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A Paleozoological Perspective on White-Tailed Deer (*Odocoileus virginianus texana*) Population Density and Body Size in Central Texas

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Abstract Archaeological and paleontological datasets are used in conservation to add time-depth to ecology. In central Texas, several top carnivores including prehistoric Native American hunters have been extirpated or have had their historic ranges restricted, which has resulted in pest-level white-tailed deer (*Odocoileus virginianus texana*) populations in some areas. Differences in body size of deer between prehistory and modernity are expected, given that a lack of predation likely has increased intraspecific competition for forage among deer, resulting in smaller body size today. In fact, modern deer from settings without harvest pressure are significantly smaller than those from harvested areas and from prehistoric deer. From a natural history perspective, this research highlights potential evolutionary causes and effects of top-predator removal on deer populations and related components of biological communities in central Texas.

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Introduction

There is general agreement that white-tailed deer (*Odocoileus virginianus* Boddaert) are overabundant throughout much of North America today and that this overpopulation is related to limited predation and historically induced changes in habitat structure and availability (e.g., references in McShea and others 1997; Ripple and Beschta 2005). Some researchers intimate that white-tailed deer populations have risen during the last few decades (Côté and others 2004); others suggest that their numbers are higher than at any time during the last few centuries (Rooney 2001); but others indicate that population densities today are lower than estimates for prehistoric times (McCabe and McCabe 1997). Various parameters are used to argue that white-tailed deer currently overpopulate areas of North America. For example, Rooney (2001) highlights their propensity to damage native flora, Allombert and others (2005) focus on the impacts of overabundant deer on invertebrate populations, and DeNicola and others (2000) discuss the growing conflict between humans and deer in increasingly crowded suburban areas. Regardless of the parameter used, there is a general consensus that white-tailed deer in many areas are overabundant, leading to a host of cascading deleterious effects permeating through ecosystems (cf. Schmitz and Sinclair 1997). Unfortunately, culling overpopulated deer herds is a controversial social and political issue that requires a delicate balancing act for wildlife managers in that segments of the public view this as a cruel solution (Rolston 1988; Rutberg 1997). This problem is common in central Texas where humans and deer are increasingly sharing the same areas.

A growing body of research uses the prehistoric faunal record from archaeology and paleontology to weigh in on modern biological conservation and ecological restoration problems (e.g., Gompper and others 2006; Graham 1988; references in Lyman and Cannon 2004; Lyman 2006a; McCabe and McCabe 1997). This article focuses on white-tailed deer in central Texas to determine whether high population density is a recent (historical) phenomenon. In order to meet this objective, the body size of modern white-tailed deer is compared to that from the prehistoric Holocene (last 10,000 years). Large predators, including Native American hunters, no longer occur in the region; we argue that their absence is a key factor leading to high population densities, and therefore, to small body size of deer in the region. In some areas of central Texas, however (e.g., Fort Hood), white-tailed deer have been managed below carrying capacity through annual sport harvest for the last half century; we predict that deer from Fort Hood should be larger than deer from relatively unmanaged central Texas populations and should be similar in size to prehistoric deer.

White-Tailed Deer in Central Texas

White-tailed deer (*O. virginianus texana*) in central Texas have been recognized as small compared to conspecifics from most areas of North America for several decades (Geist 1998; Teer and others 1965; Teer 1984, Fig. 1). A factor demonstrated to be important in the small size of deer is overpopulation in the absence of substantial predation in poor quality habitat (e.g., Kie and others 1983). Overpopulation of small deer in the region has become such a problem that during Spring 2006, a regional workshop was organized at Texas State University, San Marcos, by Texas Parks and Wildlife, The Wildlife Society, The Nature Conservancy, and numerous other vested parties to discuss adequate strategies to control deer numbers. The cause of overpopulation received attention at the workshop, but some important factors were underemphasized in that the focus of the workshop was management strategies. A causal factor in overpopulation is the absence of large-bodied predators and the resulting maintenance of a deer population that is at or near carrying capacity in much of central Texas. The

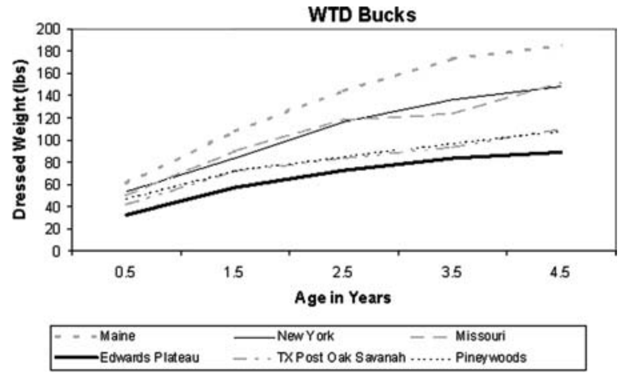

Fig. 1 Average dressed weight (lbs) by age of white-tailed deer (WTD) from several areas of North America; central Texas deer are smaller than in other areas (data from Gore and Harwell 1981; Teer and others 1965)

situation is not a simple one in that the eradication of the screwworm in the mid-twentieth century removed a ''natural'' population control mechanism (Walton 1999), and fire control in the region has altered habitat considerably (Steuter and Wright 1983). However, there is little doubt that modern harvest pressure is too light to substitute for the absence of native large predators (Cook 1984).

A key question is what were deer like prior to predator eradication, prior to modern fire management, and prior to the introduction of ranching in central Texas? At first glance, it appears that there is no easy way to answer this question in that detailed records of white-tailed deer body size, for example, for periods prior to predator eradication do not exist. However, there is a prehistoric record that can be used to approach the problem (sensu references in Lyman and Cannon 2004), that of archaeology and paleontology (henceforth referred to as paleozoology).

The Holocene (the last 10,000 years) represents a period during which central Texas contained a full post-Pleistocene predatory guild (Schmidly 1994, 2002), including wolves (*Canis lupus* Linnaeus and *C. rufus* Audubon and Bachman), coyotes (*C. latrans* Say), mountain lions (*Puma concolor* Linnaeus), black bears (*Ursus americanus* Pallas), and even jaguars (*Panthera onca* Linnaeus). Another large predator was Native American hunters, whose animal-protein diet comprised a high proportion of white-tailed deer for much of the Holocene (e.g., Baker 1998; Wolverton 2005). An important question that arises in relation to the paleozoological record is: were white-tailed deer populations less dense in central Texas during Holocene prehistory? Anecdotally, it is easy to assume that they must have been because many important predators were present and/or were more abundant than they are currently. However, the paleozoological record allows more than assumption.

If deer were less densely populated during the prehistoric period, then their body size on average should have been greater than during modernity. There are several reasons for this prediction. An important one is what Geist (1987, 1998) terms ‘‘efficiency selection.’’ In conditions where dispersal is low (e.g., in densely populated areas), female white-tailed deer tend to mate with smaller males in order to maximize energetic efficiency during gestation and in offspring (Geist 1998). It is not selectively advantageous for white-tailed deer to be large in crowded areas because physical maintenance is more costly. Shortly stated, small body size is an advantage in crowded areas because maintenance in smaller individuals requires fewer calories. Another important reason that modern white-tailed deer should be smaller than prehistoric ones is phenotypic in nature; deer in overpopulated areas tend to be small because less high-quality forage is available for young individuals during maturation, producing ‘‘stunting’’ (Teer and others 1965; Geist 1998). A full predator guild during prehistory would have thinned populations, creating a situation of reduced intraspecific competition allowing larger body size in white-tailed deer for at least two reasons. First, constraints of efficiency selection would have been relaxed, and second, in less crowded conditions more forage would have been available per individual deer during maturation, thus increasing growth rate.

This juxtaposition between prehistory and modernity regarding white-tailed deer body size clearly does not apply in areas of North America where deer habitat has expanded in quality and quantity during the historic period—for example, in response to increased agricultural land use (Hansen and others 1997; Nixon and others 1991). In such settings, removal of predators is potentially offset by an increase in available food for deer, thus relaxing the influence that crowding would have on body size (Schmitz and Sinclair 1997; Sinclair 1997). Such an offset clearly did not occur in central Texas in that deer habitat has been encroached upon by the livestock industry during the historic period rather than opened in response to industrial farming (Buechner 1944; Cook 1984).

The paleozoological record offers an opportunity to test the prediction that removal of predators in central Texas led to overpopulation and smaller body size in white-tailed deer. There is no direct measure of body size such as weight or body length that can be used to gauge size of prehistoric deer because most paleozoological specimens (individual bones and teeth) are disarticulated from the skeletons from which they originated. As a result, it is necessary to use a proxy of body size. The skeletal element used as a proxy must be chosen carefully because it must (1) adequately reflect body size; (2) be resilient enough to survive the vagaries of time; (3) be easily distinguished to species (e.g., the difference between mule deer [*Odocoileus hemionus* Rafinesque], pronghorn [*Antilocapra americana* Ord], and white-tailed deer skeletons is slim); (4) be large enough to be regularly discovered and recovered by paleozoologists; and (5) be easy to reliably measure. Prehistoric and modern skeletal specimens from various settings can then be compared to address the questions and predictions outlined above.

A good candidate is the astragalus (or anklebone) in white-tailed deer. The bone is regularly encountered at archaeology and paleontology sites, it is identifiable to species (Jacobson 2003, 2004), and it matures by 6 months of age and thus reflects maximum potential body size of deer at an early age (Purdue 1987, 1989). The last is very important because bones that mature slowly would be of little use in this analysis. Differences in size in slow-growing bones might reflect variability in size due to age, and here we are interested in whether or not adult size differs between prehistoric and modern deer in central Texas. The remainder of this article analyzes astragalus size in prehistoric and modern white-tailed deer to evaluate the prediction that prehistoric deer should be larger than modern ones from unmanaged populations as discussed above. If such is the case, we believe that deer population density may have been lower in the past than it is today, primarily as a product of higher predation pressure.

Materials and Methods

Prehistoric deer astragali were sampled from collections stored at the Texas Archaeological Research Laboratory and at the Vertebrate Paleontology Laboratory of the Texas Memorial Museum in Austin, Texas. These specimens are from sites excavated in various parts of central Texas that date to the Holocene (Table 1). Undoubtedly, it would have been ideal to measure specimens from well-dated sites restricted to one period within the Holocene (say, the last few thousand years); however, many of the specimens are from collections that never received detailed chronological analysis via relatively expensive radiocarbon dating. To determine the age of specimens would require their destruction; another alternative is to pursue study of large prehis-

Table 1 Prehistoric astragali from central Texas

County	Number of astragali
Comal	9
Coryell	6
Hays	2
Hill	15
Travis	2
Uvalde	17
Val Verde	7

toric collections of vertebrate remains that are less accessible than those used here, which will require a substantial future research effort. The paleozoological samples are from a variety of contexts, but mainly they are from palimpsest rockshelter deposits that were accumulated via a variety of human and carnivore behaviors during the Holocene (e.g., Toomey 1994). There is no reason to assume that the prehistoric sample is age or sex biased, a conclusion that is partially supported by the similar level of variability in the prehistoric and modern samples (see below). Despite the coarse time-scale of the prehistoric samples used here, the prediction framed above can be evaluated in temporally coarse terms.

Modern white-tailed deer astragali are from two areas in central Texas. The first includes suburban areas west of Austin, Texas, where deer have not been subjected to structured management during the last few decades; these deer are relatively small and occur at high population densities. For purposes of this study these deer are labeled ''unmanaged,'' and these populations appear to be at or near environmental carrying capacity, resulting in stunting (Cook 1984; Geist 1998; Teer and others 1965; Teer 1984). Astragali from unmanaged deer were collected by Orion Research and Management Services during unselective culling in 2005. The second modern sample is from Fort Hood near Killeen, Texas. This population has undergone structured and managed sport harvest for much of the last 50 years, and detailed records of population density and body size are available. The Fort Hood sample is labeled ''managed,'' and it was collected during the 2005 hunting season; its population density is assumed to be restricted below environmental carrying capacity in contrast to the unmanaged sample.

Modern astragali were collected by clipping the distal tibia and proximal metatarsal; specimens were transported to the University of North Texas Center for Environmental Archaeology, defleshed, disarticulated, boiled gently for 45 minutes to remove grease, and measured following the specifications in Figure 2. Multiple regression of six measurements on dressed body weight using modern specimens produces a significant positive relationship (multiple $R = 0.696$, $R^2 = 0.485$, $P < 0.0001$, $n = 72$), indicating that astragalus size adequately reflects body size. Prehistoric and modern samples are compared using bivariate plots of selected astragali measurements (AST 1 and AST 3) and are treated statistically using Student's *t* test. Use of AST 1 as ''thickness'' and AST 3 as ''length'' also increases the size of the prehistoric sample in that these measurements are taken near the central, robust portions of the bone and are unlikely to be damaged via destructive processes through time. All six of the measurements correlate closely to one another, and simple bivariate analysis of thickness and length is the focus of the rest of the article.

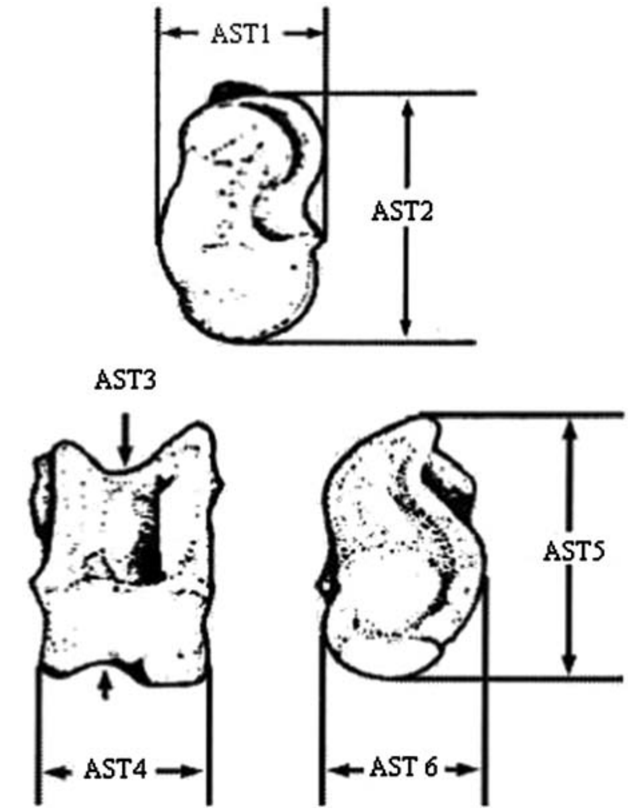

Fig. 2 Morphometric variables of the white-tailed deer astragalus used in this analysis. AST 1 is labeled ''thickness'' and AST 3 is labeled ''length'' in bivariate analyses (after Purdue 1989, p 309, Figure 1)

Results

Descriptive statistics related to each sample are provided in Table 2. Results of Student's *t* comparisons among samples are provided in Table 3. Figure 3 compares astragali from modern managed and unmanaged samples; there is some overlap, but on average

Table 2 Descriptive statistics of white-tailed deer astragali samples from modernity and prehistory (mm)

Sample	Mean	Standard deviation	Coefficient of variation	*n*
Unmanaged				
Thickness	19.88	1.00	5.02	29
Length	28.63	1.18	4.12	29
Managed				
Thickness	21.06	1.15	5.47	43
Length	29.95	1.36	4.53	43
Prehistoric				
Thickness	21.34	1.15	5.39	58
Length	29.88	1.41	4.73	58

Table 3 Results of Student's *t* tests on astragali samples

Test	*t* statistic	*P* value
Unmanaged vs. managed		
Thickness	–4.50	<0.0001
Length	–4.24	<0.0001
Dressed weight	–4.49	<0.0001
Unmanaged vs. prehistoric		
Thickness	–6.09	<0.0001
Length	–4.36	<0.0001
Managed vs. prehistoric		
Thickness	–1.19	= 0.119
Length	0.229	= 0.410

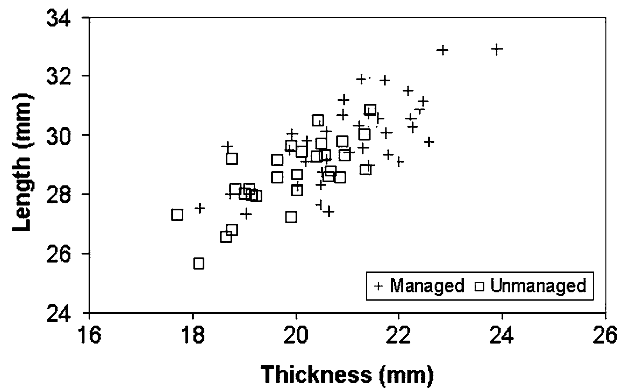

Fig. 3 Bivariate comparison of white-tailed deer astragali from modern managed and unmanaged samples

the size of astragali from the unmanaged sample is significantly smaller (Table 3). Managed and unmanaged samples are also significantly different in terms of dressed weight (Table 3). Of particular interest given the predictions outlined above is that astragali in the unmanaged modern sample are on average significantly smaller than prehistoric ones (Table 3; Figure 4). On the other hand, the managed sample from Fort Hood, which has been hunted for much of the last half-century, overlaps closely with the prehistoric sample (Figure 5) and cannot be distinguished from it statistically (Table 3). In sum, historical structured management of white-tailed deer at Fort Hood appears to have produced lower deer population densities with body-size effects akin to those of the prehistoric period. Furthermore, the absence of substantial harvest pressure in the unmanaged sample appears to have had the opposite effect in that deer are significantly smaller than during prehistory. Anecdotally, it is interesting that several wildlife biologists have noted that deer on Fort Hood are large and yet just off base, conditions are crowded and deer are small.

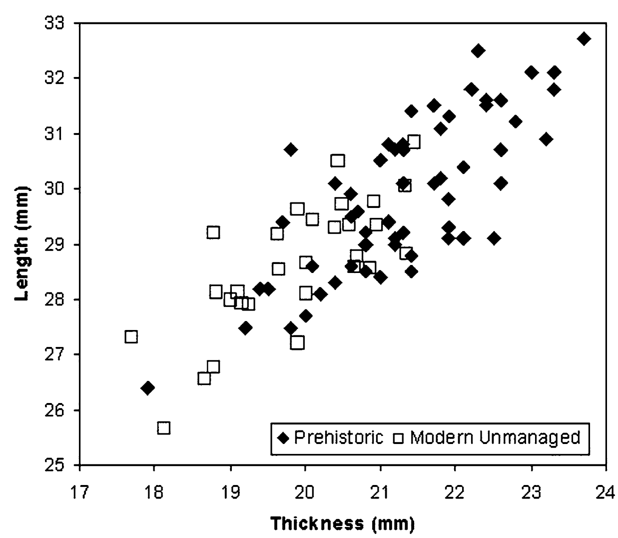

Fig. 4 Bivariate comparison of white-tailed deer astragali from modern unmanaged and prehistoric samples

Discussion

Much has been made in paleozoology of the role that the prehistoric record can or even should play in conservation biology (e.g., Graham 1988; Kay 1997; Lyman and Cannon 2004; Lyman 2006b). Similar concerns have been echoed in the conservation biology and even the philosophical literature (Callicott 2002;

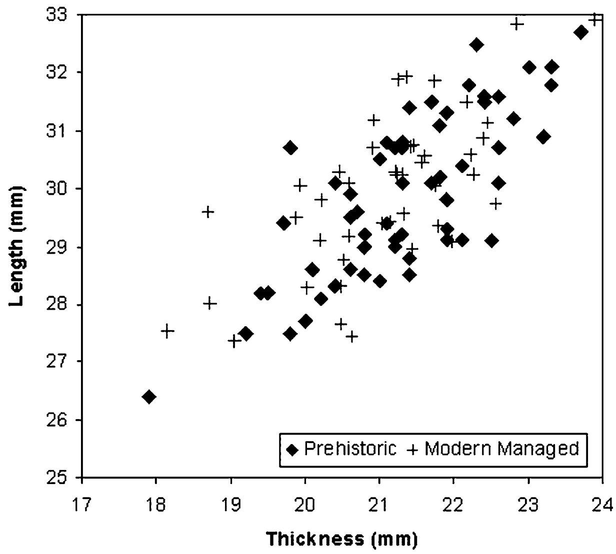

Fig. 5 Bivariate comparison of white-tailed deer astragali from modern managed and prehistoric samples

Landres 1992). Much of the discussion centers on conservation benchmarks or baselines with reference to the following question: what should the temporal baseline for modern conservation biology be (sensu Hunter 1996)? Prior to 1492 when Columbus arrived in the New World? The Pleistocene prior to human entry into the New World? We do not seek to answer these questions here. In fact, we do not see this study as much of a conservation baseline at all because temporal control of the prehistoric sample is coarse and spans the entire Holocene. What is of interest is that modern human impacts on white-tailed deer appear to be substantial if we consider deer body size an appropriate measure of human influence, i.e., via predator removal. The real issue is, why are modern deer smaller than during the rest of the Holocene? Also, why does body size increase when harvest pressure is higher? The answer seems plain and simple; unharvested deer populations are so crowded that stunting and perhaps efficiency selection occur, especially in the absence of sufficient predation.

Other potential factors that might drive changes in white-tailed deer body size include variability in habitat quality across space and through time (e.g., Langvatn and Albon 1986). Climate changed during the Holocene in central Texas and the rest of North America (Collins 2004; Ferring 1995). However, despite the use of a prehistoric sample that covers much of the Holocene, modern deer are as small as they have been or smaller than during the rest of the Holocene. Furthermore, the prehistoric sample contains approximately the same level of variability as either modern sample (see coefficients of variation in Table 2). Similarly, habitat varies across space, and the prehistoric sample spans much of the area bordering and contained within the Edwards Plateau. Again, however, coefficients of variation are similar among the modern and prehistoric samples, suggesting that despite broad spatial and temporal coverage, the prehistoric sample is not extraordinarily diverse (despite the fact that it is also the largest of the three samples). The difference in size between the unmanaged and prehistoric samples and the similarity in size between the managed and prehistoric samples are, thus, provocative.

The most visible difference between modernity and prehistory is the near total absence of large predators in much of central Texas. More important than the immediate effect of low predation pressure on white-tailed deer are the impacts of overpopulated deer on urban, suburban, and rural environments (e.g., Allombert and others 2005; Russell and others 2001; Russell and Fowler 2004). For example, crowded conditions promote overbrowsing of deciduous trees and saplings, which further reduces habitat quality and exacerbates the effects of overpopulation. The result is a downward spiral of habitat conditions in the absence of substantial harvest pressure on white-tailed deer. It is clear that culling of deer populations is a heated social and political issue that science alone cannot solve (Rutberg 1997; Walton 1999). What we hope to accomplish with this article is to add to the debate by framing just how different modern white-tailed deer populations are compared to those from the rest of the Holocene prior to predator eradication. With this type of information in hand, perhaps yet another beneficial contribution of increased harvest pressure can be realized and communicated to vested public and scientific parties, namely, that deer body size has the potential to return to what it was during the prehistoric Holocene with heavier harvest pressure in central Texas.

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