoka 2005, 2006) that use of carcass parts should intensify as humans increase harvest pressure on white-tailed deer. Our fragmentation model produced a series of predictions regarding intensification of exploitation of within-bone nutrients. All of these predictions are met at Eagle's Ridge *at ordinal scale*. It is important to note that intensity of fragmentation appears to have increased in conjunction with an improvement in boiling technology—pottery. While the exact function of early pottery in the region is unclear, it is possible that pottery was used for more intensive exploitation of withinbone nutrients through time. However, the fragmentation study is preliminary and is less convincing than the harvest pressure analysis for a few reasons.

First, the sample size for the fragmentation analysis is much smaller using less than 10 percent of the Eagle's Ridge fauna, while the harvest pressure datasets used 75% of the assemblage. Second, the differences in extent and intensity of fragmentation between the pre- and post-pottery assemblages are subtle at best; that is, the magnitudes of difference are low. Third, there is a slight increase in the percent of specimens that are burned, which may also account for fragmentation. What is provocative is that each prediction generated from the model is met in terms of the *direction* of change from the pre- to post-pottery assemblages. However, we do not argue in this paper that resource depression occurred from the mid- to late Holocene at Eagle's Ridge, but it cannot be disconfirmed.

If an increase in harvest pressure occurred, but resource depression did not, such a pattern may be related to the behavioural ecology of white-tailed deer. Since deer are relatively r-selected among cervids, their populations can withstand substantial harvest pressure. One needs to look no farther than modern eastern North America to determine that it is difficult to overhunt white-tailed deer (references in McShea et al 1997; Teer et al 1965; Teer 1984; Wolverton et al 2007). Thus, whitetails may have been a rather sustainable terrestrial vertebrate resource during the late Holocene in many areas of eastern North American, including in southeast Texas. As such, it is possible that harvest pressure on deer could have increased, but resource depression may not have occurred rapidly or at all. White-tailed deer may have been so abundant across the landscape that population declines resulting from harvest pressure may not have significantly affected encounter rates for human foragers.

Another potential explanation for a lack of strong evidence for resource intensification is the coarse temporal scale of this study. Our current dataset is large enough to examine the dataset by two time periods. However, we have analysed only a small fraction of the assemblage. Thus it is expected that the sample will increase at least tenfold. This larger sample will allow us to analyse the data aggregated into stratigraphic assemblages or by multiple 10 cm excavation level assemblages. The finer time scale will allow us to track shorter-term and/or later changes in harvest pressure or resource intensification that may be currently masked. In addition, with a larger and more complete dataset we will be able to test for resource depression using other measures of foraging efficiency, such as prey indices, richness, and skeletal element representation. If resource depression visible as a shift in prey choice does not occur, then it is likely that white-tailed deer continued to be used as a sustainable resource during the latest Holocene in southeast Texas.

Acknowledgements

References

Aten, LE 1983. *Indians of the upper Texas Coast*. New York: Academic Press.

Baker, BW 1998. Vertebrate remains from the 1/4-inch and 1/8-inch screens. In Collins, MB (ed) *Wilson-Leonard: an 11,000-year old archaeological record of hunter-gatherers in central Texas, volume 5, special studies.* Austin: University of Texas, Studies in Archaeology no 31: 1463–1509.

Bar-Oz, G & Munro, ND 2007. Gazelle bone marrow yields and Epipalaeolithic carcass exploitation strategies in the southern Levant. *Journal of Archaeological Science* 34(6):946–956.

Bayham, FE 1979. Factors influencing the Archaic pattern of animal utilization. *Kiva* 44(2–3):219–235.

Binford, LR 1978. *Nunamiut ethnoarchaeology*. New York: Academic Press.

Bozell, JR & Falk, CR 1981. *Unmodified vertebrate remains from the Pigeon Roost Creek Site (23MN732), Monroe County, Missouri: A preliminary report.* Lincoln: University of Nebraska, Department of Anthropology, Division of Archaeology, Technical Report no 81–05.

Brink, JW 1997. Fat content in leg bones of Bison bison, and applications to archaeology. *Journal of Archaeological Science* 24(3):259–274.

Broughton, JM 1994a. Declines in Mammalian foraging efficiency during the late Holocene, San Francisco Bay, California. *Journal of Anthropological Archaeology* 13(4):371–401.

Broughton, JM 1994b. Late Holocene resource intensification in the Sacramento Valley, California: the vertebrate evidence. *Journal of Archaeological Science* 21(4):501–514.

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

Broughton, JM 1999. Resource depression and intensification during the late Holocene, San Francisco Bay: evidence from Emeryville Shellmound vertebrate fauna. *University of California, Anthropological Records* 32.

Cannon, MD 2000. Large mammal relative abundance in Pithouse and Pueblo Period archaeofaunas from southwestern New Mexico: Resource depression among the Mimbres-Mogollon? *Journal of Anthropological Archaeology* 19(3):317–347.

Cannon, MD 2003. A model of central place forager prey choice and an application to faunal remains from the Mimbres Valley , new Mexico. *Journal of Anthropological Archaeology* 22(1):1–25.

Caughley, G 1977. *Analysis of Vertebrate Populations*. New York: John Wiley.

Church, RR & Lyman, RL 2003. Small fragments make small differences in efficiency when rendering grease from fractured artiodactyl bones by boiling. *Journal of Archaeological Science* 30(8):1077–1084.

Collins, MB 2004. Archaeology in central Texas. In Pertulla, TK (ed) *Prehistory of Texas*. College Station: Texas A & M University Press: 101–126

Davis, SJM 1989. Why did prehistoric people domesticate food animals? In Bar-Yosef, O & Vandermeersch, B (eds) *Investigations in South Levantine Prehistory*. Oxford: British Archaeological Reports, International Series vol 497:43–59.

Davis, SJM 2003. The zooarchaeology of Khirokitia (Neolithicc Cyprus), including a view from the mainland. In Guilaine, J & Le Brun, A (eds) *Le Néolithique de Chypre*. Actes du Colloque International. Département des Antiquités de Chypre et l'École Française d'Athènes: 253–268.

Davis, SJM 2005. Why domesticate food animals? Some zooarchaeological evidence from the Levant. *Journal of Archaeological Science* 32(9):1408–1416.

Elder, WH 1965. Primeval deer hunting pressures revealed by remains from American Indian middens. *Journal of Wildlife Management* 29(2):366–370.

Ensor, HB & Ricklis, RA 1998. Archaeological background: Culture history, previous research, and formulation of research design. In Ensor, HB (ed) *Eagle's Ridge: A Stratified Archaic and Clear Lake Period Shell Midden, Wallisville Lake Project Area, Chambers County, Texas*. Wallisville Lake Project Technical Series no 4. Plano: Geo-Marine, Inc:13–25

Ferring, CR 1995. Middle Holocene environments, geology, and archaeology in the southern Plains. In Bettis, EA III (ed) *Archaeological geology of the Archaic period in North America*. Boulder: Geological Society of America Special Paper no 297: 21–35.

Ferring, CR 2001. *The archaeology and paleoecology of the Aubrey Clovis site (41DN479) Denton County, Texas*. Fort Worth: United States Army Corps of Engineers.

Ferring, CR & Yates, BC 1997. *Archaeological investigations at five prehistoric sites at Lewisville Lake, Denton County, Texas*. Denton: University of North Texas, Center for Environmental Archaeology.

Ferring, CR & Yates, BC 1998. *Archaeological investigations at prehistoric sites at Lake Ray Roberts, Denton County, Texas*. Denton: University of North Texas, Center for Environmental Archaeology.

Gee, KL, Holman, JH, Causey, MK, Rossi, AN & Armstrong, JB 2002. Aging white-tailed deer by tooth replacement and wear: a critical evaluation of a time-honored technique *Wildlife Society Bulletin* 30(2):387–393.

Geist, V 1987. On speciation in Ice Age mammals,

with special reference to cervids and caprids. *Canadian Journal of Zoology* 65(5):1067–1084.

Geist, V 1998. *Deer of the world: their evolution, behavior, and ecology*. Mechanicsburg: Stackpole Books.

Geist, V 1999. Periglacial ecology, large mammals, and their significance to human biology. In Bonnischsen, R & Turnmire, KL (eds) *Ice age peoples of North America: environments, origins, and adaptations of the first Americans*. Corvallis: Oregon State University Press:78–94.

Geist, V & Bayer, M 1988. Sexual dimorphism in the Cervidae and its relation to habitat. *Journal of Zoology* 214(1):45–53

Grayson, DK 1991. Alpine faunas from the White Mountains, California: Adaptive change in the prehistoric Great Basin? *Journal of Archaeological Science* 18(4):483–506.

Hansen, LP, Nixon, CM, & Berringer, J 1997. Role of refuges in the dynamics of outlying deer populations: two examples from the agricultural Midwest. In McShea, WJ, Underwood, HB, & Rappole, JH (eds) *The science of overabundance: deer ecology and population management*. Washington, DC: Smithsonian Books:327–345

Hildebrand, DK 1986. *Statistical Thinking for Behavioral Scientists*. Boston: Prindle, Weber, and Schmidt Publishers.

Kie, JG, White, M & Drawe, DL 1983. Condition parameters of white-tailed deer in Texas. *Journal of Wildlife Management* 47(3):583–594.

Klein, RG & Cruz-Uribe, K 1984. *The analysis of animal bones from archaeological sites*. Chicago: University of Chicago Press.

Koike, H & Ohtaishi, N 1987. Estimation of prehistoric hunting rates based on the age composition of sika deer (Cervus nippon). *Journal of Archaeological Science* 14(3):251–269.

Lyman, RL 1987. On the analysis of vertebrate mortality profiles: sample size, mortality type, and hunting pressure. *American Antiquity* 52(1):125–142.

Lyman, RL 1994a. Relative abundances of skeletal specimens and taphonomic analysis of vertebrate remains. *Palaios* 9(3):288–298.

Lyman, RL 1994b. *Vertebrate taphonomy*. New York: Cambridge University Press.

Marean, CW & Kim, SY 1998. Mousterian large mammal remains from Kobeh Cave: Behavioral implications for Neanderthals and early modern humans. *Current Anthropology* 39(supplement):s79–s113.

Marean, CW & Cleghorn, N 2003. Large mammal skeletal element transport: applying foraging theory in a complex taphonomic system. *Journal of Taphonomy* 1:15–42.

Marshall, F & Pilgram, T 1993. NISP vs. MNI in quantification of body part representation.

American Antiquity 58(2):261–269.

McGrew, JC & Monroe, CB 2000. *An Introduction to Statistical Problem Solving in Geography*, second edition. Boston: McGraw Hill.

McMillan, RB & Klippel, WE 1981. Post-glacial environment change and hunter-gatherer societies of the southern prairie peninsula. *Journal of Archaeological Science* 8(3):215–245.

McShea, WJ, Underwood, HB, & Rappole, JH (eds) 1997. *The Science of Overabundance: Deer Ecology and Population Management*. Washington, DC: Smithsonian Books.

Miller, M & Wolverton, S 2007. Did the bow and arrow increase subsistence efficiency in north-central Texas? *Poster at the 72nd annual meeting of the Society for American Archaeology, Austin, TX.*

Monks, GG 1981. Seasonality studies. In Schiffer, MB (ed) *Advances in archaeological method and theory* vol 4. New York: Academic Press:177–240.

Moore, RG 1995. The Mossy Grove Model of Long-Term Forager-Collector Adaptations in Inland Southeast Texas. PhD Dissertation, Rice University, University Microfilms, Ann Arbor.

Morin, E 2007. Fat composition and Nunamiut decision-making: a new look at the marrow and bone grease indices. *Journal of Archaeological Science* 34:69–82.

Munro, ND 2004. Zooarchaeological measures of hunting pressure and occupation intensity in the Natufian. *Current Anthropology* 45(Supplement):s5–s33.

Munro, ND & Bar-Oz, G 2005. Gazelle bone fat processing in the Levantine Epipaleolithic. *Journal of Archaeological Science* 32(2):223–239.

Nagaoka, L 2002a. The effects of resource depression on foraging efficiency, diet breadth, and patch use in southern New Zealand. *Journal of Anthropological Archaeology* 21(4):419–442.

Nagaoka, L 2002b. Explaining subsistence change in southern New Zealand using foraging theory models. *World Archaeology* 34(1):84–102.

Nagaoka, L 2005. Declining foraging efficiency and moa carcass exploitation in southern New Zealand. *Journal of Archaeological Science* 32(9):1328–1338.

Nagaoka, L 2006. Prehistoric seal carcass exploitation at the Shag Mouth site, New Zealand. *Journal of Archaeological Science* 33(10):1474–1481.

Nagaoka, L, Wolverton, S & Fullerton, B 2008. Taphonomy of Twilight Beach seals. In Clark, G, Leach, BF, & Bulmer, S (eds) *Islands of Inquiry: Colonisation, Seafaring and the Archaeology of Maritime Landscapes*. Terra Australis 29:475–498.

Neusius, SW 1982. *Early-Middle Archaic subsistence strategies: Changes in faunal*

exploitation at the Koster Site, Unpublished PhD Dissertation, Department of Anthropology, Northwestern University.

Nixon, CM, Hansen, LP, Brewer, PA, & Chelsvig, JE 1991. Ecology of white-tailed deer in an intensively farmed region of Illinois. *Wildlife Monographs* 118.

O'Brien, MJ 2001. Archaeology, paleoecosystems, and ecological restoration. In Egan, D & Howell, EA (eds) *The historical ecology handbook*. Washington, DC: Island Press:29–53.

O'Brien, MJ & Wood, WR 1995. Prairie-timberland adapation types. In Wood, WR, O'Brien, MJ, Murray, KA & Rose, JC (eds) *Human Adaptations in the Missouri Prairie-Timberlands*. Fayetteville: Arkansas Archaeological Survey Research Series no 45:148–176

O'Brien, MJ & Wood, WR 1998. *The Prehistory of Missouri*. Columbia: University of Missouri Press.

Outram, AK 2001. A new approach to identifying bone marrow and grease exploitation: why the "indeterminate" fragments should not be ignored. *Journal of Archaeological Science* 28(4):401–410.

Outram, AK, Knüsel, CJ, Knight, S, & Harding AF 2005. Understanding complex fragmented assemblages of human and animal remains: a fully integrated approach. *Journal of Archaeological Science* 32:1699–1710.

Parmalee, PW, McMillan, RB & King, FB 1976. Changing subsistence at Rodgers Shelter. In Wood, WR & McMillan, RB (eds) *Prehistoric Man and His Environments: A Case Study in the Ozark Highland*. New York: Academic Press:141–161.

Patterson, LW 1987. Prehistoric population dynamics in southeast Texas. *Bulletin of the Texas Archaeological Society* 57:117–121.

Patterson, LW 1993. The boundary between inland and coastal margin settlement patterns in southeast Texas. *Journal of The Houston Archeological Society* 107:14–18.

Patterson, LW 1995. The archaeology of southeast Texas. *Bulletin of the Texas Archaeological Society* 66:239–264.

Payne, S 1972. On the interpretation of bone samples from archaeological sites. In Higgs, ES (ed) *Papers in Economic Prehistory*. Cambridge: Cambridge University Press: 65–81.

Purdue, JR 1980. Clinal variation of some mammals during the Holocene in Missouri. *Quaternary Research* 13(2):242–258.

Purdue, JR 1987. Estimation of body weight of white-tailed deer (*Odocoileus virginianus*) from central Illinois. *Journal of Ethnobiology* 7:1–12.

Purdue, JR 1989. Changes during the Holocene in the size of white-tailed deer (*Odocoileus virginianus*) from central Illinois. *Quaternary Research* 32:307–316.

Purdue, JR & Styles, BW 1987. Dynamics of mammalian distribution in the Holocene of

Illinois. *Report of Investigations no 41*. Springfield: Illinois State Museum.

Reitz, EJ & Keck, CA 1998. Appendix A: Animal use through time at the Eagle's Ridge Site, 41CH252. In Ensor, HB (ed) *Eagle's Ridge: A stratified Archaic and Clear Lake period shell midden, Wallisville Lake Project Area, Chambers County, Texas*. Plano: Wallisville Lake Project Technical Series no 4, Geo-Marine, Inc: A3–A65.

Ricklis, RA 2004a. Prehistoric occupation of the central and lower Texas coast. In Pertulla, TK (ed) *The prehistory of Texas*. College Station: Texas A&M University Press:155–180.

Ricklis, RA 2004b. The archaeology of the Native American occupation of southeast Texas. In Pertulla, TK (ed) *The prehistory of Texas*. College Station: Texas A&M University Press:181–202.

Sauer, PR 1984. Physical characteristics. In Halls, LK (ed) *White-tailed Deer Ecology and Management*. Harrisburg: Stackpole Books:73–90.

Schmidly, DJ 1994. *The Mammals of Texas*, revised edition. Austin: University of Texas Press.

Schwartz, CW & Scwartz, ER 2001. *The Wild Mammals of Missouri*, second edition. Columbia: University of Missouri Press and Missouri Department of Conservation.

Seagle, SW 2003. Can ungulates foraging in a multiple-use landscape alter forest nitrogen budgets. *Oikos* 103:230–234.

Severinghaus, CW 1949. Tooth development and wear as criteria of age in white-tailed deer. *Journal of Wildlife Management* 13(2):195–216.

Simard, MA, Côté, SD, Weladji, RB, & Huot, J 2008. Feedback effects of chronic browsing on life-history traits of a large herbivore. *Journal of Animal Ecology* 77:678–676.

Smith, BD 1974. Predator-prey relationships in the southeastern Ozarks-A.D. 1300. *Human Ecology* 2(1):31–43.

Smith, BD in press. Resource resiliency, human niche construction, and the long-term sustainability of pre-Columbian subsistence economies in the Mississippi River Valley corridor. *Journal of Ethnobiology*.

Stiner, MC 1990. Use of mortality patterns in archaeological studies of hominid predatory patterns. *Journal of Anthropological Archaeology* 9(4):305–351.

Stiner, MC, Munro, ND & Surovell, TA 2000. The tortoise and the hare: small-game use, the broad spectrum revolution, and Paleolithic demography. *Current Anthropology* 41(1):39–73.

Stiner, MC, Munro, ND, Surovell, TA, Tchernov, E & Bar-Yosef, O 1999. Paleolithic population growth pulses evidence by small animal exploitation. *Science* 283(5399):190–194.

Stiner, MC, Weiner, S, Bar-Yosef, O, & Kuhn, SL 1995. Differential burning, fragmentation, and preservation of archaeological bone. *Journal of*

Archaeological Science 22:223–237.

Szuter, CR & Bayham, FE 1989. Sedentism and prehistoric animal procurement among desert horticulturalists of the North American Southwest*.* In Kent, S (ed) *Farmers as Hunters: the Implications of Sedentism.* New York: Cambridge University Press:80–95.

Taber, RD, Raedeke, KJ & McCaughran, DA 1982. Population characteristics*.* In Thomas, JW & Toweill, DE (eds) *Elk of North America: ecology and management*. Harrisburg: Stackpole Books:279–298.

Teer, JG 1984. Lessons from the Llano Basin, Texas*.* In Halls, LK (ed) *White-tailed Deer Ecology and Management*. Harrisburg: Stackpole Books:261–290.

Teer, JG, Thomas, JW and Walker, EA 1965. Ecology and Management of White-tailed Deer in the Llano Basin of Texas. *Wildlife Monographs* 15.

Thorndike, RM 1982. *Data Collection and Analysis: Basic Statistics*. New York: Gardner Press.

Tull, D 1987. *Edible and Useful Plants of Texas and the Southwest*. Austin: University of Texas Press.

Wolverton, S 2002. NISP:MNE and %whole in analysis of carcass exploitation. *North American Archaeologist* 23(2):85–100.

Wolverton, S 2005. The effects of the Hypsithermal on prehistoric foraging efficiency in Missouri. *American Antiquity* 70(1):91–106.

Wolverton, S 2007. *A Paleozoological Perspective on Predator Extermination and White-tailed Deer (Odocoileus virginianus Boddaert) Overabundance in Central Texas.* Unpublished PhD Dissertation, Environmental Science, University of North Texas.

Wolverton, S 2008. Harvest pressure and environmental carrying capacity: An ordinal scale model of effects on ungulate prey. *American Antiquity* 73(2):179–199.

Wolverton, S, Kennedy, JH & Cornelius, JD 2007. A paleozoological perspective on white-tailed deer (*Odocoileus virginianus texana*) population density and body size in central Texas. *Environmental Management* 39(4):545–552.

Yerkes, RW 2005. Bone chemistry, body parts, and growth marks: evaluating Ohio Hopewell and Cahokia Mississippian seasonality, subsistence, ritual, and feasting. *American Antiquity* 70(2):241–265.

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