A PALEOZOOLOGICAL PERSPECTIVE ON PREDATOR EXTERMINATION AND WHITE-TAILED DEER (*Odocoileus virginianus* Boddaert) OVERABUNDANCE IN CENTRAL TEXAS

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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. Predator extermination has dramatically reduced the average body size of members of the extant predator guild, and large carnivores most capable of hunting white-tailed deer are extirpated. Character release in the remaining “large” predators—mesocarnivores—is a predicted outcome related to the adaptive vacuum at the top of the trophic hierarchy. 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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CHAPTER 1

INTRODUCTION

By the first half of the twentieth century white-tailed deer (*Odocoileus virginianus* Boddaert) were extirpated from much of their historical geographic range in eastern North America (DeYoung et al. 2003; Doerner et al. 2005; Ellsworth et al. 1994a, 1994b; Leberg et al. 1994; McShea et al. 1997). Post colonization harvest pressure had been too high in many areas, and deer populations eventually disappeared. In some areas, such as central and southern Texas, whitetail populations survived and persisted up to today (Schmidly 1994, 2002). These and other surviving populations were used as sources for restoration of white-tailed deer across eastern North America during the last half-century (e.g., DeYoung et al. 2003). Much of modern white-tailed deer management, thus focuses on the genetic condition (e.g., heterozygosity or lack thereof) of these restored populations. White-tailed deer are one of the most studied large mammals in the world—studies range from the genetic effects of restoration (e.g., Breshears et al. 1988; Doerner et al. 2005; Ellsworth et al. 1994 a, 1994b), to ecological and evolutionary factors that affect population dynamics (e.g., Keyser et al. 2005; Kie and Bowyer 1999; Lesage et al. 2001; Purdue et al. 2000), to the impacts that deer have on ecosystems (e.g., Côté et al. 2004; Ripple and Larsen 2000; Russell et al. 2001).

Large carnivores were exterminated in much of North America during the same period that white-tailed deer populations diminished (Ripple and Beschta 2005). Unlike deer, predators were eradicated in much of Texas in order to protect economic interests in the livestock industry, and unlike deer large predators have not been restored to most areas of North America from which they were eliminated (Schmidly 2002). In parallel fashion, much of eastern North America was opened to develop farmland during the last two centuries (Hansen et al. 1997; Nixon et al. 1991). As a result white-tailed deer were re-introduced, in many cases, to settings with dramatically higher environmental carrying capacity in the absence of large predators.

The Evolution of Deer Overabundance

Missing from this picture is that white-tailed deer were nearly predetermined to reach pest-level population densities in the lush farming regions of eastern North America and in much of the Midwest in the absence of wolves (*Canis lupus*), cougars (*Puma concolor*), and Native American hunters. This relates to the evolutionary history of white-tailed deer and the environmental history of Pleistocene and Holocene North America. White-tailed deer are the consummate generalist ungulate. As Valerius Geist (1998) in his book *Deer of the World* puts it, they are poor competitors with specialized herbivores the latter of which have restricted diets. In an evolutionary sense, however, a generalist living on the “in-betweens” is a survivor. During the Pleistocene, North America was crowded with large-bodied, specialized herbivores (see references in Martin and Klein 1984). These specialists, such as mammoths, mastodons, giant groundsloths, and camels were vulnerable targets on the evolutionary scene compared to white-tailed deer. Should the environment change dramatically, species that are too specialized (e.g., too large in body size or too restricted in diet) must evolve to survive (Guthrie 1984). In Geist’s terms, this kind of species would speciate often in its evolutionary history; specialists must become something else in order to survive through evolutionary time. Environment changed radically at the end of the last glaciation, and many herbivore and carnivore specialists became extinct (Graham and Lundelius 1984; Graham and Mead 1987). Added to this late Pleistocene setting in North America was a new, highly sophisticated and efficient predator, humans accentuating the pressure on large-bodied specialists (sensu Martin 1984; Martin and Szuter 1999).

The terminal Pleistocene was an evolutionary bottleneck that filtered out many specialized herbivores and carnivores. One survivor was the white-tailed deer, which could live in nearly any setting in temperate North America and could eat multiple types of food. They made it through the bottleneck into relatively open herbivore niche space. The Holocene North American mammalian fauna became dramatically simplified in that it now contained reduced ungulate and carnivore richness. The remaining ungulates are segregated into different portions of the landscape (e.g., bighorn sheep [*Ovis canadensis*], pronghorn antelope [*Antilocapra americana*], and deer [*Odocoileus* sp.]) or tend to be distinct in terms of body size in areas of range overlap (e.g., pronghorn antelope and bison on the Great Plains) (Hall 1981). In stark contrast, ungulate diversity in the Old World (primarily Africa) is crowded with dietary specialists.

Essentially, restored white-tailed deer populations in much of eastern North America are those of artificially fed generalists in a large predator-free exclosure that contains few other competitive ungulates. The veracity of this gross over-simplification certainly rings hollow in particular areas of North America, but on the evolutionary time scale (e.g., thousands of years or greater) the generalization holds. A potential sign of such is that introduced ungulate specialists out-compete white-tailed deer precisely because of their evolutionary histories in higher diversity communities of the Old World (Varner 2003).

White-tailed Deer in Central Texas

One exception to this generalization is the white-tailed deer population in central Texas (Figure 1.1). Central Texas deer (*O. virginianus texana*) were not extirpated in all parts of their range (Schmidly 2002). Further, farming was not an important development during the nineteenth and twentieth centuries over much of the region. Instead ranching took hold as a major land-use development (see Buechner 1944; Cook 1984). In contrast to much of eastern North America where environmental carrying capacity for deer appears to have increased during the last two centuries, in central Texas it probably decreased as habitat became increasingly devoted to livestock. Sheep and cattle occupied much of the habitat in central Texas during the historic period, which automatically reduced space and forage for white-tailed deer (Teer 1984).

Large predators, however, were as thoroughly exterminated in central Texas as elsewhere in North America. In central Texas today deer population densities are as high as or higher than anywhere in North America (Teer et al. 1965; Teer 1984). Deer are so overabundant in this marginal habitat that their body size appears to have been stunted as a result (Geist 1998; Teer et al. 1965). Central Texas white-tailed deer are some of the smallest deer in North America. Today, bit-by-bit these diminutive ungulates are eating away the remaining habitat in central Texas (Russell and Fowler1999, 2004). The problem of deer overabundance, colloquially termed “the deer problem,” is a challenging one in that Texas Parks and Wildlife, though aware of the

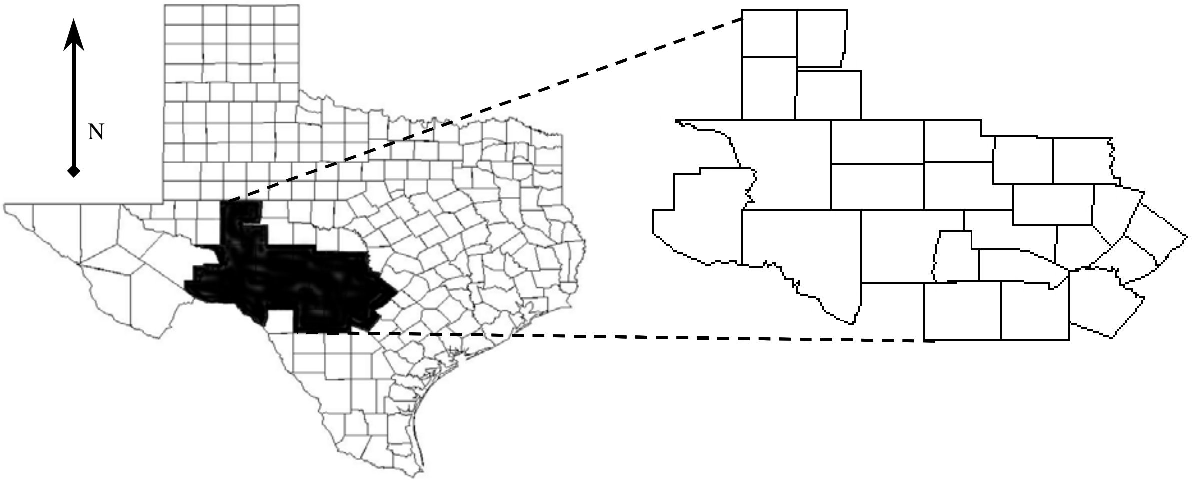

Figure 1.1 Map of Texas highlighting the Edwards Plateau. The study area comprises the Edwards Plateau and surrounding counties. Austin, Texas is located in the easternmost edge of the Edwards Plateau, and to its northeast is Fort Hood.

brewing ecological disaster, can only actively manage deer on public land. Only a small fraction of land in Texas is public (see references in Telfair 1999), thus Texas Parks and Wildlife has sought cooperation with counties and municipalities in order to raise public awareness about the effects of deer overabundance and to initiate lethal and non-lethal population control (sensu DeNicola et al. 2000; Bowker et al. 2003; Henderson et al. 2000; Whisenant 2003).

San Antonio and Austin have witnessed large-scale suburban growth during the last few decades, which has pushed development into white-tailed deer habitat. The burgeoning deer population, on the other hand, has begun to encroach on urban and suburban space (Walton 1999; Whisenant 2003; see Etter et al. 2002; Lopez et al. 2003 for other areas North America). Predators larger than coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) are generally absent (Cook 1984) and sport hunting does not exert enough harvest pressure to diminish deer population densities (Teer et al. 1965; Teer 1984; see also Riley et al. 2003).

Do Two Wrongs Make a Right?

Although recognized social, political, economic, and ecological implications pertain to the problem of white-tailed deer overabundance (Rutberg 1997), it is difficult to assess what should be done about it. Questions abound: Is it fair or natural to cull white-tailed deer populations (see summary in Rolston 1988)? Is culling simply indiscriminate killing? Can sport hunting be structured to manage deer population density? Is it ethical to promote sport hunting for pleasure under the umbrella of deer management? Would such management sanction blood lust as animal rights activists intimate (Rolston 1988)? Or would culling and/or structured harvest provide a pragmatic solution to a growing, potentially devastating, ecological problem that produces trophic cascades throughout the central Texas ecosystem? There is no easy answer to these and related questions, but there is a relatively unexplored avenue of study that potentially sheds a new light on the evolution and cause of deer overabundance in central Texas and elsewhere.

This dissertation uses the paleozoological record of archaeology and paleontology to compare what white-tailed deer and predator populations were like prior to Euro-American settlement and what they are like today in central Texas. The variables that are compared are simple in their design and straightforward in their use. *Species richness* of the carnivore guild is studied to illustrate just what is missing from the modern Texas fauna. The *body size* of surviving carnivores, in this case bobcats and coyotes, is compared between the two periods using a proxy measure (size of the mandible) to determine if large carnivore extermination has caused any phenotypic effects in these medium-sized predators. The body size of white-tailed deer is also compared between prehistory and today using size of the astragalus (ankle bone) as a proxy measure in order to gauge whether or not stunting is occurring today.

An important assumption in this study is that during the prehistoric period of the Holocene (the last 10,000 years up to Euro-American settlement) large predators (e.g., cougars and wolves) and Native American hunters likely exerted enough harvest pressure on white-tailed deer to thin their populations (Smith 1974), reduce intraspecific competition for forage, and, thus, result in large deer relative to the modern population (Wolverton et al. 2007). If so, can managed sport harvest reduce population density and thereby increase body size of modern deer? If yes, then the paleozoological record offers not just a basis for comparison, but also a warrant for action. In terms of ethics, two wrongs (predator eradication in the past and deer culling today) might in this case make a right. To some members of society killing deer is viewed as cruelty (see summary in Rolston 1988). However, if culling produces a healthier deer population that does less damage to already overtaxed habitat in central Texas, and if this action has paleozoological support, then perhaps culling the deer population is an appropriate solution to the problem of overabundance and to not do so is unethical.

It is a significant question as to whether or not paleozoological data are suited to the tasks of wildlife management (Lyman 1996, 1998; Lyman and Cannon 2004a). These data are coarse in temporal scale, patchy in terms of representativeness, and merit careful consideration in their use (especially for carnivores). Chapter 2 formalizes the research questions to be addressed in this dissertation and introduces paleozoological data in more detail. Chapter 3 is the first of three analytical chapters; it is a comparison of the prehistoric and modern predator guild in central Texas. Chapter 4 is a study of the historical record of white-tailed deer management since 1971 at Fort Hood, which is located in northern central Texas. The effects of structured harvest on deer population density and body size over the last few decades are also explored in Chapter 4. Chapter 5, in similar fashion to Chapter 3, compares modern and prehistoric samples—this time of white-tailed deer—to consider differences in population density and body size between the two periods.

Body size reflects several conditions in predators and deer. Interspecific competition between members of the predator guild is an important influence on carnivore body size. Among white-tailed deer population density and ecological carrying capacity are important influences on body size. This study attempts to exploit these relationships to the advantage of wildlife biology by framing predictions that make ecological sense and then by testing them, for better or worse, using paleozoological data.

CHAPTER 2

PROBLEM ORIENTATION AND RESEARCH EXPECTATIONS

Management of white-tailed deer populations often requires that wildlife biologists walk a fine line. On one side of that line is a sustainable harvest policy to benefit sport hunting; on the other side is pest-level overabundance (cf. Schmitz and Sinclair 1997). Sport hunting today is often the main source of predation on deer populations in many areas of North America. Although there are areas where large predators still exist (e.g., northern Minnesota, the Rocky Mountains), over much of white-tailed deer range large predators have been purposefully eradicated (Ripple and Beschta 2005).

Wildlife biologists debate the extent to which the elimination of large predators and the absence of Native American hunters influences modern white-tailed deer population density (see Côté et al. 2004; Sinclair 1997). McCabe and McCabe (1984, 1997), for example, estimate prehistoric white-tailed deer population size for North America based on archaeological and historical data. They conclude based on their estimates that white-tailed deer populations were substantially higher during prehistory (before European settlement of the New World) prior to predator extermination. Estimates of human and deer population size and density based on such data, however, are highly problematic and assumptive (Lyman and Wolverton 2002). The same archaeological faunal data could as easily, but not necessarily more accurately, be interpreted as evidence of high harvest pressure exerted by Native Americans, which would suggest a population limiting, or perhaps even regulating, factor existed in the past that is not present today (Grayson 2001).

The kinds of data required to better evaluate levels of prehistoric harvest pressure require large paleofaunal samples that are rarely encountered in the North American archaeological record (e.g., Koike and Ohtaishi 1987; Lyman 1987; Stiner 1990, 1994). What is clear is that white-tailed deer and mule deer (*Odocoileus hemionus*) were important parts of Native American subsistence to varying degrees across North America (Broughton 1999; McMillan and Klippel 1981; Smith 1974; Wolverton 2005). The archaeological record indicates if anything that Native American hunters were important predators now missing from North American ecosystems (Bayham 1979; Szuter and Bayham 1989).

In addition to the question of the importance of predator eradication, use of the term “overabundance” in relation to whitetail population density is at times criticized as being a product of social judgments rather than ecological science (Schmitz and Sinclair 1997; Sinclair 1997). Sinclair (1997), for example, correctly points out that the meaning of “overabundance” is relative to management goals, cultural perspectives, and environmental setting. Figure 2.1 highlights that there are several value judgments in addition to ecological factors that potentially contribute to management of deer populations. An important one is what Sinclair (1997:382-386; DeCalesta 1997) refers to as “cultural carrying capacity;” others include “rare-species carrying capacity” and “sport-hunting carrying capacity.” Cultural carrying capacity refers to the deer population density that is culturally acceptable in a locality or region, which might vary considerably. Sport hunting capacity is the desirable population density for providing plentiful, healthy deer to be harvested annually, and rare species carrying capacity is the population density at which deer do not harm endangered or threatened species in a

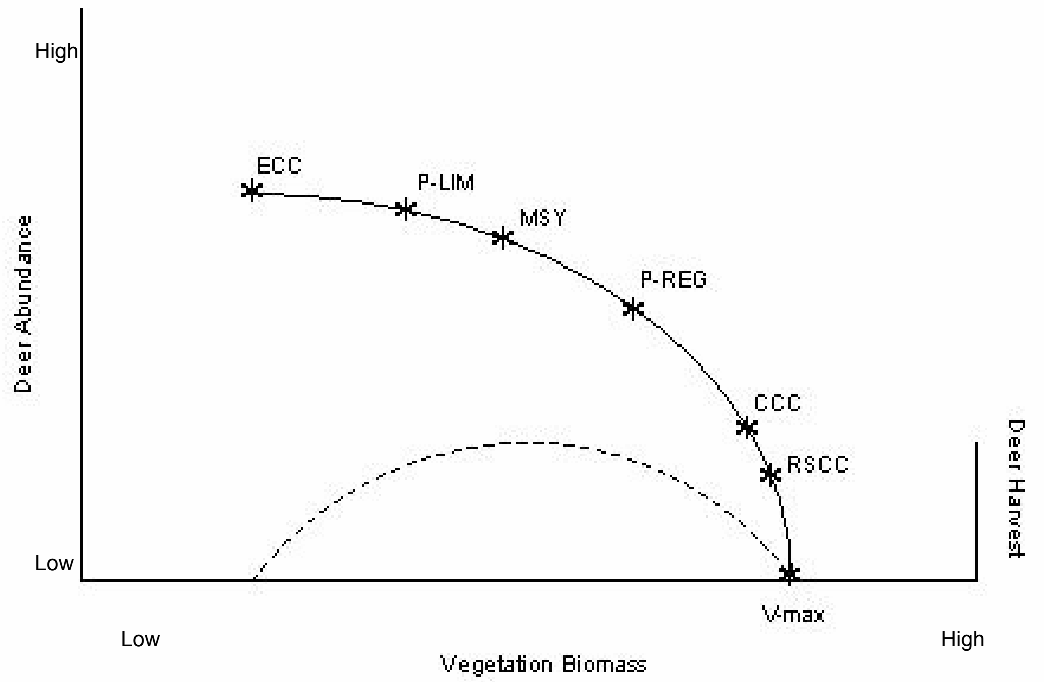

Figure 2.1 Diagram of carrying capacities related to vegetation biomass, deer abundance, and deer harvest. RSCC is rare species carrying capacity. If deer are impacting a rare species and a goal is to conserve that species, then deer numbers will have to be low and vegetation biomass will be relatively high. Deer abundance is highest at ECC when harvest pressure is low; vegetation biomass is lower with high ungulate density. At high prey densities predators can limit, but not necessarily regulate abundance (P-LIM). Maximum sustainable yield is the highest harvest pressure attained without decreasing deer density over time. At lower densities prey abundance is a function of predation rate (P-REG). Cultural carrying capacity (CCC) can vary according to societal values (after Sinclair 1997:382, figure 23.1). The dashed line represents potential deer harvest.

region. These variables are conceptual but they illustrate an important point; depending on what is valued, desirable deer population densities vary. If managers seek to conserve rare plant species that are prone to destruction by deer, then a low population density is desired. On the other hand, if managers seek to insure maximum numbers of deer for sport harvest a higher population density is desirable. Sinclair (1997) correctly points out that it is important not to confuse these values with science.

Predator Eradication and White-tailed Deer Population Irruption

It is often assumed that in the absence of large predators, ungulate populations rapidly approach environmental carrying capacity (ECC), which is defined as the maximum number of individuals supported by food availability in a region for a period of time (both time and space are analytically specified or assumed). This follows Hairston et al.'s (1960) trophic-hierarchy model, which predicts that carnivores mediate the effect of herbivores on plant communities. Without predation, it is predicted (and often assumed) that ungulate populations will reach ECC and will run rampant across the landscape eating as they go (sensu Leopold et al. 1947).

Sinclair (1997; Schmitz and Sinclair 1997) asserts that among ungulates predator limitation is more common than predator regulation. The former refers to any effects that diminish population growth in prey, and the latter are density dependent effects that diminish prey population density when growth occurs (Messier 1991). In Sinclair's (1997) usage, limitation is a minimal effect and regulation is more severe. Sinclair (1997; Rutberg 1997) understates the influence that predation has on deer population density, and his argument fails to take into account the evolutionary biology of white-tailed deer, which is different than for other ungulates for which predator-prey relationships are better known (e.g., moose [*Alces alces*], Boutin 1992; Gasaway et al. 1992; Messier 1994; and caribou [*Rangifer tarandus*] Skogland 1991). White-tailed deer are reproductive polymorphs that are not purely K strategists (sensu Southwood 1977); their evolutionary history produced a more r- selected strategy than those of most other cervids. Table 2.1 (after Geist 1998:257) lists several characteristics that are extremes of biological continua in cervids; white-tailed deer are accurately

Table 2.1 Geist's (1998:257) continua of cervid adaptations.

Dense Vegetation Adaptation *White-tailed deer*	Continua *Other Cervids*	Open Plains Adaptation *Caribou*
concentrate selector	---------------------------	nonselective roughage grazer
saltatorial runner	---------------------------	cursorial runner
solitary	---------------------------	gregarious (selfish herd)
hider	---------------------------	displayer
cryptic colors	---------------------------	"attention" designs
nocturnal	---------------------------	diurnal
small antlers	---------------------------	large antlers
small body	---------------------------	large body
r-strategist	---------------------------	K-strategist
resource defender	---------------------------	scramble competitor
no body stores	---------------------------	seasonal body stores
juvenile disperser	---------------------------	traditionalist
nonmigratory	---------------------------	nomadic
home range discrete	---------------------------	nomadic
neonates hide	---------------------------	neonates follow
small neonates	---------------------------	large neonates
low speciation	---------------------------	high speciation
long species life	---------------------------	short species life
paedomorphic	---------------------------	hypermorphic
eurytopic	---------------------------	stenotopic
low frequency of signals	----------------------------	high frequency of signals
social signals simple	---------------------------	social signals complex

described as possessing attributes to the left side of the table whereas caribou fall to the right and other cervids range between the two extremes. White-tailed-deer defensive, reproductive, and dietary strategies are relatively polymorphic (intermediate between r- and K-strategies) and opportunistic compared to pure K strategists (sensu

Southwood 1977), though ungulates in general tend to be large-bodied K strategists compared to other mammals (Wemmer 1997).

The polymorphic reproductive strategy of white-tailed deer relates to their evolution as a consummate generalist among a guild of specialist ungulates during the Pleistocene (Geist 1998:263); "this 'weed species' specializes in exploiting opportunities, not competing for resources through local contests or scrambles," which are more characteristic of K-strategists. Today, the ecological impact of this evolutionary history is that in the absence of predation and a depleted post-Pleistocene ungulate community, whitetails, as reproductive polymorphs can be expected to become overpopulated pests. In this sense, predation on white-tailed deer is far more important than Sinclair (1997) and other authors (e.g., Rutberg 1997; Schmitz and Sinclair 1997) imply. Predation limits other ungulates, such as caribou, *only at low population densities* because they are more K-selected than white-tailed deer. According to Southwood (1977:352-353, emphasis added) the expectation for reproductive polymorphs is somewhat different,

> The combination of characters at each extreme [K versus r strategists] will lead to different forms of population dynamics. The role of predators at both extremes will be small, at the r-end because of the organisms' high mobility, at the K-end because of defense mechanisms... *However, for species that are intermediate in the continuum* [e.g., white-tailed deer], *predators are important and, taken with other forms of interspecific competition, frequently maintain a population equilibrium below the carrying capacity as determined by food and space resources*. Successful biological control [of predators] and the outbreak of 'upset pests' following the destruction of predators provide many field examples to support these theoretical conclusions.

The most important implication of this statement is that white-tailed deer populations were likely controlled below ECC for most of the Holocene and were released from that control via predator extermination and the disappearance of Native American hunters—this is not a statement without theoretical support in ecology and empirical support in evolutionary biology (Kay 1994; Smith 1974; cf. Rutberg 1997; Schmitz and Sinclair 1997; Sinclair 1997). Without predation, irruptions of white-tailed populations are expected (sensu McCullough 1997).

The suggestion that predation is unimportant in regulating white-tailed deer population densities below pest level is a product of several factors. First, the use of other cervids that fall closer to the K-end of the reproductive continuum (especially caribou and moose) as models of what to expect for predator-prey relationships in white-tailed deer leads to a belief that predators only limit deer at low densities but not at high densities. It matters not that cervids in general are relatively K-selected compared to other mammals; what is important is that white-tailed deer are less so than other cervids. Predation effects on other cervids might not apply to white-tailed deer (e.g., Boutin 1992; Gasaway et al. 1992; Messier 1994; Skogland 1991; but see Messier 1991). Second, understating the role of predators on white-tailed deer populations relates to a lack of attention to the *continuum* between r and K reproductive strategies and the fact that white-tailed deer are intermediate polymorphs compared to many ungulates (see Giest 1998 and discussion above). Third, the first two reflect an oversight; the ecology of white-tailed deer is often examined without reference and consideration of evolutionary biology, which is readily available for cervids and white-tailed deer in particular (Geist 1998 and references therein). Fourth, the belief that whitetails are not necessarily overabundant in eastern North America is flawed because ECC is higher today than during prehistory as a result of the effects of farming (Hansen et al. 1997; McCullough 1997; Nixon et al. 1991). Rather than conclude that predation is unimportant based on deer and plant relationships in areas where ECC is known to have increased and on relationships studied in other ungulates, why not base that evaluation on populations in areas where farming is less important (e.g., central Texas)?

Finally, estimates of white-tailed deer population size in North America prior to the historic period (e.g., McCabe and McCabe 1984, 1997; Rutberg 1997) are probably inaccurate and highly inflated. This inaccuracy supports a belief that deer populations are under-populating North America today. Whitetails may not be at ECC in much of eastern North America (Schmitz and Sinclair 1997), but that does not mean that they are at lower population densities than during prehistory. To the contrary, it is likely that deer population densities are much higher today given that every important predator has been extirpated and that ECC has increased over much of their range—*an inescapable conclusion if evolutionary biology is taken into account*.

The pest-level population density of white-tailed deer in central Texas is a product, thus, of two factors: 1) the evolution of white-tailed deer for survival as a generalist in a Pleistocene ungulate guild crowded with specialists (Geist 1998), and 2) predator eradication and the release of population control on this reproductive polymorph. Unlike the many areas of the Midwest (e.g., Hansen et al. 1997; Nixon et al. 1991), deer population size and density is apparently not a product of a historic increase in carrying capacity related to farming in central Texas.

White-tailed Deer Overabundance in Central Texas

It is well established that central Texas white-tailed deer are very small (e.g., Geist 1998; Teer et al. 1965, Teer 1984). Stunting related to overcrowding appears to be the main cause of their small size (see Chapters 4 and 5). The situation in central Texas is complex in that fire control, livestock ranching, introduction of exotic ungulates, and predator eradication have created radically modified habitat (Cook 1984; Mungall and Sheffield 1994; Walton 1999). Overcrowding appears to have led to over-browsing, which further destroys habitat for deer and other organisms (e.g., Russell and Fowler 1999, 2004). The impacts of predator eradication on white-tailed deer, and by logical extension the surrounding biological communities, raise some important and interesting questions. For example, what are the ecological impacts of overabundance in the region? How does predator extermination affect the remaining predator guild? Also, how much change has occurred in deer body size with predator eradication and overcrowding? If body size effects (e.g., stunting) have occurred, can these and other effects of overabundance be mitigated through management of white-tailed deer populations? These kinds of questions are difficult to answer because reliable documentary records of conditions prior to the historical period do not exist making it difficult to assess modern versus pre-modern conditions in white-tailed deer and other species.

There is a record, however, that can be tapped to answer these and other questions, that of paleozoology (references in Lyman and Cannon 2004b; Lyman 2006a,b). The paleozoological record includes the sum of skeletal samples from paleontological and archaeological sites. Collections of vertebrate remains curated by archaeologists and paleontologists can be used for comparing modern populations to prehistoric ones depending on the kinds of questions asked (see discussion above related to estimation of prehistoric population size [McCabe and McCabe 1984, 1997]). Much of the analysis presented in the following chapters, therefore, focuses on body size in predators and white-tailed deer because this particular variable can be reliably studied using paleozoological samples (Dayan et al. 1991; Gompper et al. 2006; Graham 1991; Lyman 2006a; Purdue 1980, 1989). Further, body size in mammals relates to variables such as niche breadth and population density making it relevant to modern wildlife biology.

The prehistoric period ended when Euro-Americans progressively moved westward settling the western portions of North America. The prehistoric paleozoological record thus represents a period prior to predator eradication and modern human impact (e.g., roads, ranching, and industrial farming). This record comprises skeletal remains (often fragmentary ones) such that the answers it provides are often limited in number and coarse in scale. These limits, however, do not diminish the paleozoological record’s value to modern wildlife biology, conservation, and restoration; it is the “best game in town” for studying the magnitude of impact of modern Euro-American society in North America (references in Lyman and Cannon 2004b).

Using the paleozoological record to answer questions such as those outlined above requires an introduction to archaeological and paleontological sampling and an understanding of important ecological concepts that explain changes in carnivore and white-tailed deer body size. In particular, it is important to examine the role that resource competition plays in carnivore body size and the role that population density plays in white-tailed deer body size in marginal habitat. This chapter addresses these needs in an attempt to highlight how a paleozoological perspective on predator eradication and white-tailed deer overabundance can benefit management efforts in central Texas.

Paleozoological Sampling

Paleontological and archaeological vertebrate samples are acquired through excavation of prehistoric sites. Many of the vertebrate faunas from central Texas are from caves that were natural traps, carnivore dens, or human occupations sites (Lundelius and Slaughter 1971; Toomey 1994). Some of the archaeological faunas come from open-air sites excavated during regional studies of past human culture. Paleozoological bone is subject to a vast array of destructive processes at varying intensities. The study of taphonomy concerns examining the effects of behavioral, geological, and/or chemical processes that fragment, weather, and potentially destroy prehistoric bone (see Lyman 1994). Not all paleozoological faunas are created equal; some have witnessed more destructive taphonomic histories than others. As a result, the preservation of each sample must be considered carefully prior to making assumptions concerning whether or not it is representative of prehistoric human or animal behavior or past environmental conditions. That is, paleozoologists are always at the mercy of what bones preserve and which ones are recovered during excavation. Often there is no means of resampling the same fauna, and the best that can be done is to sample as extensively as possible for the periods and places of interest.

In this study relatively robust, dense skeletal elements that preserve well are used to offset taphonomic biases when possible. In the case of medium size carnivores, however, it is important to use skeletal parts that are easily identified to species. There are always trade-offs among preservation, identifiability, and recovery of particular species and their skeletal elements that must be considered when sampling the paleozoological record. White-tailed deer remains are common in paleozoological samples (especially archaeological faunas), but carnivore remains are rare because not only are they less likely to have been hunted by prehistoric human hunters than were game animals, they were rarer on the landscape (sensu Colinvaux 1978).

The available paleozoological faunas relevant to this study date primarily to the Holocene (last 10,000 years) in central Texas. It would be ideal to restrict sampling to, say, the last few thousand or even a few hundred years prior to Euro-American settlement of the region. However, the readily available record does not support such a fine-scale temporal study. The prehistoric samples of coyote, bobcat, and white-tailed deer remains used in this study are, at best, coarse averages of Holocene body size for each species. Morphometric variables and relevant characteristic of prehistoric samples used in each analysis are covered in later chapters, but suffice it to say the coarse Holocene resolution of these samples is sufficient to permit several comparisons that highlight modern human impacts related to deer population density and predator eradication in central Texas.

Predator Eradication and Carnivore Body Size

At issue is niche breadth of particular species in the predator guild (Hutchinson 1957; Whittaker et al. 1973). Predator eradication has effectively created niche vacuum-space at the top of the trophic hierarchy (sensu Palomares et al. 1995; Crook and Soulé 1999). Effects have cascaded from white-tailed deer to much of the rest of the biological community (including modern humans). It is a relatively easy task to demonstrate a decline in carnivore richness from the Holocene to modernity (see Chapter 3). However, more important is establishing the characteristics of those predators lost via extinction and extirpation. Those predators that were exterminated because they are capable of killing livestock happen to also be those most capable of preying upon white-tailed deer (cougars, wolves, jaguars, even bears). Demonstrating a reduction of the average body size of the predator guild in central Texas is an important first step in determining just what has been lost and precisely what kind of a niche vacuum has been created.

Carnivores exhibit plasticity in body size; that is, their body size can fluctuate phenotypically from generation to generation according to environmental conditions (Rosenzweig 1968). Competitive pressure among carnivores is thought to relate to body size, and body size among member species of the predator guild can be expected to diversify through *character displacement* when the guild is relatively crowded (Dayan and Simberloff 1998; Gittleman and Purvis 1998; Rosenzweig 1968; Sikes and Kennedy 1992). Character displacement involves diversification of phenotypic traits, in this case body size, in order to avoid competition for resources (Brown and Lomolino 1998;

Brown and Wilson 1956; Dayan and Simberloff 1998; Grant 1999; MacArthur and Wilson 1967). When a species or a number of species are removed from a guild, the opposite occurs. *Character release* takes place when competition decreases, and it results in “the shift in a species’ size or some other feature when it is released from selective forces imposed by the presence of another species” (Dayan et al. 1991:191). Character release can be the result of an “‘*adaptive vacuum*’ which a companion species might otherwise occupy” (Brown and Wilson 1956:58, emphasis added).

During the last 15,000 years all of the predators larger in body size than the coyote and bobcat have either gone extinct (e.g., the Pleistocene extinctions) or have been extirpated in Texas. The stage has been set for character release in the body size of mesocarnivores, in particular coyotes (*Canis latrans*) and bobcats (*Lynx rufus*). Diets of coyotes, wolves, and red wolves, for example, overlap, and the three species are closely related such that they are capable of hybridization (Bekoff 1982; Johnson and Crabtree 1999; Schmidly 1994). The disappearance of larger canids releases competitive pressure on coyotes. Another species that should be similarly affected is the bobcat, though its closest taxonomic relative in Texas is the cougar (*Puma concolor*) with which it does not hybridize. Gittleman and Purvis (1998) stress that body size in canids is more closely related to carnivore species richness than in felids; however, the situation in central Texas is not one of fewer or greater numbers of large carnivore species, it is one of their total absence. With few exceptions in few areas of the state bobcats and coyotes are the remaining “large” predators in Texas. If character release in body size were to occur in bobcats it would be with severe changes in carnivore richness like those produced by predator extermination during the historic period.

Theoretically, the paleozoological record can be studied to determine whether or not character release has occurred in mesocarnivores, but small samples used in this study limit that potential (see Chapter 3). The upper limit of their body size range should be larger during modernity than during the rest of the Holocene if release occurred. Average body size of mesocarnivores should increase as a result of this upper-limit range expansion, but more important is the expansion of mesocarnivore body size toward that of larger predators now missing from the region. Bobcats and coyotes are commonly thought to prey on small prey, but they are capable of preying on white-tailed deer and, in the case of coyotes, on elk (Crabtree and Sheldon 1999; Gese and Grothe 1995; Labisky and Boulay 1998; McCord and Cardoza 1982; Mech 1984). In central Texas, white-tailed deer are extraordinarily small; if the upper range of body size in mesocarnivores has expanded as a result of character release in the absence of competition with larger predators, then coyotes and bobcats may rely on deer as prey now more than ever (Cook 1984).

To summarize, niche space high in the trophic hierarchy in Texas is essentially vacant. Mesocarnivores are the largest predators left in most areas of Texas, including the central portion of the state. White-tailed deer overabundance in progressively worsening habitat has resulted in stunting reflected in small body size. Removal of large carnivores such as wolves and cougars has disrupted long-term evolutionary relationships in the predator guild by creating a niche vacuum. The likely candidates to fill that niche space are the mesocarnivores still present, bobcats and coyotes. If character release into that vacant niche space is occurring, then mesocarnivores from the Holocene paleozoological record should be smaller than modern ones and the upper limit of body size in modern mesocarnivores should be greater than during prehistory. Testing this hypothesis requires measuring skeletal elements of mesocarnivores and comparing their size from both periods, a subject that is returned to in Chapter 3.

Population Density and White-tailed Deer Body Size

At the community scale interspecific diversity in body size is often closely related to population density; that is, smaller bodied species tend to have higher population densities than larger bodied ones. This relationship is well documented and exists for both carnivores and herbivores (Calder 1984; Cyr 2000; Peters 1983; Peters and Raelson 1984). Figure 2.2, for example illustrates the factors relating body mass to

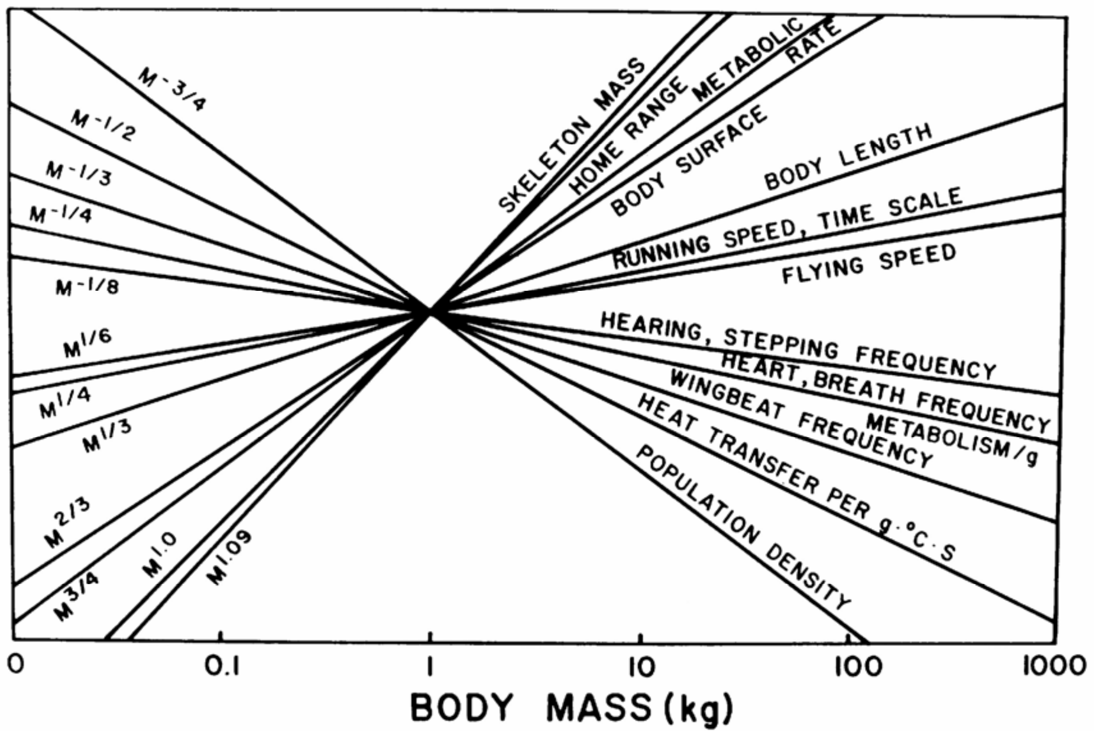

Figure 2.2 Calder's (1984:11, figure 1-2) diagram of the relationships between several biological and ecological variables and body mass in eutherian mammals.

several variables in eutherian mammals. The strongest negative factor is population density; at the interspecific scale progressively larger body mass relates to progressively lower population density.

The relationship between body mass and population density extends to the intraspecific scale as well. However, at the intraspecific scale, it is unlikely that small body size is determining high population density. On the contrary, the opposite is the case, stunting occurs when intraspecific competition for resources is high. At high population densities, white-tailed deer, for example, tend to be relatively small (Kie et al. 1983). At or near environmental carrying capacity, white-tailed deer populations should be at their highest population densities, growth rate among conspecifics should decline in crowded conditions, and body size should be relatively small if forage is overbrowsed. In general, density-related changes in life history (such as ontogenetic growth rate) occur at population-levels at or near carrying capacity (Fowler 1981).

Support for the previous statements regarding high population density and stunting is found in a study on white-tailed deer physical condition done at the Rob and Bessie Welder Wildlife Refuge in south Texas. Kie et al. (1983) examined white-tailed deer on a predator-free enclosed lot compared to those outside the enclosure. It was found that higher populations densities resulted in smaller deer that were in relatively poor physical condition within the enclosure. Similarly, Keyser et al. (2005) in a study that considered white-tailed deer from across the Midwest and Southeast found that yearling-buck dressed weight was a strong predictor of population density. Along similar lines, Lesage et al. (2001) found that forage competition (related to population density) is an important factor in determining adult body size among white-tailed deer in southeastern Quebec.

Various models of predator-prey relationships predict growth in prey populations determined by predator abundance (see Roughgarden 1979). In the absence of predators, a limit to growth is removed. Removal of large predators has not radically influenced body size of white-tailed deer in many areas of North America, despite the fact that population densities are high. This relates to what Côté et al. (2004:116, emphasis added) term “the most obvious factor contributing to rapid growth of deer populations… *increased forage*.” In many areas of North America white-tailed deer were reintroduced to predator free conditions with improved edge habitat related to increases in farming (Hansen et al. 1997; Nixon et al. 1991; Stoll and Parker 1986). In those areas “carrying capacity far exceeds current deer population levels” (Hansen et al. 1997:327; see discussion above). Along similar lines, Seal et al. (1983) witnessed few ill health effects relative to increasing population density in an enclosed population from 1972 to 1977 in Michigan as long as the herd was well fed with supplemental feed. This serves as an analog to settings where farming has increased forage in the absence of predators. Forage has not increased in a similar fashion in central Texas; deer have survived the historical period in much of the region while habitat has been encroached upon by the ranching industry and more recently by urban and suburban development. Predator extermination in this setting removed an important population control in progressively degrading habitat. White-tailed deer population density is high and body size is small as a result. Deer in central Texas are eating themselves out of habitat as time passes.

The modern condition of the central Texas white-tailed deer population should stand in stark contrast to the prehistoric population. During the Holocene the Texas predator guild included several large predators, such as *Canis lupus*, *C. rufis*, *Puma concolor*, and *Panthera onca*. Native American hunters were an additional important predator of white-tailed deer in central Texas (Baker 1998). If modern deer population density is at or near carrying capacity in the absence of substantial predation, then prehistoric deer from the Holocene should be significantly larger in body size than modern ones. Addressing this hypothesis with paleozoological data, much like with examining mesocarnivore size, requires morphometric analysis of skeletal element samples from modern and prehistoric populations. This subject is returned to in Chapter 5.

Statistical Power of Student's *t* Tests

The null hypothesis in each of the analyses is that no difference exists between the average size of prehistoric mesocarnivores (Chapter 3) and white-tailed deer (Chapter 5) between prehistory and modernity. Student's *t* test is used to compare average size of morphometric variables from samples dating to each period. An important concept that is relevant to these comparisons is *statistical power* or *power of the test*, "power is the probability of rejecting the null hypothesis when it is in fact false and should be rejected" (Zar 1974:44). There are four common reasons for failure to reject the null hypothesis: 1) there is no or a low magnitude of difference between samples, 2) α, the probability of Type I error (incorrectly rejecting the null hypothesis), is too low (here it is set at 0.05), 3) one or both of the compared samples are too small, and/or 4) sample variances are so high that extremely high magnitudes of difference must be observed for them to be significant (Hair et al. 1995).

Power of each Student's *t* test in this dissertation is determined when there is a failure to reject the null hypothesis, i.e., when no statistical difference is found. The magnitude of difference required for a significant difference in each test can be easily gauged using minimum significant difference (MSD) compared to observed difference between sample averages ($\Delta\bar{x}$). MSD can be calculated using the critical *t* value for each test, and it can be reported as %MSD by dividing MSD by the control sample average (in this case usually that of prehistoric samples[1]). $\%\Delta\bar{x}$ can be calculated in a similar fashion to %MSD, and if $\%\Delta\bar{x}$ and %MSD are similar but non-significant, then an important difference may exist between samples that is not visible statistically. That is, consideration of statistical power allows the analyst to determine what magnitude of difference would have been necessary to achieve statistical significance. If sample variances are high, then only large differences will be significant; if samples are small then significant differences will not occur unless α is elevated, which increases probability of Type I error. Statistical power can also be used to assess significant differences; if $\%\Delta\bar{x}$ is substantially higher than %MSD then not only is the test powerful, but the magnitude of difference observed is substantial.

High power tests have low %MSD in that small-magnitude differences can be detected. In the case of prehistoric sampling high power of a test reflects not only adequate sample size but confidence in the quality or magnitude of difference observed

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[1] There is no "control" but the prehistoric samples are theoretically the original condition from which body size changed. When comparisons are between unmanaged and managed deer samples (Chapter 5); the managed sample is used as the "control."

in $\Delta\bar{x}$ (Hair et al. 1995). Statistical power is returned to in Chapters 3 and 5 when Student's *t* tests are used to compare prehistoric and modern samples.

Can the Body Size Effects of Deer Overabundance be Mitigated?

Pest-level population densities of white-tailed deer in central Texas can be mitigated with higher culling rates in municipal, county, and private areas. However, a political and social issue that arises is whether or not it is ethical or fair to cull white-tailed deer (Rolston 1988). Unfortunately there are few stakeholders speaking on behalf of large carnivores several generations after they were exterminated. White-tailed deer have been managed and harvested at Fort Hood in the northern part of central Texas for roughly the last half century. Detailed historical records of annual harvests can be used to assess whether or not population density has decreased and body size has increased with management. Kie et al.'s (1983) study highlights that south Texas whitetails at lower population densities are larger and healthier, which suggests that progressive management at Fort Hood should produce the same effects. Fortunately, direct relations between body size and population density can be examined with the Fort Hood dataset, a topic that is returned to in Chapter 4.

Conclusion

White-tailed deer in central Texas are in an ecological trap that habitat destruction and predator extermination has sprung. The paucity of public land in Texas creates a setting in which structured harvest of large portions of the deer population is difficult to impossible. Numerous cities in and around Austin are now handling white-tailed deer overabundance in diverse manners (sensu DeNicola et al. 2000). Some cities transplant deer to other places, such as northern Mexico. In some cases, moving deer simply moves the problem, and some municipalities are finding it harder to find destinations for their deer. Other cities are turning to culling operations that thin white-tailed deer populations. A portion of this study relies on use of skeletal specimens recovered from culled deer, which represent historically unmanaged populations at or near environmental carrying capacity (see Chapter 5).

In a few areas, including Fort Hood, cougars are slowly re-establishing themselves. However, continued expansion of their range will introduce a new conflict between humans and large predators. It seems that the best solution is to mimic the effects of large predators through structured harvest, but this option is controversial in that many wildlife biologists find it difficult to promote sport hunting with such a goal in mind. This paleozoological study provides a backdrop for considering such action by attempting to answer the question: how much of an impact has predator eradication had on white-tailed deer in central Texas? By extension, how much of an effect has deer overabundance had on people, plant communities, and the ecosystem as a whole?

CHAPTER 3

THE HOLOCENE PREDATOR GUILD IN TEXAS

This chapter explores the effects of large predator extermination on medium-sized carnivores (here bobcats and coyotes). First, changes in carnivore species richness are examined using the paleozoological record to determine how much body-size diminution in the predator guild has occurred through time. Because the magnitude of diminution is severe, the effects on extant mesocarnivores (bobcats and coyotes) are predicted to be profound. Two variables are ecologically significant: “mesopredator release” occurs when predation on medium-sized predators by large carnivores is relaxed because of extermination of the latter (Soulé et al. 1988:84). This potentially causes a population explosion in the remaining, smaller carnivores. Mesopredator release does not receive more than cursory attention in this chapter because it does not require paleozoological data to study. Character release, change in phenotype (e.g., body size) related to the absence of competition, is a predictable parallel effect to mesopredator release, and it is studied here using paleozoological data. It is predicted that body size of modern mesocarnivores is larger today than during the Holocene and more importantly that the upper limit of body size range has expanded today.

Prehistoric changes in the predator guild are not limited to the Holocene; consideration of modern effects of predator eradication should take into account extinctions that occurred during the late Pleistocene. It is clear that average body size diminution in the predator guild occurred during the late Pleistocene through extinction of the largest carnivores, and any effects of this prehistoric change on extant predators is amplified by historic efforts to exterminate remaining large carnivores. Placed in the context of recent (last 30,000 years) evolutionary history, purposeful predator eradication by humans is a harsh blow to an already depleted predator guild. The largest extant carnivores are medium sized; character release toward larger body size is expected given the adaptive vacuum at the top of the trophic hierarchy.

Materials and Methods

Taxonomic richness in the carnivore guild is studied using the paleontological record from Halls Cave. Halls Cave, located in Kerr County within the eastern Edwards Plateau, produced a large fauna that provides a relatively complete record of the late Pleistocene and Holocene central Texas carnivore guild (Toomey 1993). Here the cave's fauna is divided into two assemblages that are compared to historic (Hs) period and modern (M) faunas reported by Schmidly (1994). HC1 is the late Pleistocene/early Holocene fauna from Halls Cave, and HC2 is the early through late Holocene prehistoric fauna from the cave.

The quantitative unit used to express changes in carnivore richness is "number of taxa" or NTAXA (Grayson 1991; Grayson and Delpech 1998; Nagaoka 2001). Average carnivore weight per period is calculated using median weights for each species reported by Schmidly (1994) and Brakefield (1993 [for large felids]). Weight of the North American lion (*Panthera atrox*) is estimated from that of the extant African lion (*P. leo*). The upper weight limit of *Canis lupus* is used as an estimate for the dire wolf (*Canis dirus*), an assumption based on the fact that morphometrically dire wolf skeletal parts are larger than those of gray wolves (see below). Weights of saber-toothed cats

Table 3.1 Median and estimated weights for carnivores HC1 = late Pleistocene/early Holocene Halls Cave, HC2 = Holocene Halls Cave, Hs = historic (Schmidly 1994), and M = modern (Schmidly 1994).

Taxon	Common Name	Weight (kg)	Assemblage
Included			
Canis latrans	coyote	17	HC1, HC2, Hs, M
Canis rufus	red wolf	30	HC1, HC2, Hs
Canis lupus	gray wolf	50	HC1, HC2, Hs
Vulpes vulpes	red fox	4	HC1, HC2, Hs, M*
Urocyon cinereoargenteus	gray fox	4	HC1, HC2, Hs, M
Ursus americanus	black bear	150	HC1, HC2, Hs†
Bassariscus astutus	ringtail	1.25	HC1, Hs, M
Procyon lotor	raccoon	8.5	HC1, HC2, Hs, M
Mustela sp.	weasels	0.65	HC1, HC2, Hs, M
Spilogale sp.	spotted skunks	0.53	HC1, HC2, Hs, M
Mephitis mephitis	striped skunk	4	HC1, Hs, M
Conepatus leuconotus	hog-nosed skunk	1.9	HC2, Hs, M
Puma concolor	puma or cougar	64	HC1, HC2, Hs†
Leopardus weidii	margay	2.5	HC1, Hs
Lynx rufus	bobcat	7	HC2, Hs, M
Panthera onca	jaguar	101.5	HC1, Hs
Late Pleistocene			
Canis dirus	extinct dire wolf	80	HC1
Panthera atrox	extinct North American lion	153	HC1
Not included			
Vulpes velox	swift fox	2	Hs, M
Ursus arctos	grizzly bear	245	Hs
Nasua narica	coati	4.5	Hs, M
Taxidea taxus	badger	7	Hs, M
Mustela nigripes	black-footed ferret	1.13	Hs
Lontra canadensis	river otter	6.5	Hs†
Mephitis macroura	hooded skunk	0.65	Hs†
Leopardus pardalis	ocelot	12.5	Hs
Herpailurus yaguarondi	jaguarundi	6	Hs†
Homotherium sp.	extinct sabertooth	Unknown	none
Smilodon sp.	extinct sabertooth	Unknown	none

* Postcrania indistinguishable from *U. cinereoargenteus*; *V. vulpes* arguably exotic.
† Exterminated or rare in Texas today, assumed to be absent in central Texas.

(*Homotherium* and *Smilodon*) are not estimated because there are no closely related extant taxa to serve as analogs. Median weights and estimates for modern and extinct carnivores are listed in Table 3.1. Average weights of the predator guild per temporal

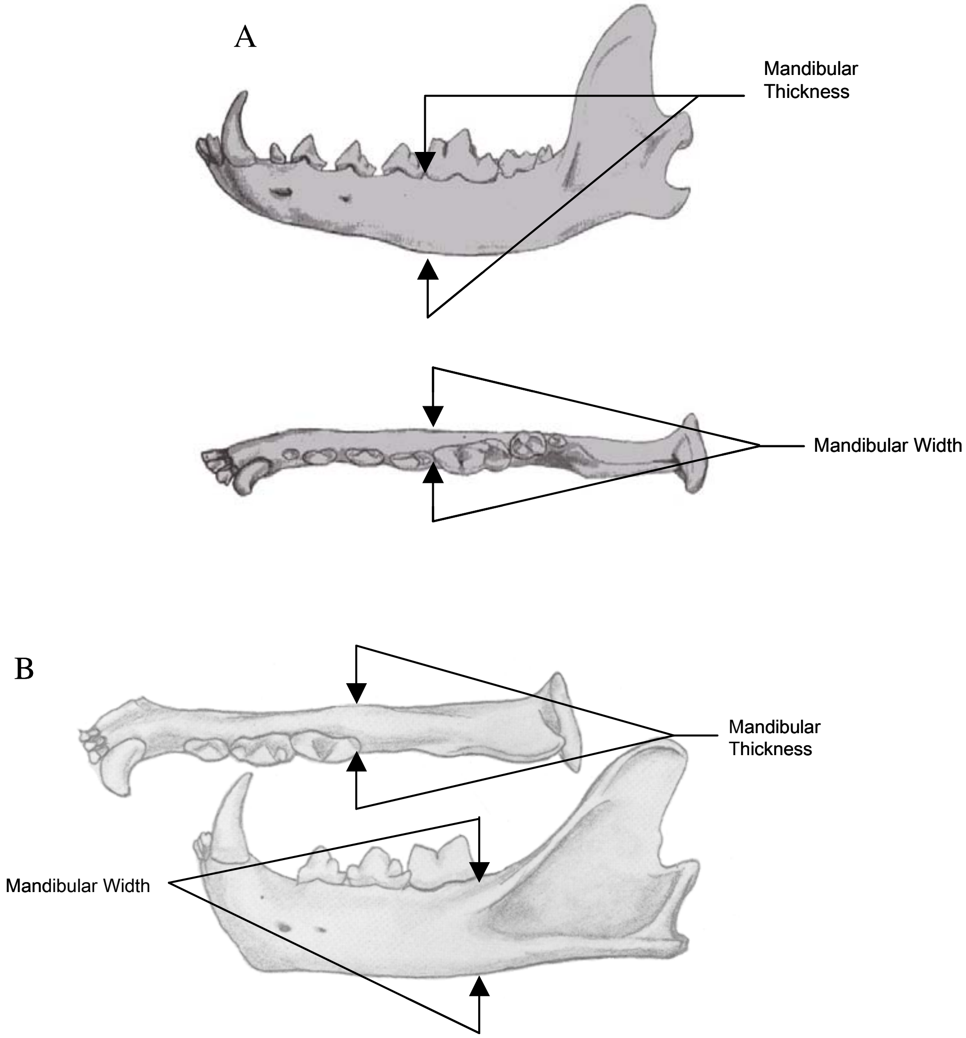


Figure 3.1 A) mandibular thickness and width (mm) taken on canid mandibles anterior to the first lower molar on the medial side. B) mandibular thickness and width (mm) taken on felid mandibles posterior to the first lower molar. Drawings from Gilbert (1990:251 and 254).

assemblage are reported in Table 3.2. Those carnivore taxa dating to the historic and modern periods that were excluded from this analysis did not occur in Halls Cave.

Measurements were made on the mandible in order to compare modern and prehistoric mesocarnivores to each other and to larger predators (Appendix A). The mandible is used here, particularly in the case of the coyote, because it can be more easily identified to species than post-cranial elements (Krantz 1959; Nowak 1979) and because cranial measurements are indicative of body size in carnivores (Van Valkenburgh 1990). The mandible is measured instead of teeth because it more closely reflects body size especially in canids (Van Valkenburgh 1990). For sake of simplicity, similar measurements are used on all felid and canid specimens (Figure 3.1); felid mandibular thickness and width are easily and reliably taken posterior to the M_1. Canid dentition is more crowded, and thickness and width are taken anterior to the M_1 as a result. Student's *t* tests are used to assess statistical differences between prehistoric and modern samples. Statistical power of tests is determined using %MSD and %$\Delta 0$ (see discussion in Chapter 2).

In terms of taphonomy, these portions of the mandible are relatively robust and are likely to preserve and to be identified to species in paleozoological faunas compared to other portions of the mandible, cranium, and skeleton. Prehistoric mesocarnivore mandibles appear to have been from adults, but sex is unknown. Many of the modern and prehistoric mesocarnivore specimens are from central Texas, but others from adjacent areas are used to provide larger samples (Appendix A). The small size of the prehistoric samples somewhat limits an ability to address whether or not character release has occurred since predator eradication.

Paleozoological and modern specimens, including living and extinct large carnivores (*Canis dirus*, *Smilodon* sp., *Homotherium* sp., and *P. atrox*), are from collections curated at the Texas Memorial Museum Laboratory of Vertebrate Paleontology. Extant large felids (e.g., *Panthera tigris*, *P. leo*, and *P. pardus* [African leopard]) were included in this analysis as analogs for large felids that lived during the late Pleistocene in North America; they serve as a reference highlighting the body size decrease in the predator guild during the last 20,000 to 30,000 years.

Changes in the Predator Guild

In terms of body weight individuals of species in the modern carnivore guild in Texas represents a fraction of the average size of earlier predator guilds (Table 3.2). The individuals in the modern guild are between eleven and twenty-five percent of the average body weight of the late Pleistocene assemblage depending on whether or not cougars are included in the modern assemblage (Table 3.2). Using the same criteria, the modern predator guild is between seventeen and thirty-seven percent of the average body weight of the historic-period guild reported in Schmidly (1994) excluding those taxa at the bottom of Table 3.2 that were not recovered at Halls Cave. The average weight of the three modern species that were excluded is only 4.5 kilograms indicating that their inclusion would amplify the decrease in average predator size during modernity. Further, if *Ursus arctos* is included in the historic assemblage the difference between the historic and modern assemblages would be magnified. It is clear that the magnitude of average-body-size diminution in carnivores within the last two hundred years is similar in scale to that of the late Pleistocene extinction event (Figure 3.2).

Table 3.2 NTAXA and average weights per temporal assemblage.

Assemblage	Average Weight (kg)	NTAXA
HC1	41.93	16
HC2	28.13	12
Historic	27.93	16
Modern	4.88 (10.26)*	10 (11)*

* Number in parentheses includes *P. concolor*.

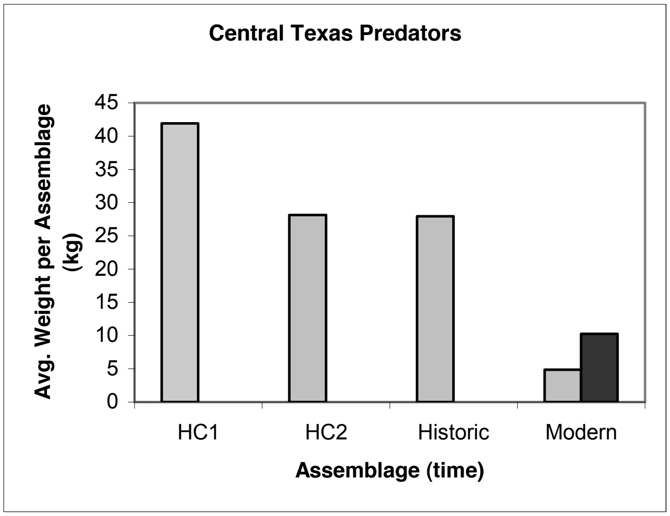


Figure 3.2 Diminution in average body weight of the predator guild through time without cougars in the modern assemblage (gray) and with cougars (black).

NTAXA of historic predators in Texas was 25 species; Table 3.1 actually underestimates this value by 2 species because weasels are combined as *Mustela* sp. and spotted skunks are combined as *Spilogale* sp., which produces historic period carnivore richness of 27 species (Schmidly 1994). Today there are 21 species of carnivore in the state including *Mephitis macroura*, *Lontra canadensis*, *Puma concolor*, *Leopardis pardalis*, *Herpailurus yaguarondi*, and *Ursus americanus*, all of which are rare at best. Richness of common carnivores is more appropriately estimated at 15 species when those rare species are excluded, which is slightly above half the richness of the historic predator guild. More important is the large body size of those predators missing from or rare in modern Texas, which include gray wolf, red wolf, cougar, and jaguar.

Diminution in Carnivore Size and Character Release

The decline in body size of predators during the late Pleistocene and Holocene is apparent in the morphometric analysis of canid and felid mandibles (Tables 3.3 and 3.4;

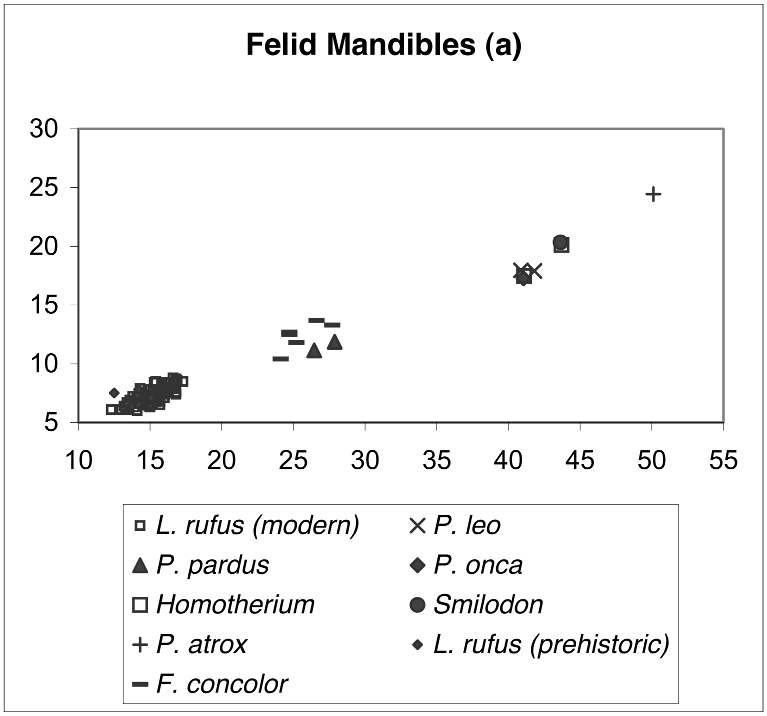
Table 3.3 Descriptive statistics of measurements on canids.

Sample	Mean	Standard Deviation	Coefficient of Variation	n
Modern Coyote				
Thickness	18.62	1.68	9.03	66
Width	8.84	0.78	8.87	66
Prehistoric Coyote				
Thickness	17.59	1.49	8.47	17
Width	8.84	0.71	7.88	17
*Wolves**				
Thickness	36.50	3.57	9.77	10
Width	17.29	1.99	11.5	10

* contains two *Canis lupus* mandibles and eight *C. dirus* mandibles.

Table 3.4 Descriptive statistics of measurements on felids.

Sample	Mean	Standard Deviation	Coefficient of Variation	n
Modern Bobcat				
Thickness	15.07	1.06	7.04	77
Width	7.22	0.70	9.69	77
Prehistoric Bobcat				
Thickness	14.02	0.79	5.63	10
Width	6.98	0.49	6.98	10
Modern Puma concolor				
Thickness	25.50	1.37	5.37	6
Width	12.40	1.18	9.52	6
Modern Panthera				
Thickness	35.93	6.87	19.13	6
Width	15.83	3.37	21.31	6
Extinct Pleistocene Felids				
Thickness	43.92	3.69	8.41	5
Width	19.92	2.90	14.57	5



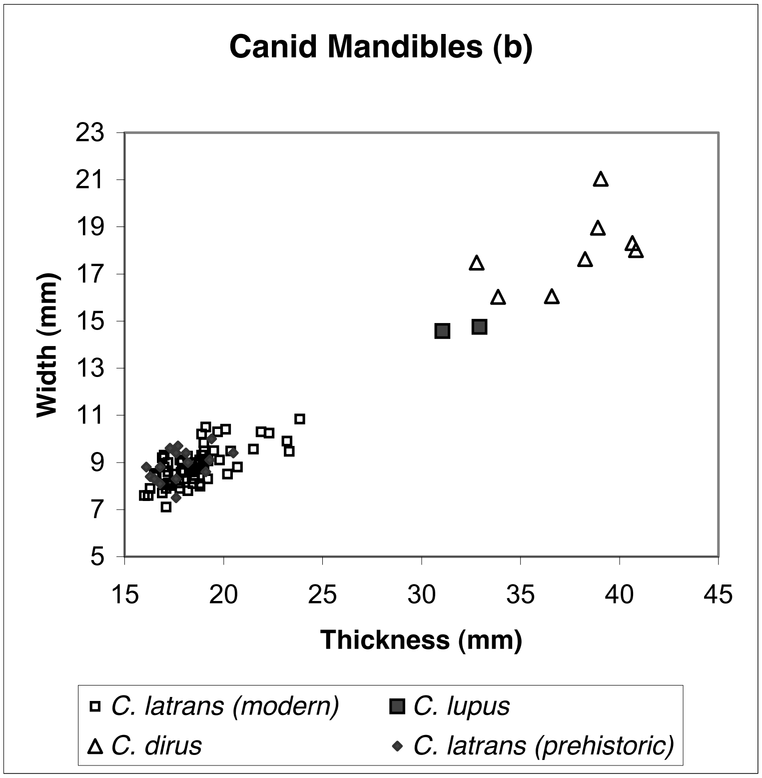


Figure 3.3 A) comparison of mandibular thickness and width among extant, extirpated, and extinct felids in Texas. B) comparison of mandibular thickness and width among extant, extirpated, and extinct canids in Texas.

Figure 3.3). Morphometric data from skeletal elements have the advantage of providing a proxy measure for extinct carnivore body size, which is difficult to assess for sabertooth cats in particular. The extant mesocarnivores (on average) are substantially smaller than even those predators living in Texas during the historic period. The Pleistocene extinction event and historic predator eradication have created an enormous niche vacuum at least in terms of carnivore body size.

Character release in the body size of extant mesocarnivores is a likely consequence of such profound changes in the predator guild. Figure 3.4 compares mandibular thickness and width of modern and prehistoric coyotes. Figure 3.5 illustrates a similar relationship for bobcats. In terms of thickness modern bobcats and coyotes are significantly larger than prehistoric ones (Table 3.5A). Average width of modern bobcat mandibles is larger than for prehistoric bobcats, but the difference is not

Table 3.5 Results of Student's *t* tests on mesocarnivore samples and variable ranges.

A. Test	*t*-statistic	*p*-value	$\Delta \bar{x}$ (%)	MSD (%)
Bobcats				
Modern vs. Prehistoric				
Thickness	3.02	0.002	1.05 (7.49%)	0.58 (4.12%)
Width	1.06	0.15	0.24 (3.44%)	0.38 (5.37%)
Coyotes				
Modern vs. Prehistoric				
Thickness	2.29	0.01	1.03 (5.86%)	0.75 (4.25%)
Width	-0.02	0.49	0 (0%)	0.83 (9.39%)

B. Sample	Prehistoric Ranges	Modern Ranges
Bobcats		
Thickness	12.5 – 15.1	12.3 – 17.3
Width	6.4 – 7.8	6 – 8.8
Coyotes		
Thickness	14.2 – 20.5	16 – 23.9
Width	7.5 – 10	7.1 – 10.8

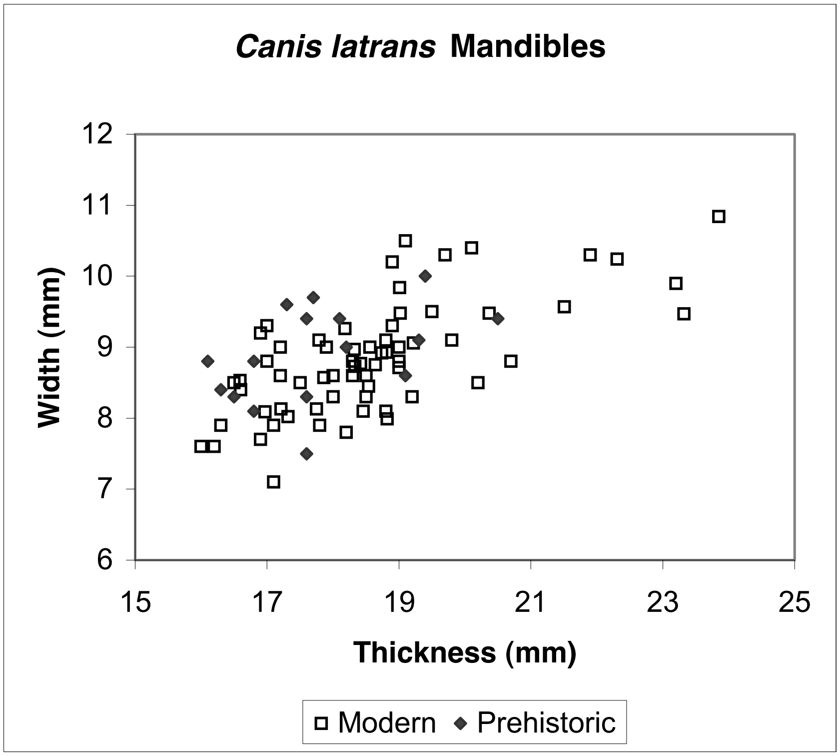


Figure 3.4 Modern versus prehistoric coyote mandible size in Texas.

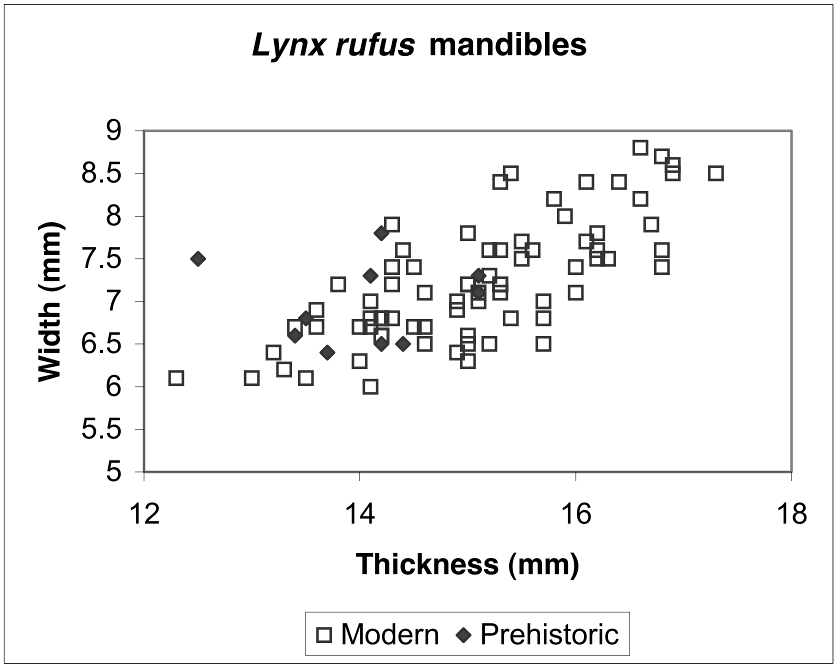


Figure 3.5 Modern versus prehistoric bobcat mandible size in Texas.

statistically significant (Table 3.5A). Prehistoric and modern coyote mandible widths are the same on average. An important prediction of character release is not only that average size of mesocarnivores should have been larger today than during prehistory but that the upper-range limit (maximum size) of modern mesocarnivores should be larger. Although not all measurements highlight significantly larger mesocarnivores today, the upper limits are greater in modern than in prehistoric samples for each variable (Table 3.5B), which is consistent with the prediction that character release occurred (see also Figures 3.4 and 3.5).

Statistically significant differences of between three and ten percent $\Delta\bar{x}$ can be detected with these samples (Table 3.5A), which suggest that these tests are high in power (see Chapter 2 for discussion of statistical power). Those differences that are statistically significant (e.g., coyote and bobcat mandibular thickness) are from more powerful tests as highlighted by relatively low %MSD. Non-significant differences in mandibular width for both species are likely caused by small sample sizes and relatively high variances compared to those for thickness (Tables 3.3 and 3.4). $\%\Delta\bar{x}$ for bobcat mandibular width is close to %MSD suggesting that a larger prehistoric sample might produce a significant difference. $\%\Delta\bar{x}$ of zero for coyote mandibular width suggests that there is no ecologically important difference between the two samples; however, small sample size similarly cannot be disconfirmed as causing decreased statistical power of this particular test. Overall, low %MSD across these samples indicates that significant relationships should be easily detected at most magnitudes of difference between modern and prehistoric samples.

Summary

Species richness of the central Texas carnivore guild is substantially lower today than it was during prehistory. Those predators that are missing from the guild today tend to be relatively large; in particular, carnivores most capable of preying upon adult deer are absent or rare in most of Texas. This has created an “adaptive vacuum” at the top of the trophic hierarchy that magnifies the absence of prehistoric Native American hunters. This scenario should result in character release in the body size of modern mesocarnivores because carnivores tend to be phentoypically plastic in terms of size (Rosensweig 1968). Average size of coyotes and bobcats, using the proxy of mandible size, appears to have increased between prehistory and today. More important is the range expansion of the upper limit of mandible size. However, these results are only provocative because character release cannot be disconfirmed. The prehistoric samples are small and are not wholly restricted to central Texas; confident support that character release occurred is not yet warranted but it is interesting that bobcats and coyotes exhibit the same pattern. Larger prehistoric samples are required to more rigorously test whether or not character release has occurred.

Discussion

A growing body of literature focuses on ecosystem-scale effects of predator removal and reintroduction (Boyce and Anderson 1999; Crabtree and Sheldon 1999; Ripple and Beschta 2005; Ripple and Larsen 2000). A frequently debated issue that is still unresolved is just how important large predators are in regulating prey populations. It is clear that at high prey population densities large predators become satiated and thus have less of a regulatory effect (Boyce and Anderson 1999; Schmitz and Sinclair 1997). Lost in this debate is the influence of predator loss, not at the taxon level, *but at the guild level*. Much of North America has effectively lost a majority of the predator guild, and that majority tends to be those carnivores that are most capable of preying upon medium to large ungulates (see previous section). This guild included Native American hunters. These changes in the predator guild are in part attributable to the late Pleistocene extinctions; the largest carnivores likely became extinct in tandem with their megaherbivore prey. However, more recent extirpations and extinctions are products of purposeful extermination by modern humans. On an evolutionary scale, the ecological damage is massive, and should not be underestimated simply because modern experiments and studies are inconclusive or contradictory in terms of the role that a particular carnivore species plays in an ecosystem for a short period of time (e.g., Gasaway et al. 1992; Messier 1994; Skogland 1991). Those studies are very important in terms of understanding the proximate effects of predator-prey interactions, but they cannot fully demonstrate evolutionary impacts of predator eradication.

Another angle on this debate examines irruptions in mesocarnivore populations produced by large-carnivore extirpation and extinction (Palomares et al. 1995; Litvaitis and Villafuerte 1996). Character release, which is studied here, is conceptually related to but not the same as “mesopredator release” (Soulé et al. 1988:84; Rogers and Caro 1998; Crooks and Soulé 1999). The latter intimates that as larger predators are exterminated in an area, population densities of smaller predators increase. In some areas of the world it is thought that mesocarnivore population explosions have threatened or exterminated rare bird species (see Crooks and Soulé 1999; Rogers and

Caro 1998; Soulé et al. 1988). Mesopredator release is a predictable impact of large carnivore extermination on the remaining portion of the predator guild in an area.

The effects of mesopredator release should be expanded to include other evolutionary predictions. If exterminated carnivores played a role in population regulation of, say, medium to large ungulates, then ungulate populations should increase in population density with their extirpation, which appears to be the case in central Texas (see Chapters 4 and 5). On the other hand, what about mesopredators themselves? Character release in body size might occur if body size and diet breadth overlap between medium and large carnivores. Diets of medium and large carnivores overlap; wolves, for example, are opportunistic enough to take small prey such as cottontail rabbits (Johnson and Crabtree 1999; Paradiso and Nowak 1982). Coyotes and bobcats take white-tailed deer as prey (Cook 1984) and occasionally prey upon elk (*Cervus canadensis*) in the Yellowstone Ecosystem (Crabtree and Sheldon 1999; Gese and Grothe 1995). If large carnivores are exterminated, those previously shared resources are more available to mesocarnivores. In the short term, a loss of competition creates a higher availability of prey to mesocarnivores perhaps releasing the upper limits of their body size range. Over the long term (e.g., thousands of years), a lack of interspecific crowding in the predator guild should lead to expansion into formerly occupied niche space and perhaps even to speciation among mesocarnivores. Predator eradication produces predictable effects that are evolutionary in proportion.

It is one thing to predict effects, and yet quite another to demonstrate that predictions of the evolutionary effects of mesopredator release do or do not hold. The dataset explored in this chapter does not allow sufficient confidence to assert that character release has occurred during modernity. However, neither can character release be disconfirmed. The paleozoological samples probably exist (unexcavated sites or unanalyzed existing collections) with which to better test whether or not character release in the body size of central Texas mesocarnivores has occurred. More important, however, are expectations concerning potential ecological effects of high mesocarnivore population densities in a region that has already witnessed unquantifiable modern human impact (e.g., via suburban development and ranching). The effects of large predator extermination on mesocarnivores are not clearly documented in this study, though several implications are set forth for more extensive analysis in the future. The fact that such evolutionary predictions can be framed with reference to the influence of extermination on the remaining predator guild highlights the potential for paleozoology to contribute to ecology and wildlife biology.

CHAPTER 4

MODERN WHITE-TAILED DEER AT FORT HOOD

Fort Hood comprises 339 square miles of central Texas north of Austin in Bell and Coryell counties. Ecologically the area represents a confluence of the Blackland Prairie, the Edwards Plateau, and the Cross Timbers (Figure 4.1). White-tailed deer from throughout much of central Texas are small compared to other parts of North America, and deer from the Edwards Plateau are the smallest in the region (Figure 4.2). Later in Chapter 5, modern deer from Fort Hood are compared to modern, unmanaged deer from Travis County and to prehistoric deer from throughout central Texas. Travis County contains portions of the Blackland Prairie and the eastern Edwards Plateau; the prehistoric sample draws from the paleozoological record from all three ecoregions that intersect at Fort Hood today. Modern Fort Hood white-tailed deer, thus offer an interesting and important sample with which to study historic changes in central Texas deer. Further, in Chapter 5, Fort Hood deer harvested in 2005 provide a modern, historically harvested sample to contrast to prehistoric deer in terms of body size.

This chapter is an evaluation of changes in deer body size with sustained harvest management during the last three and a half decades. The Natural Resources Branch of the Directorate of Public Works at the fort maintains detailed harvest data from those decades. Of particular interest here is that dressed weight, sex, and approximate ontogenetic age of each deer killed during hunting seasons have been and continue to be kept. Although dressed weight reflects body size, it is somewhat problematic in that this variable changes with age, sex, and nutritional condition of deer. Important for this study is that the detailed dataset from Fort Hood allows control of age and sex in order

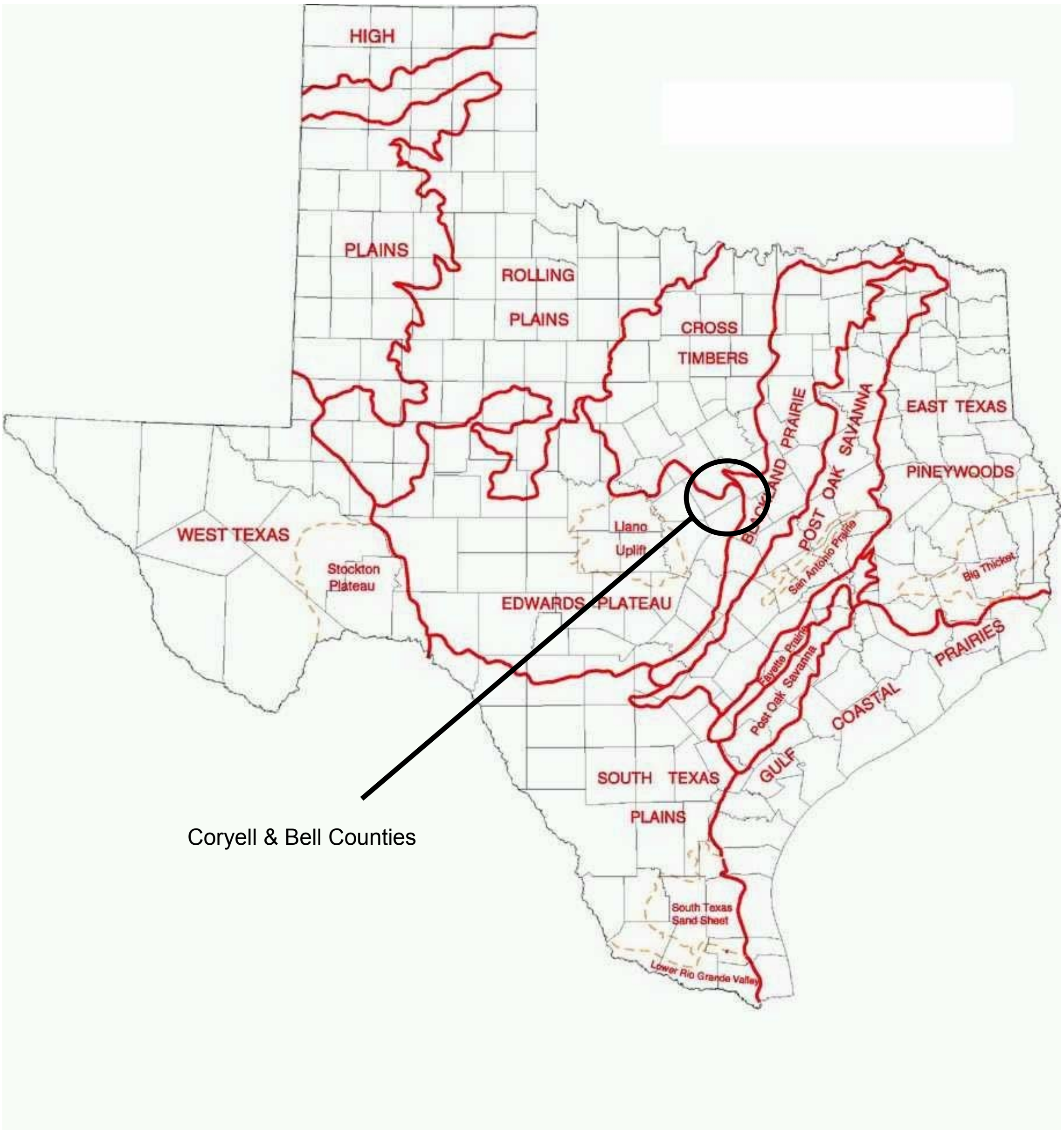


Figure 4.1 Map of the ecoregions of Texas. The Blackland Prairie, Edward's Plateau, and Cross Timbers converge in central Texas.

to study historic changes in body size. Also of interest is spotlight-survey census data that provide an indication of deer population density through time and for different areas of the fort; this dataset is incomplete and limited but offers a unique and important context within which to consider deer body size.

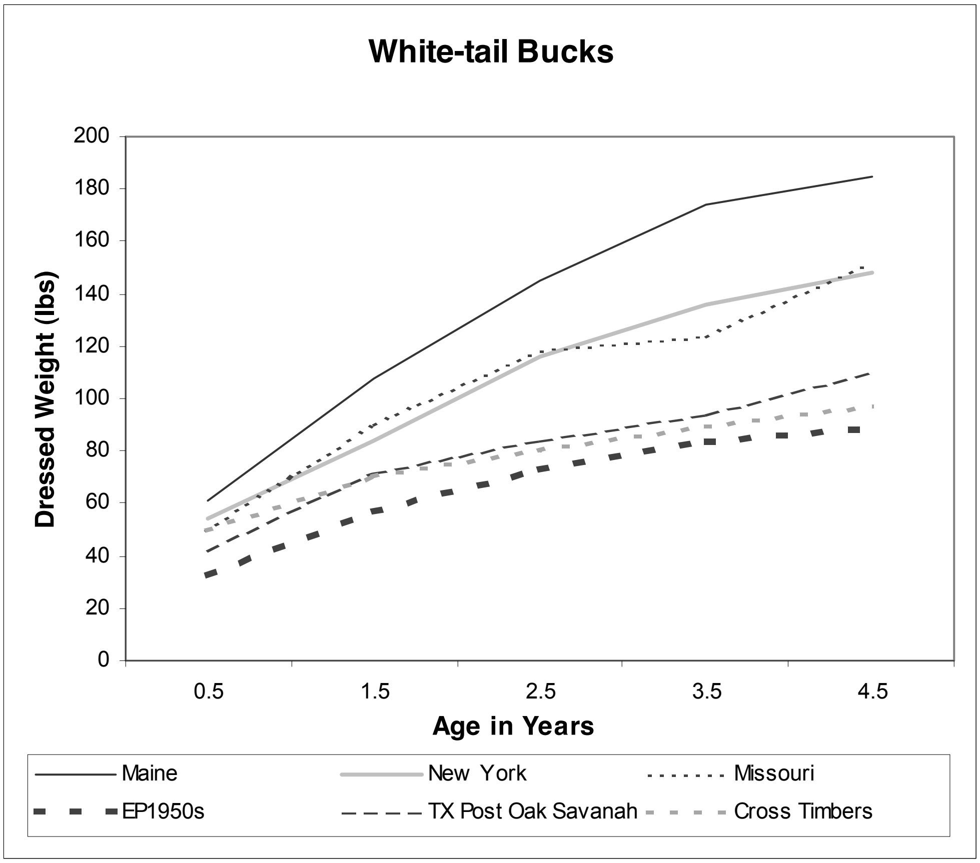


Figure 4.2 Bivariate plot of dressed weight of white-tail bucks by age for several regions of the United States (EP = Edwards Plateau). Data from Teer et al. (1965) and Gore and Harwell (1981).

This chapter begins with some basic predictions concerning the history of white-tailed deer body size during the last three and a half decades at Fort Hood, enters into analysis of body size (dressed weight) during the same period, and finishes by considering data on population density and its relationship to body size in white-tailed deer. Chapter 4 dovetails closely with consideration of modern and prehistoric deer body size in Chapter 5.

Predictions

White-tailed deer populations were thin or perhaps even extirpated at Fort Hood by the first half of the twentieth century. The population was restored during the mid-twentieth century with native central Texas *Odocoileus virginianus texana*, and the population has been harvested by modern sport hunters for much of the second half of the twentieth century. Census records do not exist for Fort Hood for prior to the 1980s, and the dataset is patchy thereafter. However, Teer et al.'s (1965) detailed study highlights an extremely high density of white-tailed deer in the Edwards Plateau at mid-century. Those same deer were extraordinarily small in body size compared to whitetails from other parts of the country (Figure 4.2). Data from Texas Parks and Wildlife's Big Game Investigations (Gore and Harwell 1981) reveal that deer in the Edwards Plateau remained small compared to other areas of the state in the 1970s and 1980s.

Whitetails at Fort Hood during the 1970s were also relatively small compared to deer from other parts of the state. In fact, Fort Hood deer were quite similar in body size to those from the Edwards Plateau in the 1970s (see discussion below). This highlights one or perhaps two important conditions at Fort Hood early in its management history. It is quite possible that deer were overabundant at the fort after a successful mid-century reintroduction. Further, it is likely that small deer were reintroduced from other areas of central Texas.

Whatever the cause of small body size, it is predicted that as structured harvest progressed during the following decades body size of Fort Hood deer should have increased. Why? Because if deer were small to begin with, subjection to managed conditions should have provided the Fort Hood population with progressively better habitat and forage through time. Second, if deer were overcrowded prior to the 1970s, then progressive management during the following decades should have thinned their population and lowered density, also providing better habitat and more forage per individual through time. This situation should be in contrast to areas farther south near Austin where structured management of the deer population did not occur thus creating a condition of extreme overpopulation (see Chapter 5). Finally, bucks are larger than does and have more extensive home ranges (Marchinton and Hirth 1984); thus, high population density is likely to produce more pronounced diminution in bucks than does. Similarly, release from the effects of crowding should produce a more substantial increase in body size in bucks than in does.

If the body size predictions are met, then other predictions should also hold concerning Fort Hood white-tailed deer. First, deer density should decrease with progressive harvest during the last few decades. Second, deer from areas of the fort with lower density should produce larger whitetails. The former can only be evaluated at a very coarse scale because of the patchy temporal record of survey data from the last two decades. The latter is evaluated using data from two harvest seasons, 1990 and 1991, for which spatial and census data are more detailed.

As shall become clear, each of the predictions outlined above holds for Fort Hood white-tailed deer. The most impressive implication to evolve out of this study is the significant influence of population density on white-tailed deer body size in central Texas. There is no doubt that at the inter-regional scale numerous climate- and habitat-related variables drive body size differences in cervids (e.g., Langvatn and Albon 1986; Geist 1987, 1998), but at the intra-regional to local scales (e.g., within central Texas) population density is an extremely important factor (see Kie et al. 1983; Lesage et al. 2001).

Methods

Dressed weight (lbs) that was taken on the same scale each year during deer harvest check-in at Fort Hood is used as an indicator of body size. Dressed weight is carcass weight after the animal has been field dressed (gutted) but prior to extensive butchery. Age of deer was and continues to be determined via tooth wear following Severinghaus (1949; e.g., Schwartz and Schwartz 1981). Although wear rates vary according to habitat and though assignment of wear to age classes is subjective, the age classes serve as an ordinal-scale (older-than, younger-than) indicator of age (cf. Gee et al. 2002). Tooth wear undoubtedly becomes less accurately predictive of age the older deer become; that is, the more wear that has occurred the less contingent the wear might be on deer age. For that reason, when wear-age-classes are used analyses are restricted to younger ages classes (up to the 4.5-year class), and when possible, analysis is limited to only the 1.5-year class, which exhibits the least wear, hence the least variability. Further, the 1.5-year class marks the full eruption of permanent teeth, and this is a relatively stable indicator of physiological development up to that point (Schwartz and Schwartz 1981). Use of later age classes requires the assumption that progressively greater tooth wear reflects a longer lifespan, which is generally true but increases in variability with age of deer.

Data produced on deer size by age for ecoregions of Texas in 1980 comes from Gore and Harwell (1981). Data for the Edwards Plateau and for other regions of the United States is from Teer et al. (1965). Fort Hood census data were gathered by wildlife biologists at the Natural Resources Branch of the Directorate of Public Works at Fort Hood via spotlight survey for the purpose of determining yearly harvest strategies. Here they are used to evaluate population density across the fort and through time. The survey data are divided into three subregions of the fort, the East Region, the West Region, and West Fort Hood (WFH).

White-tailed Deer Body Size at Fort Hood

Since 1971, the first year for which data are compiled, deer body size has steadily—nearly monotonically—increased (Figure 4.3), which would appear to support the first prediction outlined above (see summary data in Appendix B). However, the distribution in Figure 4.3 could be biased if, say, there are more does represented early in the sequence and fewer later. Another potential bias is age; it is possible that earlier in its history the dataset is dominated by juveniles. Figure 4.4, however, leaves no doubt that deer body size increased through time at Fort Hood. The trend persists when the sample is limited to deer that are 1.5 years old and it occurs in bucks and does independently; both positive relationships are statistically significant though the magnitude of change was greater for bucks than for does. The same trend is apparent in older age classes among bucks and does from 1975 to 2005 (Figure 4.5). Whitetail bucks and does at Fort Hood in 1975 approximated the body size of deer in the Edwards Plateau, but by 2005 they are as large as or larger than deer in the Cross Timbers ecoregion and farther east in the Post Oak Savanna (Figure 4.6).

These data highlight a substantial change in white-tailed deer body size at Fort Hood during the last four decades though not much of one occurred in the Edwards

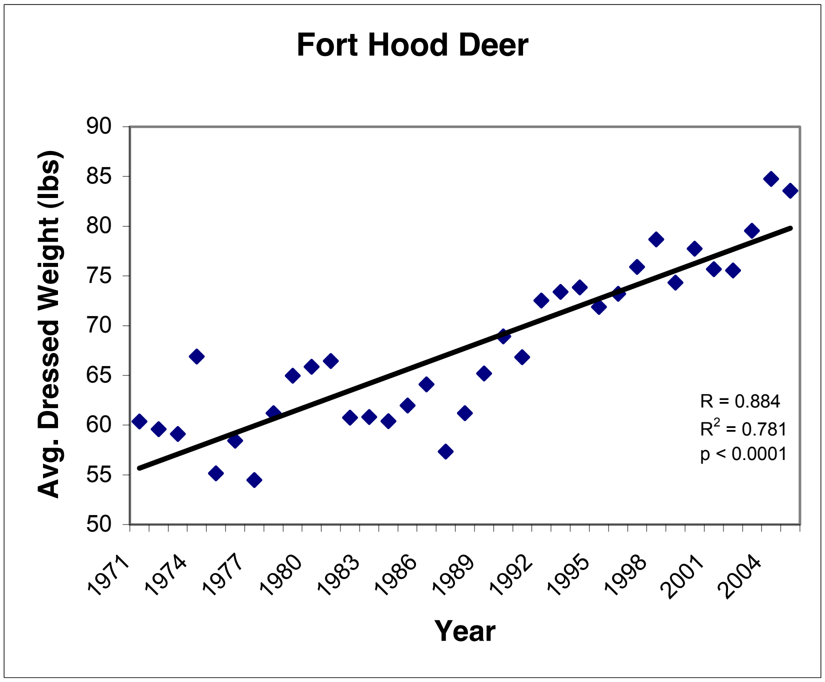


Figure 4.3 Bivariate plot illustrating an increase in average white-tailed deer dressed weight from 1971 to 2005 at Fort Hood.

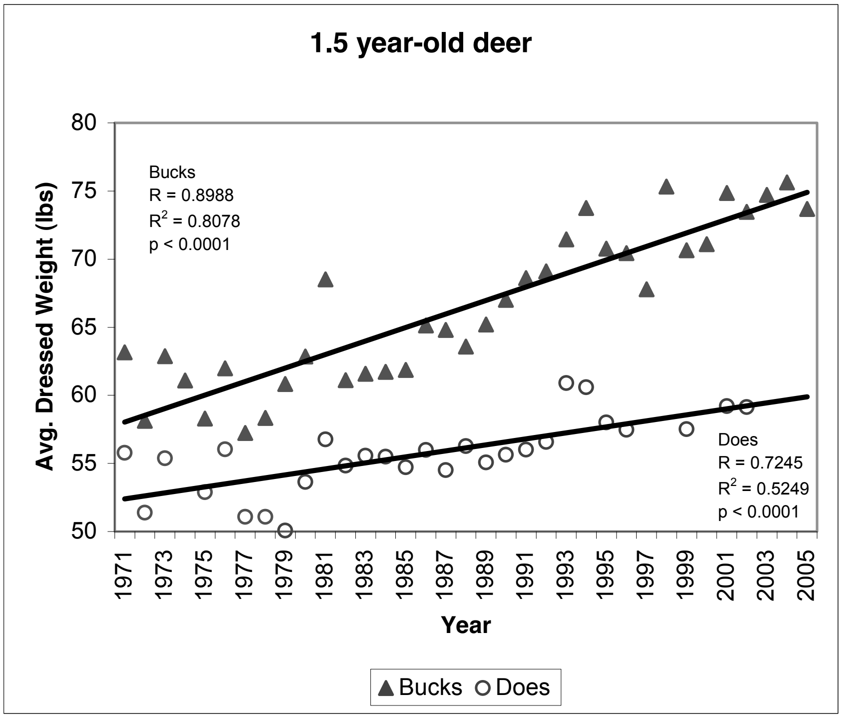
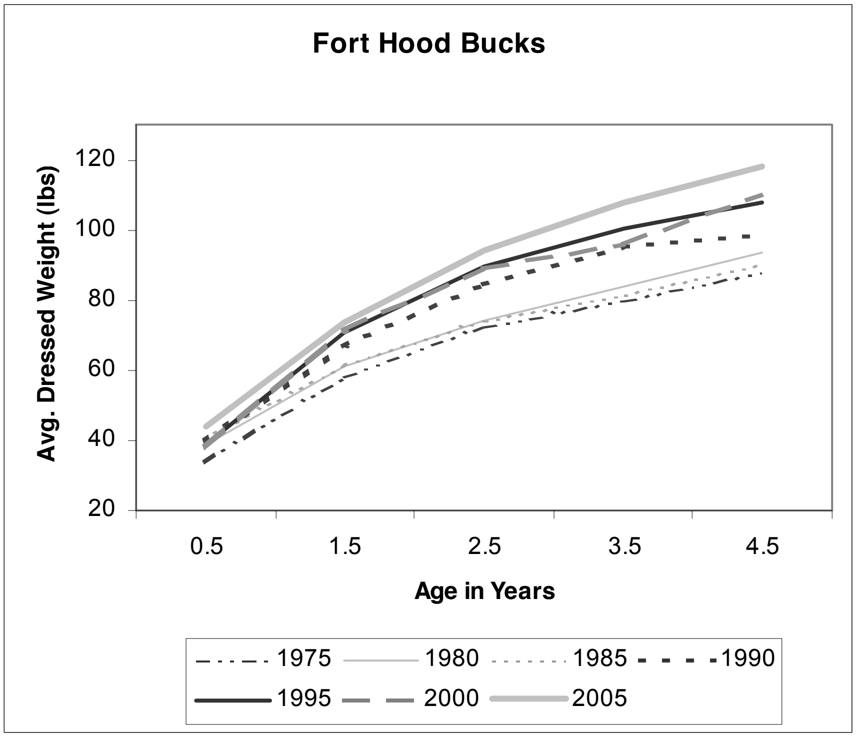


Figure 4.4 Bivariate plot illustrating an increase in average 1.5 year old white-tailed deer dressed weight for bucks and does from 1971 to 2005.



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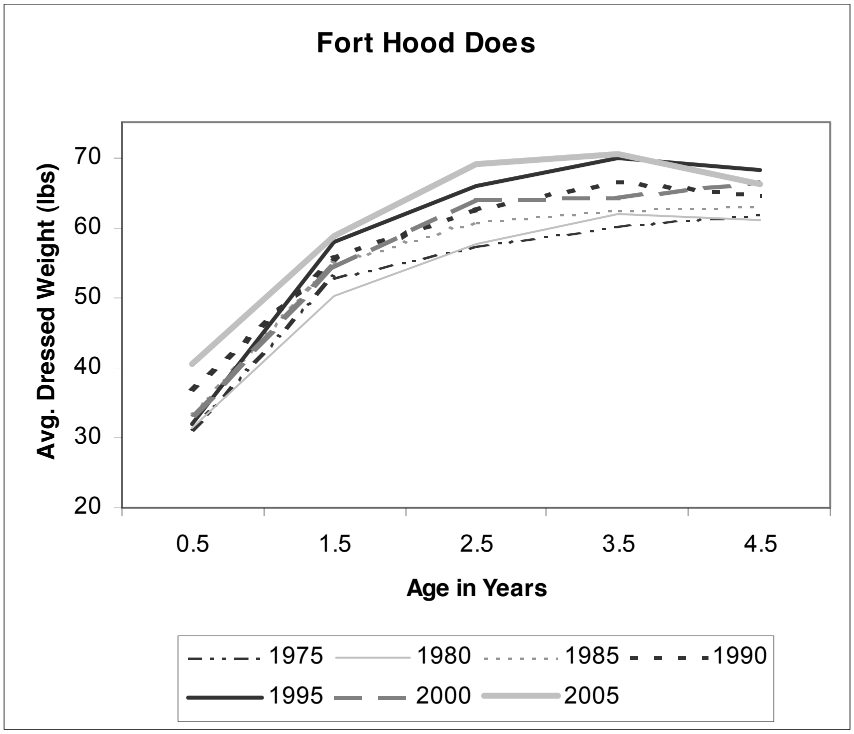


b

Figure 4.5 Bivariate plot of a) buck and b) doe dressed weight by ontogenetic age in five year increments from 1971 to 2005 for Fort Hood.

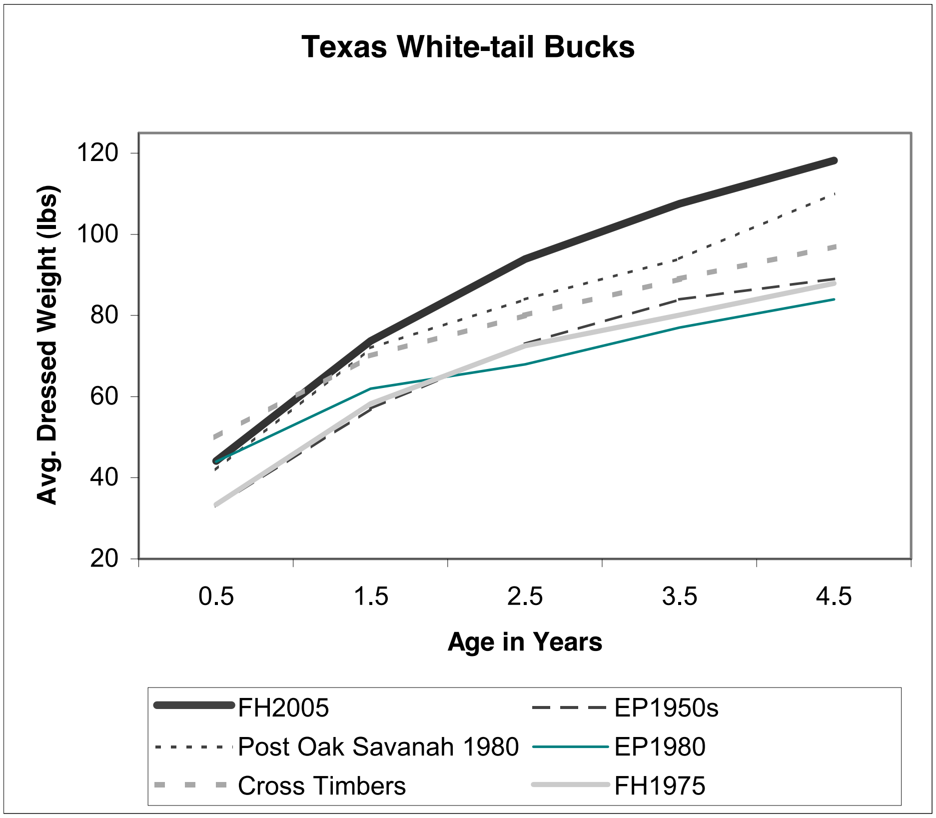


Figure 4.6 Bivariate plot of white-tail buck dressed weight by ontogenetic age for the Edwards Plateau (EP1950s and EP1980), the Cross Timbers, the Post Oak Savanna, and Fort Hood (1971 and 2005). Ecoregional data are from Teer et al. (1965) and Gore and Harwell (1981).

Plateau from the 1950s to 1980 (Figure 4.6). Following the first prediction outlined above, deer body size increased as the history of management progressed. But is the Fort Hood trend related to a decrease in population density during the same period? Itis tempting to deduce such a change from the body size data, but other variables (e.g., habitat improvement) might better explain the trend. In fact, it is probable that deer habitat did improve at Fort Hood during the last half century; however, as shall become clear in the next section, such improvement likely relates to a decrease in deer population density during the same period.

Population Density and Deer Body Size at Fort Hood

The temporal record of deer population density at Fort Hood is patchy; however, there are two distinct periods represented. The first period is from 1981 to 1991 and the second period is from 1997 through 2005. For the first period white-tailed deer body weight averaged nearly fifteen pounds less than the later period. Spotlight surveys estimate over ten more deer per 1,000 acres on average during the first period than during the second period (Table 4.1). Figure 4.7 illustrates yearly population-density estimates for the fort, and it is clear that despite extensive variability population density decreased across the base as a whole. The relationship between time and estimated population density is treated non-parametrically using Spearman's rank-order correlation because of the time gap in data from 1992 to 1996 (Table 4.2). Statistically significant decreases in estimated population density occurred through time for the fort as a whole and for the East and West regions. West Fort Hood also witnessed a decrease though it was not statistically significant. These data indicate that as body size increased after 1971 at Fort Hood, population density decreased.

Given that West Fort Hood consistently exhibited higher estimated population density than the East or West regions during the last two and a half decades, it is also expected that deer from West Fort Hood should be smaller in body size. Accessible spatial data are only compiled for the 1990 and1991 hunting seasons; these data demonstrate that bucks and does harvested from West Fort Hood are consistently smaller than those harvested from the East and West regions (Figure 4.8). Deer harvested from the East and West regions, on the other hand, are similar in size to one another. These data corroborate that high population density is closely related to small

Table 4.1 Estimated population density and body size for two periods at Fort Hood.

Period	Deer / 1000 acres	Avg. dressed weight (lbs)
1981-1991	36.03	63.09
1997-2005	25.36	78.42

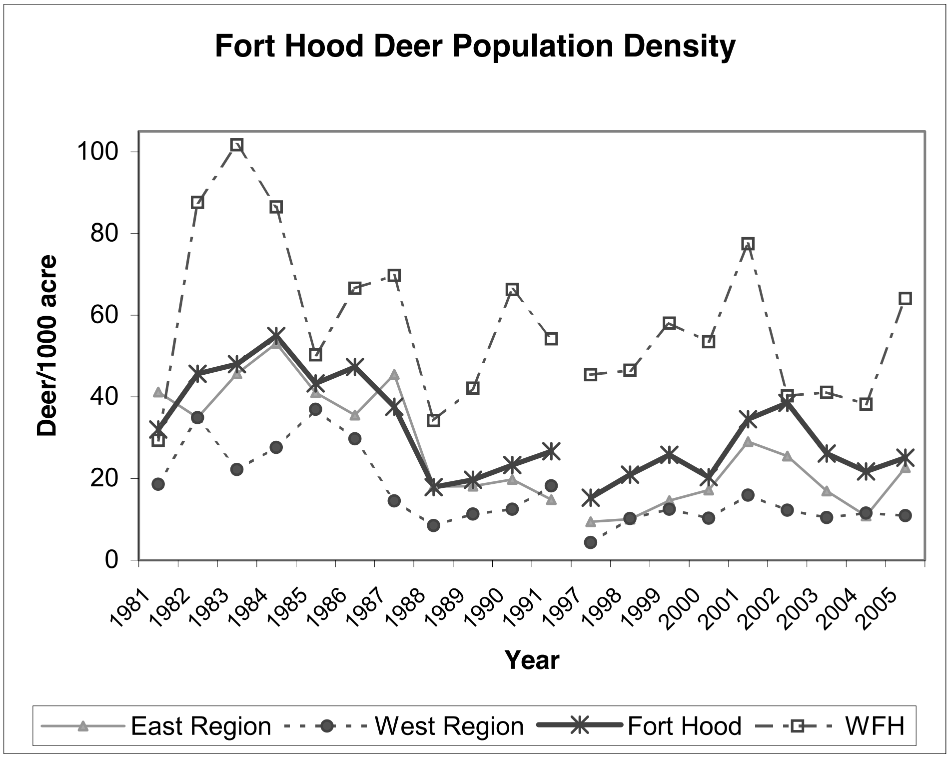
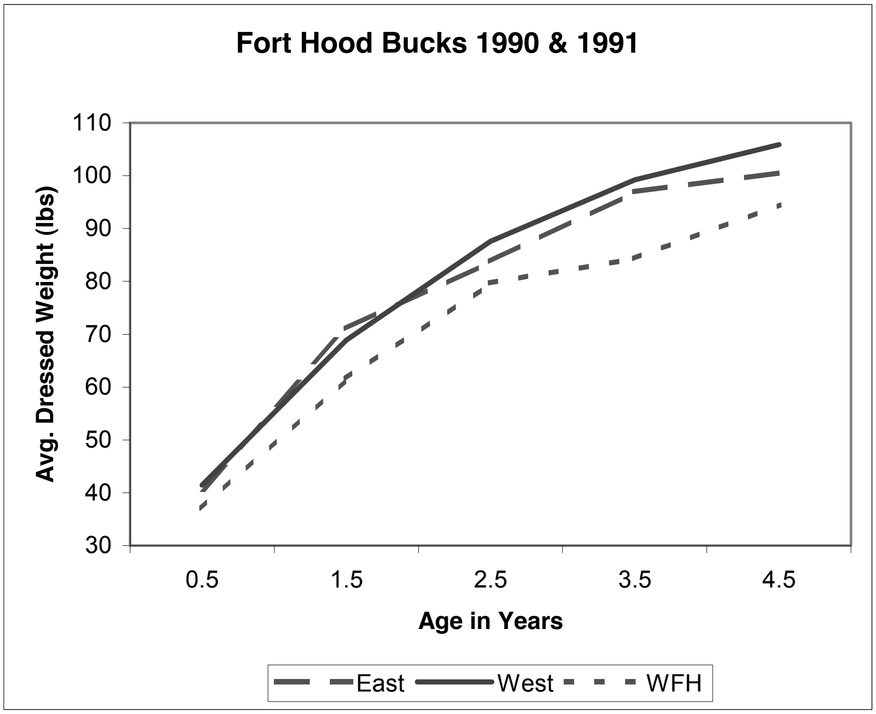


Figure 4.7 Bivariate plot of estimated white-tailed deer population density by for Fort Hood and its subregions for 1990 and 1991 (WFH = West Fort Hood).

Table 4.2 Spearman's rank order correlation between ranked time and estimated population density.

Fort Hood	East Region	West Region	West Fort Hood
$R_s = 0.484$ $R_s^2 = 0.235$ $p = 0.031$	$R_s = 0.648$ $R_s^2 = 0.420$ $p = 0.002$	$R_s = 0.642$ $R_s^2 = 0.412$ $p = 0.002$	$R_s = 0.305$ $R_s^2 = 0.093$ $p = 0.191$



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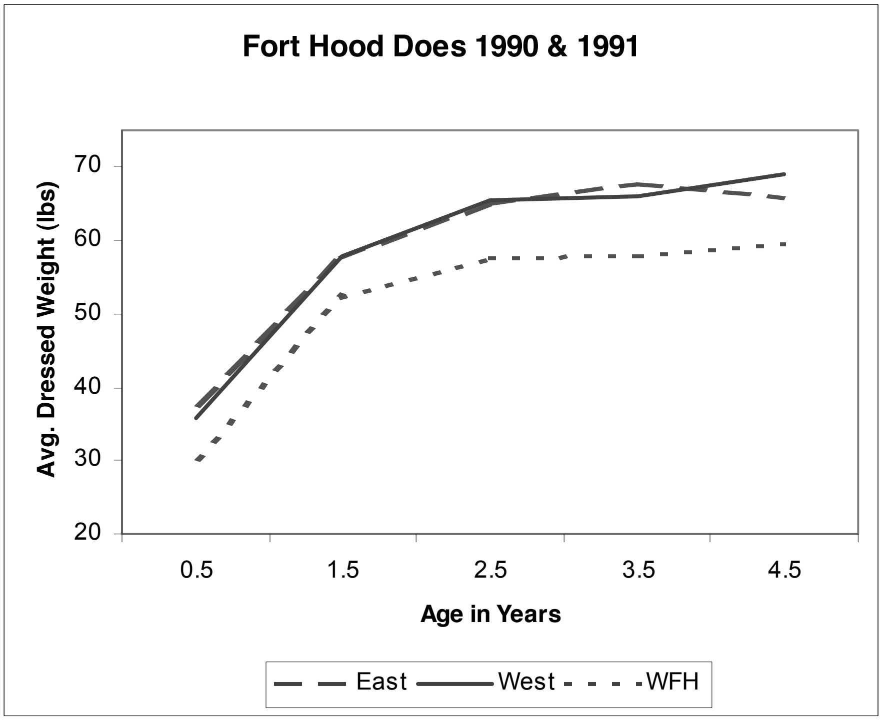

b

Figure 4.8 Bivariate plots of average dressed weight by ontogenetic age for a) bucks and b) does from subregions of Fort Hood.

body size in white-tailed deer at Fort Hood.

Summary

Although habitat diversity cannot be ruled out as an important local factor in the body size disparity between West Fort Hood and other portions of the base, in every situation discussed in this chapter relatively small body size correlates closely with high population density. For example, sustained harvest at Fort Hood appears to have lowered population density and average dressed weight of bucks and does has significantly increased since the 1970s. The same is true for West Fort Hood in that it is the subregion that has consistently produced the highest estimated population density and the smallest deer during the last two and a half decades. These patterns are not a product of age or sex biases in the datasets in that those variables are analytically controlled by considering bucks and does separately and by demonstrating age-independent body size trends. Nonetheless an important future study will be to examine differences in habitat quality between West Fort Hood and other parts of the fort. Further it will be necessary to determine whether or not potential habitat differences relate to overabundant deer and associated overbrowsing.

Discussion

Structured harvest of white-tailed deer has a profound effect on their body size; however, the effect is more substantial and rapid for bucks than for does. This difference in response to harvest pressure by bucks and does is to be expected given distinctive ways that each sex uses habitat. Bucks have larger home ranges than highly philopatric does (Comer et al. 2005; Geist 1998; Marchinton and Hirth 1984; Purdue et al. 2000). Bucks also require more space and food than does because they are larger on average. Overcrowding reduces dispersal opportunities among bucks and thus more likely causes diminution than in does. In the absence of large predators in central Texas, management offers a release from high population density, an increase in available habitat and food per individual, and as a result an increase in body size, especially for bucks.

An overabundance of deer produces effects that span well beyond that of phenotypic plasticity in body size. High population density leads to several disturbances that echo through the ecosystem. For example, overabundant deer populations restrict recruitment of deciduous saplings and create room for competitive species such as junipers (*Juniperus* sp.). Dense populations of deer also compete directly with humans for habitat often inhabiting yards in suburban and urban settings (Etter et al. 2002; Henderson et al. 2000; Lopez et al. 2003; Walton 1999). Deer movements along roadside edges result in automobile wrecks, and in rural settings deer cause damage to agricultural crops. Management of white-tailed deer would not likely eliminate these impacts; however, it is true that sustained harvest limits their numbers and reduces their undesirable environmental and cultural impacts. Unfortunately, there is no simple solution because a segment of society prefers not to support culling of overabundant populations despite their deleterious effects.

Given that culling of white-tailed deer populations is a socially, economically, and politically charged issue, it is important to consider the longer term effects of predator eradication and high deer population density. Geist (1987, 1998) theorizes that a reduction in dispersal ability among whitetails eventually results in a longer-term evolutionary effect that he terms “efficiency selection.” In crowded conditions does face evolutionary trade offs between body size, offspring body size, and reproductive energetic efficiency. That is, evolution turns toward maintenance of reproduction at the cost of body size. There may even be sexual selection at work in that it is reproductively advantageous for does to “choose” relatively small bucks to mate with. Smaller bucks lead to smaller fawns that have a greater probability of surviving in overcrowded conditions. Efficiency selection to maintain reproductive energy leads to genetically smaller deer. In the strictest sense of the carrying capacity concept, body size diminution effectively bends the rule in that the number of deer that can survive increases because each individual is smaller.

Predators thin prey populations, which controls their density. It is of interest, then, to examine body size of central Texas deer from a period when large predators were common. The prehistoric period known to archaeology and paleontology offers an opportunity to compare deer body size before and after predator eradication. Removing a substantial portion of the predator guild has created a niche vacuum at the top of the trophic hierarchy. The resulting changes are evolutionary in proportion; they are not simply management issues. By radically altering the predator guild, modern humans have impacted the course of evolution in white-tailed deer, competing herbivores, carnivores, surrounding plant and insect communities, and the ecosystem as a whole. The paleozoological record of paleontology and archaeology provides a unique source of data with which to examine these long-term evolutionary changes, whether they be phenotypic, genotypic, or ecological in nature.

CHAPTER 5

A PALEOZOOLOGICAL PERSPECTIVE ON DEER OVERABUNDANCE

It is clear that predator eradication caused substantial changes to the predator guild in central Texas during the last century. The remaining carnivores represent a fraction of the body size range of native Holocene predators from the region (see Chapter 3). It is also clear that white-tailed deer body size is phenotypically plastic, particularly in response to habitat conditions and population density (see Chapter 4). This chapter considers modern white-tailed deer body size in reference to that during prehistory in order to determine effects of predator eradication on deer population density and body size (Wolverton et al. 2007). An important impact of predator eradication and habitat modification throughout many areas of central and eastern North America is an explosion of white-tailed deer populations (McShea et al. 1997). Overabundance of deer in central Texas is important for numerous politically, socially, and ecologically significant reasons, which is the subject of the following chapter. Here the focus is analysis of prehistoric (Holocene) versus modern white-tailed deer body size in central Texas. Examining the modern white-tailed deer population under the lense of a long-term perspective reveals the magnitude of changes that have occurred since predator eradication. This study also adds a new dynamic to debates on potential solutions to this modern management problem (sensu DeNicola et al. 2000). Further, this analysis strengthens the argument that white-tailed deer overabundance is a modern phenomenon closely correlated to human impacts during the historic period.

Predator eradication in Texas eliminated control on white-tailed deer populations with the exception of that provided by human harvest pressure. In central Texas the absence of predators has exacerbated overcrowding of white-tailed deer such that they now occupy rural, suburban, and urban areas often at pest levels (Walton 1999). A reasonable assumption is that intraspecific competition among modern white-tailed deer is higher than in times prior to predator eradication. A corollary is that in marginal habitat overcrowding of deer should result in smaller body size. Indeed it is clear that as deer on Fort Hood witnessed progressive decades of structured harvest, their body size increased (see Chapter 4). It appears this is at least partially the result of lower population density related to harvest pressure. The modern Fort Hood population offers an interesting comparison to unmanaged populations just to the south near Austin. Both deer populations are of the same subspecies (*Odocoileus virginianus texana*), and the clearest difference between the two is the presence of yearly harvesting at Fort Hood and the virtual absence thereof to the south near Austin. The purpose of this analysis is to compare samples from these two areas to one another and to compare each to skeletal samples from the central Texas paleozoological record.

Two patterns are expected in these comparisons; first it is predicted that deer from suburban areas near Austin, Texas are smaller than those from Fort Hood precisely because the latter are regularly harvested. Second, the Fort Hood sample should more closely approximate white-tailed deer size during the prehistoric period (the Holocene, 10,000 years ago up to the historic period) prior to predator eradication. The implication is that Native Americans and native large predators, such as wolves and cougars, controlled white-tailed deer populations at lower densities producing larger deer. The same outcome, however, would result if environmental carrying capacity was higher during the prehistoric Holocene and decreased due to modern impacts. Because predator extermination is known to have occurred, it is assumed to be at least a partial cause of deer overabundance. That it is not possible to determine prehistoric environmental carrying capacity, however, does not diminish its importance. In order to compare modern and prehistoric deer size this analysis relies on the measurement of skeletal elements (bones) likely to be preserved in paleozoological settings and that are identifiable as white-tailed deer (Jacobson 2003, 2004; Lawrence 1951).

Age-Dependent vs. Age-Independent Body Size

Comparison of prehistoric and modern white-tailed deer body size is difficult to accomplish because typical measures of size, such as weight, cannot be recorded for prehistoric individuals. Further, body weight (often dressed weight) varies by physical condition of deer, thus estimates of weight from measurements of skeletal elements are prone to an indeterminable degree of inaccuracy. It might be possible to use skeletal measures, such as length of the axial skeleton, but this is not easily nor typically done in wildlife management of white-tailed deer (cf. Teer et al. 1965). Moreover, skeletal elements from paleozoological settings tend to be disarticulated from their skeleton of origin. A commonly used measure of size is weight, and a replacement for it must be relatively easy to obtain, reliably recorded in modern and prehistoric samples, and indicative of body size. Purdue (1987, 1989) determined that measurements of the astragalus, or anklebone, meet these criteria in white-tailed deer. Further, use of this bone offers a few other advantages in comparative analysis of modern and prehistoric deer body size.

Body weight is age- and condition-dependent, which means that as deer age they tend to weigh more and that their weight shifts according to quality and quantity of their diets (Kie et al. 1983). The astragalus, however, reaches its maximum size at roughly six months of age in white-tailed deer (Purdue 1987, 1989). Further, astragalus size is less condition-dependent in adults than body weight because it does not fluctuate with diet quality and quantity. Figure 5.1 highlights this relationship in modern deer from central Texas; there is no correlation between either astragalus thickness or length with age. However, there is a highly significant correlation between dressed body weight and age in modern bucks (Figure 5.2)[2]. Astragalus size does, however, correlate with dressed weight, which demonstrates that it is indicative of body size (Figure 5.3). The correlation between dressed weight and astragalus size is not strong precisely because weight varies with age and condition and astragalus size is age-independent. The size of the astragalus thus represents two things: first it represents the growth of an individual early in its life or its phenotypic and genotypic potential to grow during the first six months of its life. Second, in that the astragalus matures early and is a limb element, its size places a contingency on attainable body size during the rest of the individual's life (sensu Calder 1984). That is, the limb and body cannot be larger than the astragalus can mechanically support. Thus, astragalus size is an indicator of maximum potential body size, which is a direct consequence of an individual's genotypic and environmental potential for growth during its first six months.

The fact that the astragalus is a measure of maximum potential body size in adults is of value for several reasons. First, use of the astragalus removes the age-

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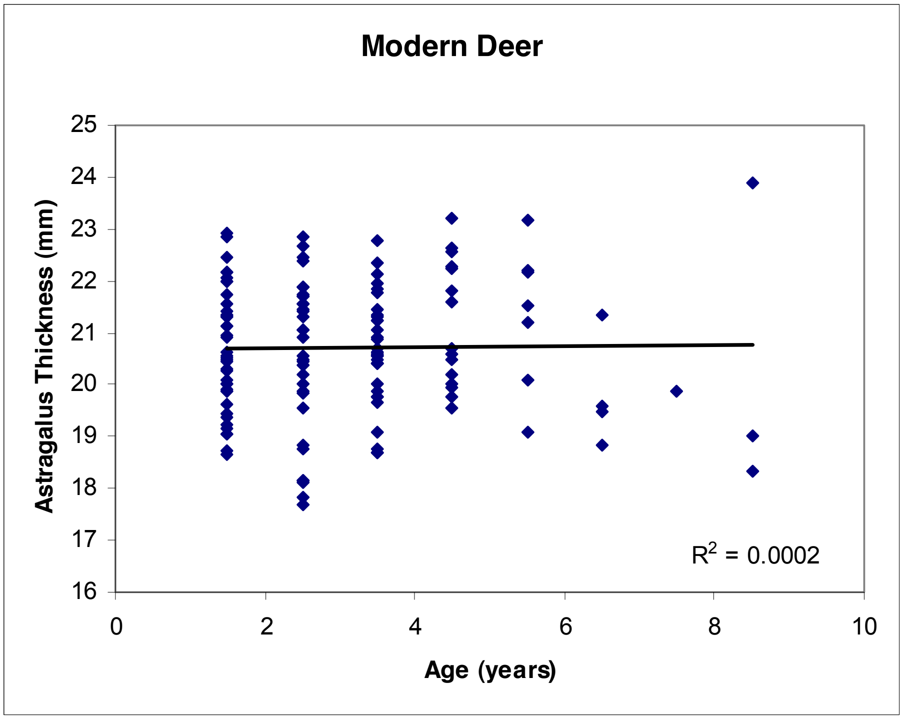
[2] Does are excluded in the weight analysis to remove the effects of sexual dimorphism in that does and bucks exhibit clearly distinct body weight trajectories with age.



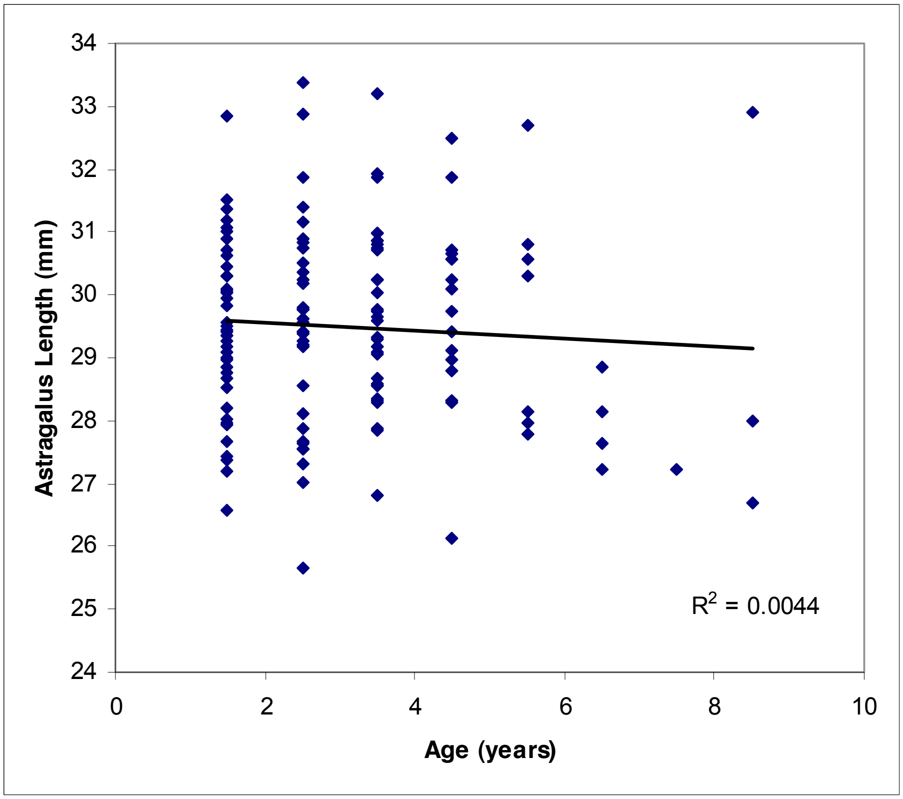


Figure 5.1 Bivariate plots of astragalus size (thickness and length) in modern deer from central Texas. There is no relationship between astragalus size and age.

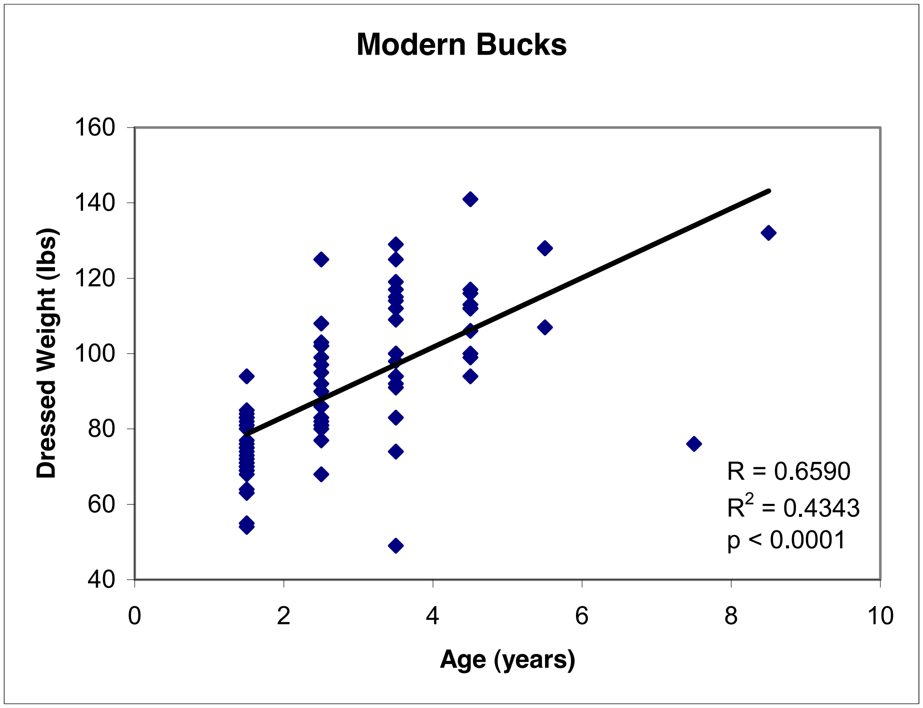


Figure 5.2 Bivariate plot illustrating the positive relationship between dressed weight and age in modern white-tailed deer bucks from central Texas.

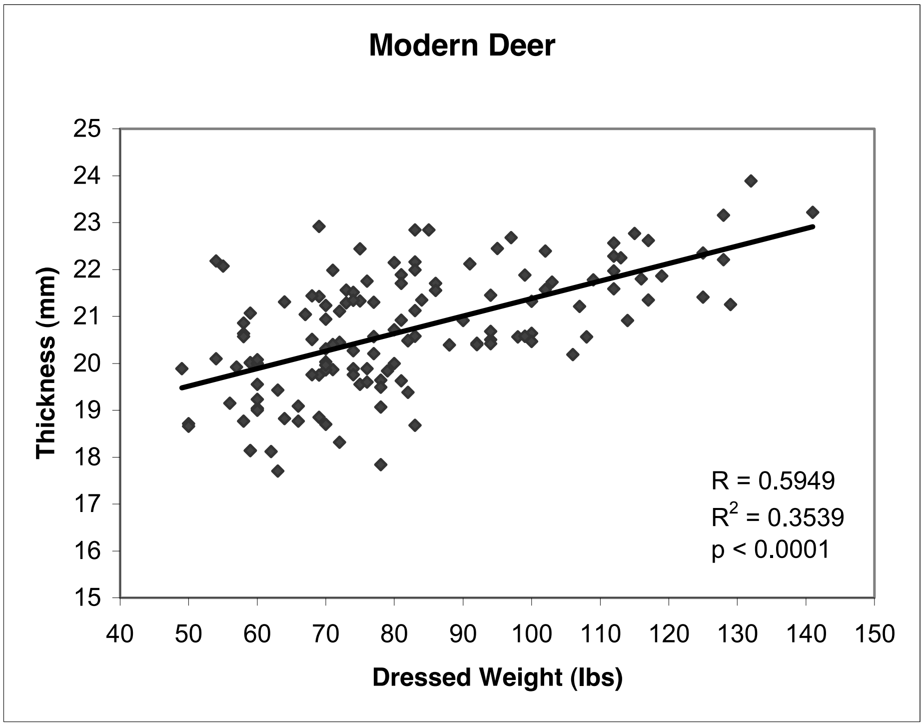


Figure 5.3 Bivariate plot illustrating the positive relationship between dressed weight and astragalus thickness in modern white-tailed deer.

dependent effects inherent in other measures of size, such as body weight. This is important because prehistoric astragali cannot be accurately aged, thus prehistoric samples comprise deer of many ontogenetic ages. If astragalus size varied with age, one would not be able to determine whether or not differences between samples are products of age biasing[3]. Further, sampling astragalus size offers a snapshot of growth conditions in a restricted period of individual's lives (the first six months).

Given that body size of white-tailed deer is related to population density, it is a reasonable assumption that growth rate during the first six months is similarly affected by population density. In crowded conditions, growth rate should be slower, producing smaller astragalus size and smaller maximum potential body size as a result. For the remainder of this chapter "body size" is used interchangeably with "astragalus size," which represents a "proxy measure of maximum potential body size."

Materials and Methods

Samples of astragali were measured in order to gauge the age-independent body size of prehistoric and modern white-tailed deer. Raw data on the measurements are recorded in Appendix C. Six measurements are illustrated in Figure 5.4, and of these AST 1 is used as "thickness" and AST 3 is used as "length" in this analysis. These two measurements were chosen because they are reliable and replicable and they are taken on parts of the astragalus that readily preserve in paleozoological settings. The last is a product of the measurements' locations at the center of the astragalus rather than along the margins where destruction more readily occurs. Using AST 1 and 3

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[3] It would have been ideal to choose a similar element for mesocarnivores in Chapter Three; however, in that case selection of the mandible was required in order to use an element that could be identified to species.

maximizes the number of specimens available for measurement in the prehistoric sample.

Prehistoric deer astragali are 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 5.1). Many of the specimens are from collections that never received detailed chronological analysis via relatively expensive radiocarbon dating. To date the specimens would require their destruction. Despite the coarse time-scale of the prehistoric samples used here, the predictions framed above can be evaluated (see discussion of coefficients of variation below).

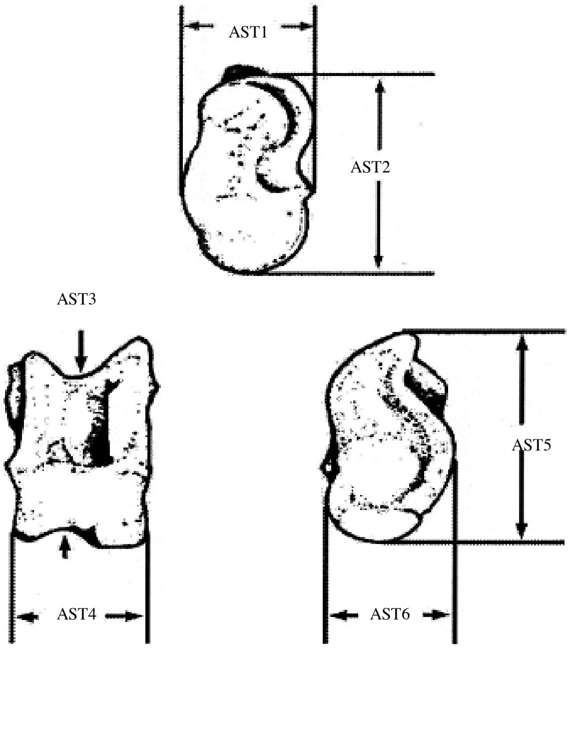

Figure 5.4 Measurements taken on modern and prehistoric white-tailed deer astragali (mm). AST 1 is used here as “thickness” and AST 3 is used as “length” (see text for discussion).

Table 5.1 Prehistoric astragali from central Texas.

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

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 at or near environmental carrying capacity. For purposes of this study these deer are labeled “unmanaged.” Astragali from unmanaged deer were collected by Orion Research and Management Services during 2005.

The second modern sample is from Fort Hood near Killeen, Texas. This population has undergone structured management and harvest for much of the last fifty years restricting population density below carrying capacity, and detailed records of population density and body size are available (see Chapter 4). The Fort Hood sample is labeled “managed,” and it was collected during the 2005 hunting-season. Modern astragali were collected by clipping the distal tibia and proximal metatarsal; specimens were transported to the University of North Texas, Laboratory of Zooarchaeology, defleshed, disarticulated, boiled gently for forty-five minutes to remove grease, and measured following the specifications in Figure 5.4.

Modern samples are stratified by sex in comparison to one another because the unmanaged sample has a higher representation of females, which skews its body-size distribution toward smaller individuals. Consideration of males and females separately allows examination of potential body size differences between the two samples independent of the effects of sexual dimorphism. The managed and unmanaged samples are also analyzed without separation of males and females because astragali in the prehistoric sample are of indeterminate sex and, as a result that sample must be considered as a whole. In this case the “lowest common denominator” is the prehistoric sample, which cannot be sexed. It is assumed that bucks and does are represented in the prehistoric sample, but this cannot be verified. However, the coefficients of variation suggest variability in the prehistoric sample that is similar to modern samples with pooled sexes (Table 5.2). Prehistoric and modern samples are compared using bivariate plots of astragalus length and thickness and are treated statistically using Student’s *t* test. Coefficients of variation are used to assess the level of variability in each sample.

Results

Descriptive statistics related to each sample are provided in Table 5.2. Results of Student’s *t* comparisons among samples are provided in Table 5.3. Figure 5.5 compares astragali from modern managed and unmanaged samples; astragali from the unmanaged sample are significantly smaller (Table 5.3). Does from the unmanaged sample are smaller on average than those from the managed sample, but the difference is not statistically significant for thickness and is marginally significant for length. Visual inspection of the distribution (Figure 5.6) indicates that there are several specimens from the unmanaged sample that extend beyond the smaller end of the managed-doe distribution. Figure 5.7 compares managed and unmanaged bucks, and the latter is significantly smaller in terms of thickness and marginally significantly smaller in terms of

Table 5.2 Descriptive statistics of white-tailed deer samples from modernity and prehistory (mm).

Sample	Mean	Standard Deviation	Coefficient of Variation	n
Managed Total				
Length	29.92	1.47	4.90	82
Thickness	21.12	1.18	5.59	82
Managed Doe				
Length	28.73	1.02	3.54	23
Thickness	19.89	1.02	5.15	23
Managed Buck				
Length	30.32	1.38	4.56	61
Thickness	21.54	0.94	4.38	61
Unmanaged Total				
Length	28.86	1.43	4.95	53*
Thickness	20.07	1.15	5.71	53*
Unmanaged Doe				
Length	28.25	1.24	4.40	31
Thickness	19.63	1.10	5.60	31
Unmanaged Buck				
Length	29.77	1.24	4.15	21
Thickness	20.73	0.91	4.40	21
Prehistoric Total				
Length	29.88	1.41	4.73	58
Thickness	21.33	1.15	5.39	58

* Includes one individual of unknown sex.

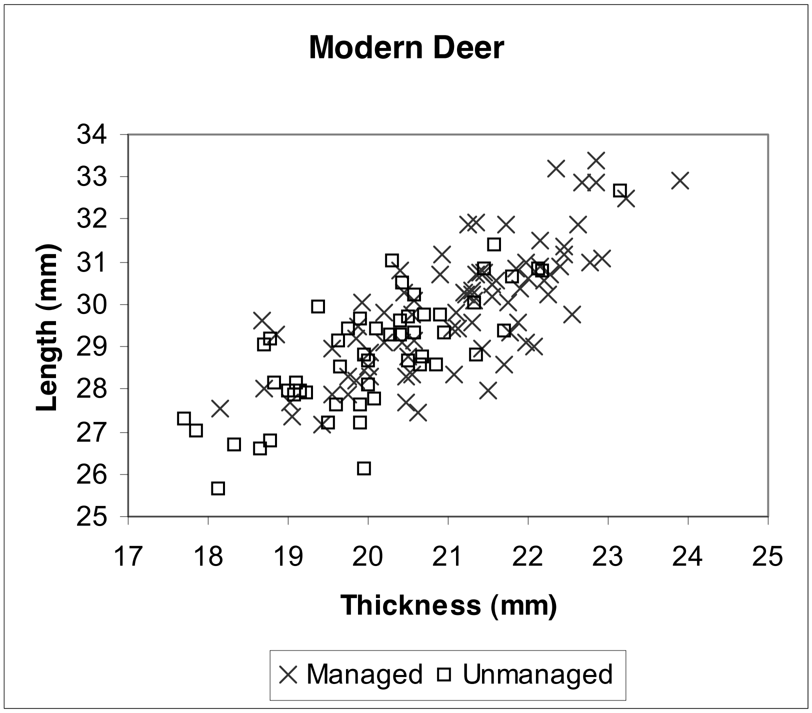

Figure 5.5 Bivariate plot of astragalus thickness and length for modern managed and unmanaged white-tailed deer.

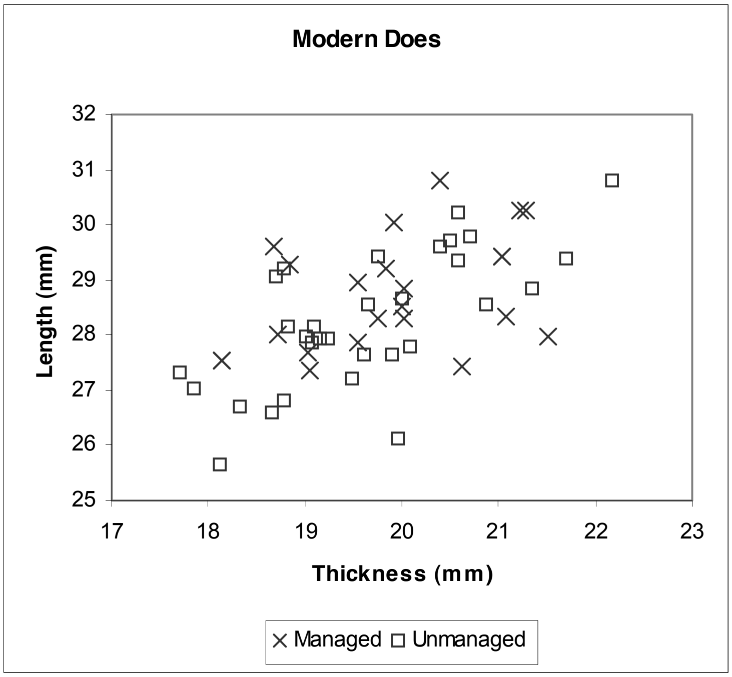

Figure 5.6 Bivariate plot of astragalus thickness and length for managed and unmanaged does.

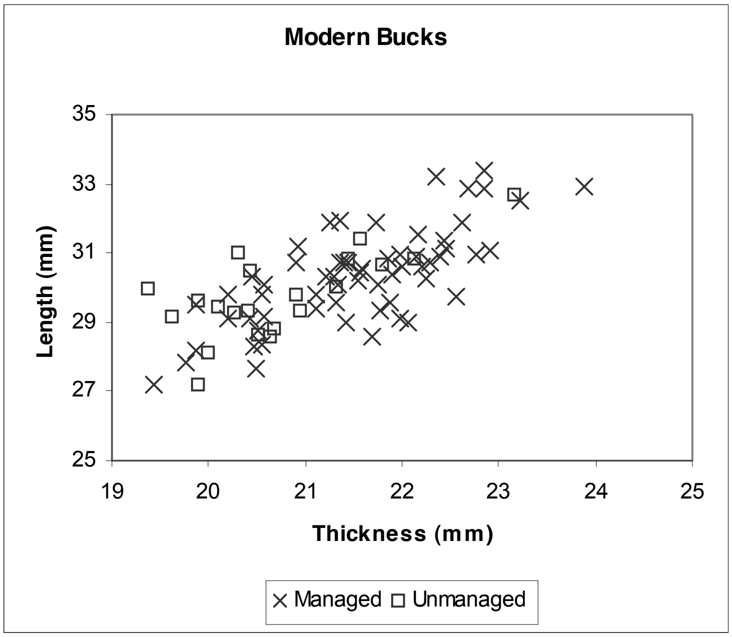

Figure 5.7 Bivariate plot of astragalus thickness and length for managed and unmanaged bucks.

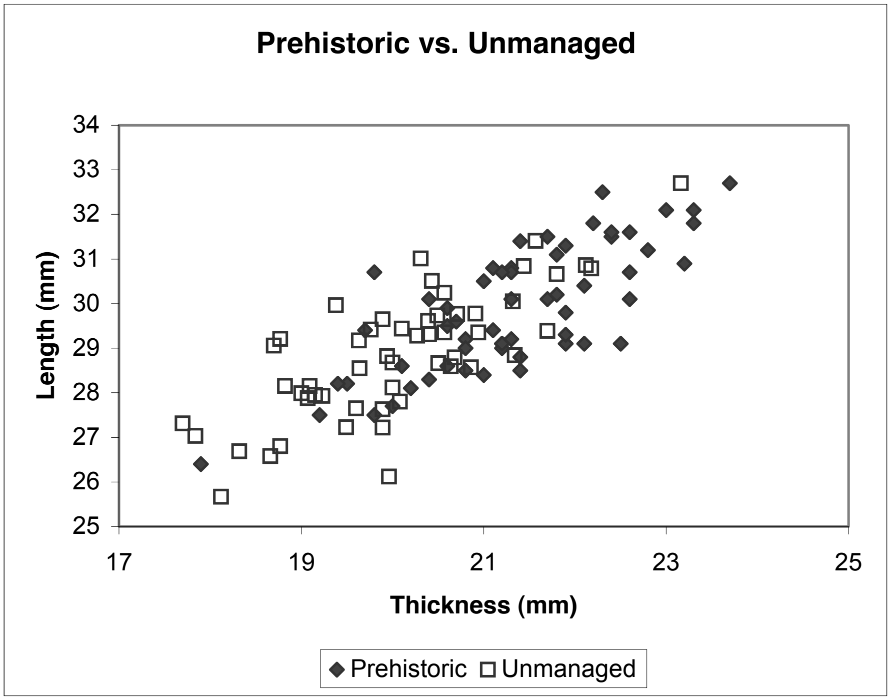

Figure 5.8 Bivariate plot of astragalus thickness and length for unmanaged and prehistoric white-tailed deer.

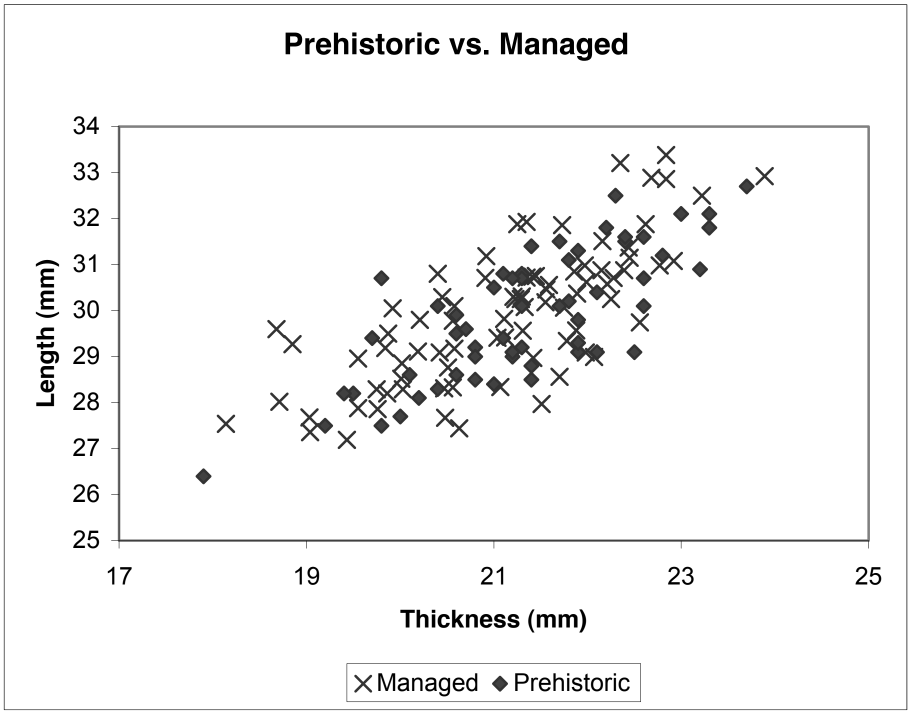

Figure 5.9 Bivariate plot of astragalus thickness and length for managed and prehistoric white-tailed deer.

length (Table 5.3).

Of particular interest given the predictions outlined above, is that astragali in the unmanaged modern sample are significantly smaller than prehistoric ones (Table 5.3; Figure 5.8). 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 5.9) and cannot be distinguished from it statistically (Table 5.3).

Table 5.3 Results of Student's *t* tests on astragali samples.

Test	*t*-statistic	*p*-value	$\Delta\bar{x}$ (%)	MSD (%)
Total				
Unmanaged vs. Managed				
Length	-4.133	<0.001	1.05 (3.51%)	0.42 (1.41%)
Thickness	-5.108	<0.001	1.05 (4.97%)	0.34 (1.62%)
Unmanaged vs. Prehistoric				
Length	-3.758	<0.001	1.01 (3.38%)	0.45 (1.50%)
Thickness	-5.789	<0.001	1.27 (5.95%)	0.35 (1.71%)
Managed vs. Prehistoric				
Length	0.174	0.431	0.04 (0.13%)	0.38 (1.28%)
Thickness	-1.067	0.144	0.22 (1.03%)	0.34 (1.60%)
Does				
Unmanaged vs. Managed				
Length	-1.575	0.061	0.49 (1.71%)	0.52 (1.82%)
Thickness	-0.901	0.186	0.26 (1.31%)	0.49 (2.44%)
Bucks				
Unmanaged vs. Managed				
Length	-1.600	0.057	0.54 (1.78%)	0.55 (1.85%)
Thickness	-3.398	<0.001	0.81 (3.76%)	0.40 (1.83%)

Each of the Student's *t* tests on white-tailed deer astragalus samples exhibits high statistical power in that differences between one and two and a half percent are detectable as statistically significant (Table 5.3). $\%\Delta\bar{x}$ in most of the tests is two to four times that of %MSD indicating that not only are most of the observed differences between means statistically significant, but they are also large in magnitude (Table 3.5). Non-significant differences between managed and unmanaged doe astragalus size likely reflects the relatively small managed sample from Fort Hood (Table 5.2). The low %MSD in the managed versus prehistoric test suggests that the test is powerful and that there is no difference in average astragalus size between the samples.

Summary

Deer from Fort Hood are larger than those from unmanaged areas near Austin. The difference occurs in bucks and does; however, as in the historical study in Chapter 4 bucks exhibit a more dramatic difference in body size because contingencies on their use of habitat are more restrictive related to their requirements for larger home ranges and for more food. Bucks literally “have more to lose” in crowded conditions than does, and this is reflected in their marked body size decrease in unmanaged conditions.

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. Further, 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 (Kevin Cagle, personal communication). The small body size of white-tailed deer in areas of central Texas where noticeable overcrowding occurs is a modern phenomenon. An important modern human impact is predator eradication because it removed a control on deer population density, though it did not occur isolated from plausible reductions in environmental carrying capacity likely to be exacerbated by overabundant deer.

Discussion

It is of interest 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. An important question is why are modern deer smaller today 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 native predators. 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, unmanaged modern deer are as small as they have been or smaller than during the rest of the Holocene. The time-averaged character of the prehistoric sample allows consideration of modern samples in reference to a relatively generalized Holocene condition. However, the prehistoric sample contains approximately the same level of variability as either modern sample (see coefficients of variation in Table 5.2).

Habitat similarly varies across space, and the prehistoric sample spans much of the area bordering and contained within the Edwards Plateau. Again, 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 comparable in size to the modern samples). The difference in astragalus 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. It is conceivable that environmental carrying capacity was higher during much of the prehistoric Holocene in central Texas and that today poorer habitat contributes to stunting. In fact, it is likely that habitat today is of poorer quality than during prehistory because of ranching, urban and suburban development, deer fencing, introduction of competitive exotic ungulates (Buechner 1944; Cook 1984; Mungall and Sheffield 1994), and overbrowsing by deer in fragmented habitat. A depleted predator guild is perhaps too easy to focus on because it is a visible, empirical difference between the prehistoric and modern periods. It is extremely provocative, however, that increases in harvest pressure at Fort Hood have made a substantial difference in deer population density and body size in a relatively short period of time. Thus, it is important not to underestimate the importance of predation.

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., Russell and Fowler 1999, 2004 for central Texas; Allombert et al. 2005 [mule deer, *O. hemionus*]; Alverson et al. 1988; Anderson et al. 2001; Augustine and DeCalesta 2003; Côté 2005; DeCalesta 1994; McShea and Rappole 2000; Pellerin et al. 2006; Potvin et al. 2003; Seagle 2003; see summaries for other regions in Côté et al. 2004, Rooney and Waller 2003, and Russell et al. 2001). Effects across North America range from alteration of forest nitrogen budgets related to use of farm crops as food by deer in Indiana (Seagle 2003), to extirpation of an island black bear population in Quebec (Côté 2005), to substantial damage to forest trees and flowers (Augustine and DeCalesta 2003; Rooney 2001; Russell and Fowler 2004).

Crowded conditions in central Texas promote over-browsing of deciduous trees and saplings (e.g., *Quercus buckleyi*), which further reduces habitat quality and exacerbates the effects of overpopulation (Russell and Fowler 1999, 2004). 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. This study adds 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 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.

CHAPTER 6

CONCLUSION

> Numbers do not seem to work well with regard to deep time. Any number above a couple of thousand years—fifty thousand, fifty million—will with nearly equal effect awe the imagination to the point of paralysis.
>
> *McPhee*

Environmental scientists are trained that statistical significance is not the same as ecological significance. Statistically significant effects are those that occur at a probability greater than that of chance alone. If a relationship, difference, or effect is statistically significant it might not be ecologically significant. Ecologically significant effects are tied to ecological theory and not necessarily to probability theory. For example, there is a statistically significant difference between astragalus size in white-tailed deer from managed and unmanaged populations in central Texas. Unmanaged deer are also statistically significantly smaller than deer from managed populations and from prehistoric deer. But are these differences ecologically important? Similar questions might be asked of the marginally statistically significant and insignificant differences in size between modern and prehistoric mesocarnivores. Perhaps those differences *are* ecologically important. Where should lines be drawn to delineate effects that are ecologically important and those that are not? Certainly, environmental and ecological scientists are fully capable of monitoring changes in biological communities created by human impact (e.g, Allan 2004; Cairns and Pratt 1993; Chessman and Royal 2004; Russell and Fowler 2004; Wallace and Webster 1996).

Perhaps environmental scientists should not create artificial boundaries around ecologically important effects. A good reason for not doing so is that ecosystems evolve (Landres 1992; Lyman and Cannon 2004a). An important effect in one time and place might not be such in other contexts. Given that contingency plays a pivotal role in evolution, the most significant effects of modern human impacts are those that radically influence the trajectory or evolution of an ecosystem (Lyman and Cannon 2004a). *Evolutionary significance* is a useful descriptor of such effects, and it is defined here as permanent or irreversible changes to an ecosystem through preventable human influence (e.g., choices). An example of such a choice is predator extermination; the effects of predator removal are important in that the evolutionary history of an intact predator guild is terminated. Species are extinguished, yes, but the guild—established over evolutionary time—is also radically transformed and must rapidly evolve in the face of change. The previous guild becomes extinct and a new one takes its place.

These kinds of environmental changes are typically not at the forefront of attention in modern society because humans do not live long enough lives to witness these and other evolutionary effects. It is possible to recognize such changes if environmental science adds a unique perspective to its repertoire of interdisciplinary science, namely what has been termed a disclosive perspective (Borgmann 2000; Oelschlaeger 1991, 2000), which can be equated with historical science (sensu Ereshefsky 1992; Simpson 1963).

A Disclosive Perspective

The opening quotation by John McPhee illustrates the challenge and reward of working with datasets that span long periods of time. A disclosive view is one that *must* incorporate time depth because those who adopt it assume that contingency matters (sensu Gould 1986). Since ecosystems evolve, contingency applies (Landres 1992). In

Borgmann's (2000:104 and 105) words, an understanding of contingency "restores a sense of depth" and encourages "reverence" for humans' fleeting lives because "through geology [and other forms of evolutionary or historical science] we come face-to-face with powers that dwarf whatever strength and skill we may claim for ourselves." Borgmann (2000), Oelschlaeger (1991, 2000), and other environmental philosophers argue that what is missing in our modern global society is a sense of reverence. For if we had reverence for the processes and products of evolution, we would more fervently prevent human impacts of evolutionary significance. Paleozoology, like ecology, can contribute extensively to environmental science by providing datasets that explore contingency, and by doing so it helps support a disclosive perspective and the reverence for life, environment, and evolution that such a perspective offers.

Future Directions in Central Texas Paleozoology

That contingency is centrally important in evolutionary change is exemplified by the fact that predator removal influences white-tailed deer in particular ways in different areas of eastern North America. Deer body size decreased in central Texas as conditions appear to be far more crowded today than during prehistory. Environmental carrying capacity in the region has declined during the historic period too, exacerbating the effects of crowding.

Large predators were similarly exterminated in other areas. The same comparison as made in Chapter 5 using white-tailed deer astragali sampled from the modern and prehistoric periods in central Missouri exhibits no statistically significant difference in terms of length and that modern deer are significantly larger in terms of thickness (Figure 6.1; Table 6.1). Hansen et al. (1997; Nixon et al. 1991) intimate that despite high population densities in north central Missouri, modern deer populations are not approaching carrying capacity largely because farming has created new, richer habitat and forage than existed during prehistory. Despite the fact that modern deer in Missouri are not stunted in the absence of predators, should it be argued that deer are not overabundant? Schmitz and Sinclair (1997; Sinclair 1997) suggest that deer overabundance is only of concern when populations approach environmental carrying capacity and potentially degrade habitat via overbrowsing, which might occur in managed or unmanaged populations. On the evolutionary time-scale, however, are the effects of predator eradication in Missouri any different than in central Texas? Clearly, visible body-size effects on deer differ between populations from the two regions, but this difference does not eliminate the fact that in Missouri—like in central Texas—much of the predator guild is missing.

Although the effects of predator eradication on white-tailed deer body size differ between the two regions, the effects on mesocarnivores should be relatively similar. That is, character release in the body size of mesocarnivores is as expected in Missouri as in Texas. Why? Because character displacement is the result of closely related species living in closely related niches in the same area. Through time those species evolve, through competitive exclusion, to minimize direct competition for prey, and in carnivores this often results in differentiation along the body size gradient. When the large end of the gradient is spontaneously removed over a short period of time (e.g., via predator extermination), niche space is opened for the remaining carnivores and character release occurs (sensu Grant 1999). An important future direction then is to

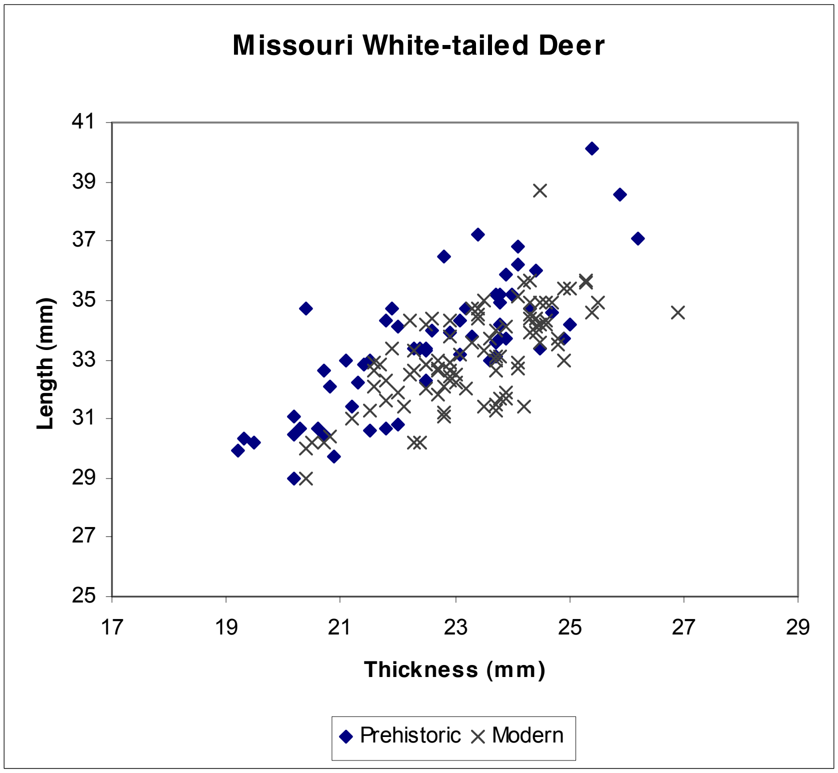

Figure 6.1 Prehistoric and modern white-tailed deer astragalus size in central Missouri (data from Wolverton 2001).

Table 6.1 Descriptive statistics and Student's *t* test results for Missouri white-tailed deer (mm).

Sample	Mean	Standard Deviation	Coefficient of Variation	n
Modern				
Length	33.49	2.27	6.79	59
Thickness	22.58	1.70	7.55	59
Prehistoric				
Length	33.15	1.60	4.82	97
Thickness	23.31	1.25	5.37	97
Modern vs. Prehistoric	*t*-statistic	*p*-value	$\Delta \bar{x}$ (%)	MSD (%)
Length	-1.11	0.134	0.34 (1.02%)	0.51 (1.52%)
Thickness	3.07	0.001	0.73 (3.23%)	0.40 (1.75%)

locate and study larger samples of prehistoric remains of coyotes and bobcats in Texas, but also in other areas such as Missouri in order to test whether or not this character release prediction holds. Larger samples are important because it is clear from comparison of Student's *t* tests used in this dissertation that statistical power is reduced using small samples (see analyses in Chapters 3 and 5). Paleozoological data are a logical choice, if not the only option, with which to further evaluate these relationships.

Conclusion

An evolutionary or paleozoological perspective on deer overabundance and predator extermination provides a unique lense through which to examine cause and effect of modern human culture on wildlife. Paleozoological datasets provide an opportunity to explore the evolutionary contingencies behind modern human impacts and to complement existing ecological studies. It has long been recognized that white-tailed deer in central Texas are overabundant and stunted, as well as damaging to existing habitat. Prior to this study little attention has been paid to how the modern whitetail population compares to that existing prior to Euro-American arrival in the region. It is important to recognize that because evolutionary causes and effects are contingency-bound no single study, such as this one, explores the evolutionary significance of deer overabundance in all areas (e.g., eastern North America). Rather, the paleozoological record should be studied at spatial and temporal scales relevant to particular research problem-orientations.

A disclosive perspective provided by studying deep time (sensu Borgmann 2000; McPhee 1998) is a powerful addition to environmental science; however, the most important impact of adopting this kind of evolutionary perspective is external to science. Humans' lives are too short to comprehend the long-term possibilities of environmental degradation unless particular attention is called to such effects. That said, the potential for environmental science, and science in general, to help solve global environmental issues is just now coming to fruition. Regional ethnocentrism works against a global perspective, but in its pursuit of objectivity science pulls people together in that it transcends such ethnocentrism (sensu Dunnell 1982). In this age, it is important not to ignore any potential dataset or perspective that potentially contributes to raising environmental consciousness and awareness; paleozoology is one such perspective.

APPENDIX A

MORPHOMETRIC DATA ON MESOCARNIVORE MANDIBLES

Data in this appendix relate to material covered in Chapter 3. All carnivore specimens included in this analysis are curated at the Texas Memorial Museum, Vertebrate Paleontology Laboratory (VPL) in Austin, Texas. Data collection took place during multiple visits to the VPL from 2004 to 2006; the author recorded all of the measurements. Prehistoric and modern bobcat (*Lynx rufus*) and coyote (*Canis latrans*) mandibles were measured using Swiss Precision SPI Dialmax calipers; large felids and canids were measured during a later visit using Mitutoyo Digimatic calipers (Model CD-6). Measurements follow those illustrated in Figure 3.1. Table A1 records data on prehistoric and modern canids, and Table A2 lists data for prehistoric and modern felids. County locations without state designation are in Texas; a few canid specimens were recovered in New Mexico (e.g., a dire wolf and three prehistoric coyote mandibles). Two of the large Pleistocene felid specimens (*Panthera onca* and *P. atrox*) are casts of the original mandibles, which is highlighted in Table A2; location data on Old World cats are unavailable.

Table A1 Canidae

Specimen	Thickness (mm)	Width (mm)	Location
Modern Coyote			
M1031	16.9	7.7	Brewster
M1037	16.2	7.6	Presidio
M1053	18.8	8.1	Brewster
M1069	17.2	8.6	Wichita
M1070	18.2	7.8	Wichita
M1091	23.2	9.9	Wichita
M1615	19.5	9.5	Hays
M1659	18.8	9.1	Presidio
M1660	17.8	7.9	Presidio
M1752	19	9	Anderson
M1756	19.8	9.1	Presidio
M1758	21.9	10.3	Presidio
M1775	18.9	10.2	Hill
M1776	19.7	10.3	Hill
M1777	20.2	8.5	Hill
M1781	20.1	10.4	Hill
M1860	20.7	8.8	Travis
M1959	17.2	9	Brewster
M1961	18.9	9.3	Brewster
M1962	19.2	8.3	Brewster
M1964	16.3	7.9	Brewster
M1965	18.3	8.6	Brewster
M1971	17.5	8.5	Presidio
M2046	18.3	8.8	Brazos
M2046	18.56	9	Brazos
M2073	20.37	9.48	Bexar
M2090	16.97	8.09	Presidio
M2207	18.74	8.92	Brewster
M2227	18.18	9.26	Brewster
M2327	18.42	8.77	Brewster
M2353	19.02	9.48	Presidio
M2358	17.32	8.02	Presidio
M2360	18.54	8.45	Presidio
M2409	17.21	8.13	Fayette

M2529	16.59	8.53	Pecos
M2530	18.33	8.73	Pecos
M2534	18.46	8.1	Pecos
M2541	19	8.71	Pecos
M2542	18.32	8.97	Pecos
M3357	17.86	8.57	Presidio
M3359	22.31	10.24	Colorado
M3381	21.51	9.57	Colorado
M3383	23.85	10.84	Menard
M3972	23.32	9.47	Bastrop
M3977	18	8.6	Bastrop
M3978	17.75	8.13	Bastrop
M3981a	19.01	9.84	Bastrop
M3981b	19.22	9.06	Bastrop
M3983	17.79	9.1	Bastrop
M4004	18.64	8.75	Bastrop
M4005	18.82	7.99	Bastrop
M4072	18.81	8.93	Bastrop
M441	16.6	8.4	Hays
M442	17.9	9	Hays
M444	17	8.8	Hays
M6336	16	7.6	Knox
M702	16.9	9.2	Wichita
M7307	18.5	8.3	Culberson
M732	19.1	10.5	Henderson
M791	17.1	7.1	Val Verde
M823	19	8.8	Val Verde
M921a	18	8.3	Knox
M921b	16.5	8.5	Knox
M965	17	9.3	Travis
M989	18.5	8.6	Brewster
M997	17.1	7.9	Presidio

Prehistoric Coyote			
40452-40	19.1	8.6	Delta
908-4324	16.8	8.1	Uvalde
908-4325	16.3	8.4	Uvalde
908-1084	17.6	8.3	Uvalde
933-2454	17.6	9.4	Bexar
933-3563	16.1	8.8	Bexar
933-670	19.4	10	Bexar
933-3398	16.8	8.8	Bexar
933-1622	16.5	8.3	Bexar
40449-68	18.2	9	Travis
40848-496	17.6	7.5	Val Verde
220-36	14.2	7.9	Jesse Cox Ranch, unknown
41228-136	18.1	9.4	Eddy, New Mexico
41228-137	20.5	9.4	Eddy, New Mexico
41228?	17.3	9.6	Eddy, New Mexico
40685-380	17.7	9.7	Mason
40685-379	19.3	9.1	Mason
Wolf and Dire Wolf			
M6540L (wolf)	32.94	14.75	Unknown
M6540R (wolf)	31.06	14.58	Uknown
933-1907R	39.05	21.05	Bexar
933-2L	38.91	18.97	Bexar
1193-6/210R	33.87	16.03	Roosevelt, New Mexico
30967-300L	40.66	18.31	San Patricio
30967-300R	40.83	18.01	San Patricio
31021-4R	38.27	17.64	Rancho La Brea, California
31021-5L	36.59	16.06	Rancho La Brea, California
40449-563L	32.78	17.48	Travis

Table A2 Felidae

Specimen	Thickness (mm)	Width (mm)	Location
Modern Bobcat			
369	15.3	7.2	Kerr
375	14.2	6.8	Kerr
653	16.8	7.4	Kinney
819	15.7	6.5	Val Verde
820	16.6	8.8	Val Verde
863	13.2	6.4	Motley
1076	13	6.1	Val Verde
1808	14.9	6.4	Brewster
1809	14.6	6.7	Brewster
1811	14.3	6.8	Brewster
1889	15.7	6.8	Cent. Tex.
2049	14.4	7.6	Hudspeth
2092	16.6	8.2	Presidio
2111	16.4	8.4	Brewster
2423	15.7	7	Menard
2604	16.9	8.5	Travis
2604	17.3	8.5	Travis
2605	14.6	7.1	Williamson
2649	14.3	7.4	Burnet
2649	14.2	6.8	Burnet
2656	13.3	6.2	Uvalde
2657	16.3	7.5	Uvalde
2658	16	7.1	Uvalde
2801	14	6.3	Williamson
3356	15.2	7.6	Presidio
3422	16.7	7.9	Menard
3914	14.9	7	Pecos
3915	16.2	7.6	Travis
4746	14	6.7	Travis
4747	14.1	6.8	Lee
4748	15.3	7.6	Atascosa
4749	15.4	8.5	Washington
4750	14.3	7.2	Bastrop
4751	15.4	6.8	Caldwell

4752	14.5	6.7	Gonzalez
4753	15	6.5	Val Verde
4757	15.3	7.1	Caldwell
4758	15.5	7.5	Caldwell
4762	15.9	8	Fayette
4764	16	7.4	Atascosa
4765	14.2	6.6	Caldwell
4767	14.1	6	Caldwell
4769	16.2	7.8	Webb
4774	16.9	8.6	Lee
4775	13.8	7.2	Caldwell
4776	16.1	7.7	Webb
4777	15.1	7.1	Webb
4778	14.1	6.7	Webb
4780	13.6	6.9	Webb
4782	15.3	8.4	Webb
4785	14.3	7.9	Colorado
4786	15	7.2	Duval
4789	15	6.3	Colorado
4790	15	7.8	Bastrop
4791	15.1	7	Williamson
4792	14.9	6.9	Caldwell
4793	13.6	6.7	Lee
4794	15.5	7.7	Hays
4795	14.1	7	Williamson
4797	15	7.2	Hays
4799	15.2	6.5	Williamson
4801	12.3	6.1	Live Oak
4802	13.5	6.1	Milam
4804	14.2	6.6	Fayette
4805	16.1	8.4	Fayette
4807	13.4	6.7	Travis
4812	15	6.6	Val Verde
4847	15.3	7.2	Lee
4965	15.1	7.1	Caldwell
4966	15.8	8.2	Fayette

4967	14.6	6.5	Travis
4968	16.8	8.7	Burnet
4969	14.5	7.4	Webb
4970	16.8	7.6	Fayette
6012	15.2	7.3	Caldwell
6992	16.2	7.5	Llano
7310	15.6	7.6	Texas
Prehistoric Bobcat			
908-4179	15.1	7.3	Uvalde
908-4181	13.5	6.8	Uvalde
908-85	13.7	6.4	Uvalde
908-3476	12.5	7.5	Uvalde
908-4180	15.1	7.1	Uvalde
4050-1600a	14.2	7.8	Kendall
4050-1600b	14.1	7.3	Kendall
4050-584	14.4	6.5	Kendall
40848-414	13.4	6.6	Val Verde
40848-415	14.2	6.5	Val Verde
Old World Felids			
Panthera pardus *(leopard)*			
M2016L	27.87	11.87	
M2016R	26.46	11.13	
P. leo (lion)			
M916L	40.86	17.94	
M916R	41.81	17.9	
P. tigris (tiger)			
M6574L	39.02	17.66	
M6574R	39.56	18.48	

Late Pleistocene Felids			
Panthera onca *(jaguar)*			
MZ41357-1L (cast)	41.06	17.28	Perry, Missouri
P. atrox (N. Amer. Lion)			
31021-22L (cast)	50.11	24.44	Rancho La Brea, Ca.
Homotherium serum			
933-2456L	41.1	17.45	Bexar
933-1233R	43.7	20.11	Bexar
Smilodon fatalis			
30967-198R	43.63	20.33	San Patricio

APPENDIX B

FORT HOOD WHITE-TAILED DEER DRESSED WEIGHT DESCRIPTIVE STATISTICS

Data in this appendix correspond to analyses presented in Chapter 4. Table B1 lists dressed-weight data for all deer harvested from Fort Hood from 1971 to 2005. Table B2 is a record of dressed-weight data for 1.5 year-old bucks from the same period, and Table B3 is the corresponding table for 1.5 year-old does. Table B4 records dressed-weight data from 1990 and 1991 for the East Region of the fort, Table B5 for the West Region, and Table B6 for West Fort Hood.

Table B1 Descriptive statistics for Fort Hood white-tailed deer dressed weight 1971 – 2005.

Year	Mean	Standard Deviation	Coefficient of Variation	n
1971	60.35	18.15	30.07	2712
1972	56.60	16.49	29.14	2120
1973	59.10	17.34	29.35	1575
1974	66.91	17.22	25.74	852
1975	55.14	16.57	30.05	2602
1976	58.42	15.54	26.61	1472
1977	54.47	14.67	26.92	842
1978	61.20	17.14	28.02	286
1979	64.96	20.33	31.29	414
1980	65.87	18.95	28.77	417
1981	66.46	17.57	26.43	447
1982	60.77	16.74	27.55	544
1983	60.81	19.02	31.28	563
1984	60.27	16.47	27.32	678
1985	61.87	16.21	26.20	828
1986	64.10	16.98	26.49	890
1987	57.24	16.35	28.57	894
1988	61.08	18.11	29.65	516

1989	64.68	20.30	31.39	503
1990	68.93	19.83	28.77	446
1991	66.70	20.69	31.02	533
1992	72.52	18.87	26.02	371
1993	73.39	18.25	24.87	379
1994	73.85	19.35	26.21	487
1995	71.87	20.10	27.96	572
1996	73.20	18.29	24.99	541
1997	75.89	23.81	31.37	269
1998	78.68	20.73	26.35	307
1999	74.33	20.79	27.97	400
2000	77.76	20.72	26.65	432
2001	75.69	20.55	27.15	455
2002	75.54	20.58	27.24	497
2003	79.54	22.00	27.67	352
2004	84.77	21.65	25.54	358
2005	83.55	23.82	28.51	253

Table B2 Descriptive statistics for 1.5 year-old Fort Hood whitetail bucks dressed weight 1971 – 2005.

Year	Mean	Standard Deviation	Coefficient of Variation	n
1971	63.15	8.33	13.20	514
1972	58.12	9.93	17.08	414
1973	62.88	8.07	12.83	416
1974	61.09	9.01	14.76	451
1975	58.30	7.74	13.28	489
1976	61.98	7.48	12.06	329
1977	57.24	7.67	13.39	97
1978	58.34	8.65	14.82	73
1979	60.82	8.28	13.61	89
1980	62.85	9.36	14.89	102
1981	68.51	7.83	11.43	102
1982	61.11	8.19	13.41	156
1983	61.59	8.81	14.30	81

1984	61.73	9.53	15.44	119
1985	61.87	8.67	14.01	134
1986	65.14	8.17	12.54	186
1987	64.79	8.91	13.75	150
1988	63.59	8.77	13.78	83
1989	65.21	9.22	14.14	75
1990	67.00	9.15	13.65	99
1991	68.61	8.81	12.84	119
1992	69.09	9.12	13.20	139
1993	71.46	7.17	10.03	102
1994	73.74	8.25	11.19	148
1995	70.76	8.26	11.67	129
1996	70.43	8.98	12.75	139
1997	67.78	10.72	15.81	60
1998	75.33	9.02	11.98	123
1999	70.64	9.06	12.82	87
2000	71.10	8.63	12.14	94
2001	74.86	9.05	12.09	76
2002	73.48	7.48	10.19	80
2003	74.71	9.60	12.84	49
2004	75.62	9.03	11.95	52
2005	73.69	6.81	13.61	49

Table B3 Descriptive statistics for 1.5 year-old Fort Hood whitetail does dressed weight 1971 – 2005.

Year	Mean	Standard Deviation	Coefficient of Variation	n
1971	55.78	7.15	12.81	310
1972	51.38	9.23	17.96	263
1973	55.38	6.30	11.37	170
1974	no data	no data	no data	no data
1975	52.90	6.82	12.88	356
1976	56.03	5.74	10.24	217
1977	51.07	6.51	12.75	112
1978	51.09	8.81	17.24	34
1979	50.07	7.81	15.60	41

1980	53.63	9.29	17.32	41
1981	56.76	5.85	10.31	46
1982	54.85	6.18	11.26	61
1983	55.57	7.05	12.69	61
1984	61.73	9.53	15.44	119
1985	54.73	6.43	11.76	100
1986	56.00	5.58	9.96	91
1987	54.50	6.63	12.17	139
1988	56.28	7.18	12.77	76
1989	55.07	5.77	10.48	61
1990	55.63	5.09	9.14	43
1991	56.02	8.97	16.01	44
1992	56.57	7.79	13.76	35
1993	60.90	5.53	9.08	31
1994	60.60	6.86	11.32	53
1995	58.00	6.55	11.28	54
1996	57.48	6.35	11.04	46
1997	52.06	5.12	9.83	16
1998	56.57	5.28	9.34	23
1999	57.52	7.89	13.71	31
2000	54.25	5.32	9.81	16
2001	59.21	7.11	12.00	42
2002	59.13	7.69	13.01	46
2003	60.33	6.45	10.68	21
2004	60.83	8.35	13.72	18
2005	58.87	8.01	13.61	23

Table B4 Descriptive statistics for East Region Fort Hood whitetail dressed weight 1990 & 1991.

Age (years)	Mean	Standard Deviation	Coefficient of Variation	n
Bucks				
0.5	40.63	4.61	11.36	24
1.5	71.04	7.772	10.87	98
2.5	83.77	11.66	13.92	44
3.5	97.00	13.92	14.35	36
4.5	100.57	16.90	16.81	23
Does				
0.5	37.78	5.00	13.22	32
1.5	57.60	6.38	11.08	37
2.5	64.87	6.61	10.19	46
3.5	67.57	6.70	9.92	35
4.5	65.80	5.69	8.65	20

Table B5 Descriptive statistics for West Region Fort Hood whitetail dressed weight 1990 & 1991.

Age (years)	Mean	Standard Deviation	Coefficient of Variation	n
Bucks				
0.5	41.43	7.95	19.19	14
1.5	68.85	6.80	9.88	61
2.5	87.58	11.95	13.64	38
3.5	99.21	15.46	15.58	28
4.5	105.89	9.61	9.08	9
Does				
0.5	35.75	6.79	18.99	24
1.5	57.81	8.61	14.90	21
2.5	65.46	6.79	10.37	33
3.5	65.91	6.75	10.25	21
4.5	69.00	5.39	7.81	5

Table B6   Descriptive statistics for West Fort Hood whitetail dressed weight 1990 & 1991.

Age (years)	Mean	Standard Deviation	Coefficient of Variation	n
Bucks				
0.5	37.00	7.63	20.63	17
1.5	61.61	9.81	15.92	59
2.5	79.72	12.31	15.44	29
3.5	84.33	13.83	16.40	18
4.5	94.5	15.36	16.26	8
Does				
0.5	30.42	6.92	22.76	24
1.5	52.14	5.99	11.48	29
2.5	57.61	7.51	13.04	33
3.5	57.92	8.50	14.67	25
4.5	59.43	6.53	10.99	7

APPENDIX C

Odocoileus virginianus MODERN AND PREHISTORIC ASTRAGALI DATA

Modern astragali were collected on two trips to Fort Hood at the game warden station by the author in 2005; astragali from deer 1.5 years and older were collected. Gaps in the dataset reflect deer that were checked in before or between the two collection-visits or represent deer killed by hunters who did not wish to participate in the project. Specimens from the unmanaged population in Travis County were collected during unselective culling by Orion Research and Management Services, Inc. during the 2005 season. Measurements taken on the astragali are illustrated in Chapter 5 (Figure 5.4). Modern astragali were measure using Mitutoyo Digimatic calipers (Model CD-6); prehistoric specimens were measured at an earlier date using Swiss Precision SPI Dialmax calipers. Table A3.1 catalogues the Fort Hood sample, Table A3.2 is a record of the unmanaged Austin sample, and Table A3.3 lists the astragali measurements for prehistoric deer from central Texas. Prehistoric specimens are curated at the Texas Memorial Museum, Vertebrate Paleontology Laboratory in Austin Texas in 2005 and 2006. Astragali from modern deer used in this study are curated at the University of North Texas, Laboratory of Zooarchaeology.

Table C1

Managed Specimen	AST1	AST2	AST3	AST4	AST5	AST6	Sex	Dressed Weight (lbs)	Age (years)
Fort Hood (2005)									
61	21.7	33.64	28.56	23.54	36.69	21.42	Buck	81	2.5
62	22.62	37.06	31.88	24.9	39.05	21.96	Buck	117	4.5
63	21.97	35.5	30.98	23.69	38.69	21.77	Buck	112	3.5
64	20.45	34.54	30.29	22.83	37.43	20.69	Buck	72	1.5
65	21.86	35.03	30.85	25.03	38.58	21.01	Buck	119	3.5
67	21.12	34.83	29.42	23.46	38.77	21.6	Buck	83	1.5
68	22.16	36.15	31.51	24.29	38.8	21.4	Buck	123	5.5
69	22.44	35.21	31.37	24.54	38.13	22.39	Buck	75	1.5
70	20.56	34.59	29.78	22.58	37.3	20.58	Buck	108	2.5
71	19.84	33.38	29.19	22.87	35.69	19.9	Doe	79	2.5
72	21.33	34.72	30.08	23.61	36.44	20.31	Buck	75	1.5
73	22.92	35.18	31.08	25.07	38.38	21.37	Buck	69	1.5
74	22.07	33.89	28.99	22.42	34.98	19.02	Buck	55	1.5
75	20.02	33.7	28.85	22.21	35.29	19.87	Doe	59	1.5
76	20.19	33.69	29.11	23.4	36.98	20.22	Buck	106	4.5
77	21.55	34.61	30.18	23.98	37.18	20.94	Buck	86	2.5
78	21.88	33.96	29.57	24.51	37.12	21.09	Buck	99	2.5
79	21.07	33.81	28.34	22.32	35.78	20.83	Doe	59	3.5
80	21.11	33.72	29.82	23.09	36.12	20.83	Buck	72	1.5
82	20.01	33.14	28.52	21.1	35.92	20.09	Doe	59	1.5
83	22.77	35.62	30.98	25.62	38.5	21.63	Buck	115	3.5
84	20.91	35.25	30.71	23.44	38.07	20.79	Buck	114	3.5
87	22.39	35.73	30.88	24.06	38.46	20.94	Buck	102	2.5
88	19.55	32.23	27.88	20.99	33.92	18.97	Doe	75	2.5
89	18.85	31.27	29.27	21.99	33.69	18.74	Doe	69	2.5
90	20.58	34.28	29.17	23.26	33.2	19.92	Buck	83	3.5
91	23.89	36.68	32.92	25.07	38.26	21.69	Buck	132	8.5
92	22.45	35.13	31.15	24.33	38.84	20.52	Buck	95	2.5
93	21.99	35.07	30.62	22.73	37.33	21.16	Buck	83	1.5
94	21.73	35.92	31.86	23.87	38.83	20.94	Buck	103	2.5
95	22.56	34.49	29.74	22.88	36.19	19.88	Buck	112	4.5

96	21.41	33.92	30.74	23.98	37.25	20.85	Buck	125	2.5
98	18.14	31.61	27.54	20.13	34.24	18.01	Doe	59	2.5
99	20.48	32.37	27.67	21.36	31.8	19.49	Buck	82	2.5
101	21.04	34.36	29.41	22.74	36.84	20.51	Doe	67	2.5
102	21.98	33.48	29.09	22.19	34.46	20.63	Buck	71	1.5
103	21.45	34.99	30.75	24.39	37.44	21.68	Buck	94	3.5
104	20.03	33.26	28.29	22.22	36.13	20.45	Doe	70	4.5
106	20.51	33.76	28.76	22.49	35.46	19.88	Buck	68	1.5
107	21.3	34.6	30.31	22.93	37.8	20.31	Buck	77	1.5
108	19.87	34.49	29.5	23.76	35.43	20.41	Buck	71	1.5
109	20.47	32.81	28.31	20.77	34.7	19.43	Buck	100	4.5
110	21.42	32.67	28.97	22.58	35.61	20.1	Buck	69	1.5
111	21.21	35.26	30.3	23.88	36.99	20.8	Buck	107	5.5
112	22.15	35.58	30.88	23.69	37.5	21.34	Buck	80	1.5
113	20.21	32.61	29.8	22.29	34.74	19.08	Buck	77	2.5
114	19.86	31.77	28.2	23	35.6	20.46	Buck	70	1.5
115	23.22	36.93	32.5	25.88	40.21	21.89	Buck	141	4.5
116	21.78	33.35	29.34	24.59	35.6	21.55	Buck	109	3.5
118	20.63	32.37	27.44	22.28	34.9	19.25	Doe	58	1.5
119	18.68	32.89	29.6	22.73	36.27	20.01	Doe	83	3.5
120	19.03	31.82	27.68	21.53	33.62	18.61	Doe	60	1.5
121	22.68	37.08	32.89	25.47	39.76	21.06	Buck	97	2.5
122	21.35	35.87	30.72	23.76	37.29	20.91	Buck	84	1.5
123	20.92	35.47	31.18	23.25	38.1	20.16	Buck	81	1.5
124	19.76	33.07	27.86	22.1	35.34	19.03	Doe	74	3.5
125	22.35	36.65	33.21	24.34	39.45	21.22	Buck	125	3.5
126	21.25	36.35	31.88	23.79	39.04	22.38	Buck	129	3.5
127	22.84	37.9	32.86	23.59	40.75	23.14	Buck	85	1.5
128	21.35	35.3	31.93	23.73	36.96	21.14	Buck	117	3.5
129	21.29	35.03	30.25	23.59	36.64	20.38	Doe	73	2.5
130	21.31	33.9	29.56	23.06	37.04	20.79	Spike	64	1.5
131	19.04	32.19	27.36	22.89	34.2	18.35	Doe	60	1.5
132	19.92	35.05	30.05	22.73	37.3	19.91	Doe	57	1.5
135	21.75	34.87	30.06	21.37	36.72	20.86	Buck	76	1.5
136	22.84	38.3	33.38	24.53	40.83	22.48	Buck	83	2.5
137	21.89	35.63	30.37	24.16	37.53	20.29	Buck	81	2.5
138	20.58	34.67	30.1	23.42	37.06	21.36	Buck	99	4.5

139	22.28	35.66	30.71	24.66	37.58	21.4	Buck	112	4.5
152	20.56	32.69	28.33	22.98	35.82	20.17	Buck	98	3.5
238	19.55	32.09	28.96	22.06	35.58	18.75	Doe	60	4.5
240	22.21	34.85	30.58	24.28	37.69	22	Buck	128	5.5
241	22.25	34.13	30.25	23.17	36.31	20.99	Buck	113	4.5
242	20.4	36.08	30.8	21.77	37.54	20.24	Doe	71	3.5
243	21.56	34.84	30.46	24.71	36.92	20.98	Buck	73	1.5
244	19.75	32.64	28.29	21.81	35.57	19.86	Doe	69	3.5
246	18.71	32.06	28.02	21.03	33	17.79	Doe	50	1.5
247	21.23	35.87	30.25	24.04	37.9	21.82	Doe	70	3.5
249	19.43	30.73	27.19	21.88	32.65	19.4	Buck	63	1.5
250	21.59	35.22	30.56	23.93	36.81	20.72	Buck	112	4.5
252	21.51	32.82	27.97	22.67	35.52	19.53	Doe	74	5.5
253	20.42	32.65	29.09	22.08	34.87	20.54	Buck	94	3.5

Table C2

Unmanaged

Specimen	AST1	AST2	AST3	AST4	AST5	AST6	Sex	Dressed Weight (lbs)	Age (years)
Austin (2005)									
4058	19.23	32.45	27.93	22.26	33.97	19.14	Doe	60	1.5
5000	19.63	33.93	29.17	22.19	35.95	19.27	Buck	81	1.5
5001	20.43	34.43	30.51	23.15	37.4	20.55	Buck	92	2.5
5002	20.91	33.5	29.78	23.49	37.21	20.18	Buck	90	2.5
5003	21.34	33.77	28.84	22.38	35.91	20.53	Doe	74	6.5
5004	17.7	31.59	27.31	22.04	34.23	18.85	Doe	63	2.5
5006	18.12	30.53	25.67	20.07	32.51	18.89	Doe	62	2.5
5007	20	33.56	28.68	22.83	34.93	20.75	Doe	60	3.5
5009	19.09	32.24	28.15	21.95	34.76	19.47	Doe	66	5.5
5013	19.89	32.19	27.22	23.39	35.42	19.79	Buck	76	7.5
5015	20.86	33.45	28.57	22.02	35.29	20.26	Doe	58	3.5
5016	21.44	35.03	30.84	23.69	37.66	21.24	Buck	68	2.5
5017	20.4	35.08	29.31	23.79	37.39	20.7	Buck	92	3.5
5018	19	32.15	27.99	21.78	33.94	19.23	Doe	60	8.5
5020	20	33.17	28.12	23.52	35.03	19.92	Buck	80	2.5
5022	20.68	34.45	28.79	23.39	36.64	20.53	Buck	94	4.5
5024	21.32	33.93	30.05	23.56	36.8	21.37	Buck	100	3.5
5025	18.77	33.84	29.21	22.1	36.27	19.88	Doe	58	2.5

5026	20.94	34.02	29.35	22.88	35.66	20.3	Buck	70	1.5
5027	19.89	34.91	29.65	23.55	34.87	21.55	Buck	49	3.5
5028	19.15	32	27.95	22	32.82	18.53	Doe	56	1.5
5029	18.66	31.44	26.58	20.84	34	18.57	Doe	50	1.5
5030	18.77	31.54	26.8	21.06	33.92	19.23	Doe	66	3.5
5032	20.64	33.63	28.59	22.55	35.56	19.76	Buck	100	3.5
5033	20.57	33.12	29.35	22.24	35.42	19.92	Doe	58	1.5
5034	20.49	34.7	29.73	23.12	36.51	20.91	Doe	82	3.5
5035	20.1	34.17	29.44	22.87	36.14	20.31	Buck	54	1.5
5037	18.82	32.71	28.15	21.47	35.75	20.34	Doe	64	6.5
5038	18.32	30.95	26.69	21.26	32.05	18.94	Doe	72	8.5
5040	17.84	31.48	27.03	21.33	34.07	18.51	Doe	78	2.5
5041	19.38	33.41	29.96	23.08	36.16	20.24	Buck	82	1.5
5043	19.6	31.39	27.65	21.99	33.77	19.16	Doe	76	6.5
5044	20.31	35.31	31.01	24.11	37.44	20.69	Buck	70	1.5
5046	22.12	35.82	30.86	23.65	37.72	21.56	Buck	91	3.5
5048	19.89	33.14	27.63	22.66	35.12	19.69	Doe	74	2.5
5050	19.96	30.97	26.12	22.22	32.5	18.98	Doe	70	4.5
5052	20.27	34.1	29.28	24.37	37.18	20.55	Buck	74	1.5
5053	20.39	35.06	29.61	23.6	36.85	20.42	Doe	88	2.5
5054	21.7	35.55	29.39	23.89	37.04	21.37	Doe	86	2.5
5055	19.49	31.64	27.23	22.27	33.8	18.78	Doe	78	6.5
5056	20.71	34.42	29.77	22.53	36.46	20.82	Doe	80	3.5
5058	19.07	32.68	27.88	21.96	35.02	19.55	Doe	78	3.5
5059	20.5	33.9	28.66	22.49	34.91	19.43	Buck	94	1.5
5060	18.7	33.36	29.06	22.17	34.83	19.58	Doe	70	3.5
5061	23.16	37.77	32.7	25.89	39.46	21.07	Buck	128	5.5
5062	21.8	35.83	30.66	23.65	39.19	22.11	Buck	116	4.5
5063	22.18	35.31	30.79	23.25	37.15	20.5	Doe	54	5.5
5064	21.57	36.35	31.41	24.28	37.39	21.34	Buck	102	2.5
5066	20.57	35.18	30.24	23.55	36.94	20.71	Doe	77	3.5
5067	20.08	32.26	27.8	22.44	33.78	19.41	Doe	60	5.5
5070	19.76	34.76	29.42	23.12	36.75	20.2	Doe	68	4.5
no number	19.64	33.17	28.55	22.02	35.27	20.67	Doe	78	3.5
5005	19.94	34.23	28.82	22.94	36.08	20.3	NR*	NR	NR

* NR = “not recorded.”

Table C3

Prehistoric

Specimen	AST1	AST2	AST3	AST4	AST5	AST6	County
40425-122	20.6	34.5	29.5	24.5	37.6	21.3	Val Verde
40425-1228	21.1	34.4	29.4	22.6	36.2	21	Val Verde
40425-1229	20.8	34.2	29.2	22.8	36.1	20.7	Val Verde
4054465	21.1	34.6	30.8	23.7	37.2	20.4	Hill
405444	20.8	33.9	29	23.7	35.8	20.4	Hill
40544315	21.4	32.5	28.5	23	36.5	20.7	Hill
40544218	21.3	36.8	30.8	22.9	38.5	20.9	Hill
40544115	21	33.1	28.4	22.2	35.7	20.2	Hill
4054420	19.5	32.9	28.2	22	35.2	18.9	Hill
4054463	23	36.2	32.1	26.9	39.4	21.6	Hill
40544143	21.7	35.8	31.5	24	38.7	20.3	Hill
40544-317	19.8	32.3	30.7	22.4	34.8	20.9	Hill
40544-225	21.3	33.3	30.1	22.5	35.8	20.4	Hill
40544-115	22.5	34.5	29.1	23.8	36.5	21.3	Hill
40544-64	21.2	32.8	29.1	21.5	35.2	19.7	Hill
42198169a	21.4	35.7	28.8	24	36.7	20.4	Val Verde
42198169b	21.9	34.8	29.8	22.9	38.2	20.1	Val Verde
42198-1575	21	32.8	30.5	23.7	38	21.1	Val Verde
48123804	21.9	36.3	31.3	24.8	39	21.8	Uvalde
40534193	20.7	33.4	29.6	23.3	35.9	19.6	Hill
40534194	21.2	34.7	29	23	36.4	19.4	Hill
40534195	20.1	34	28.6	22.9	36.8	19.5	Hill
4128436	20.4	32.7	28.3	23	35	19.4	Hays
4128423	23.2	35.8	30.9	24.9	38.8	21.5	Hays
4320210	23.7	38.2	32.7	26	40.7	21.6	Coryell
4320211a	21.2	34.2	29.1	23.2	37	20.1	Coryell
4320211b	21.3	33.8	29.2	23.5	37.4	20.8	Coryell
4320249	22.8	36.3	31.2	24.5	39.7	20.8	Coryell
4320248	22.1	35.4	30.4	23.8	37.2	19.6	Coryell
40449-50	20.8	32.7	28.5	21.6	34.5	20.2	Travis
40449-107	19.7	33.7	29.4	22.3	36.8	20.6	Travis
908-120	19.8	31.8	27.5	22.4	34	19.5	Uvalde
908-3968	20.6	32.9	29.9	22.9	35.4	22	Uvalde

908-3969	22.3	36.7	32.5	24.7	39.9	21.6	Uvalde
908-3332	22.6	35.1	30.7	26.2	38.7	22.4	Uvalde
908-3970	22.2	36.4	31.8	25.3	37.9	20.9	Uvalde
908-3968b	23.3	36.8	31.8	24.1	38.7	21.6	Uvalde
908-3329	21.8	35.3	30.2	23.7	37.1	20.6	Uvalde
908-1566	21.8	34.4	31.1	20.8	38.5	20.9	Uvalde
908-130	21.9	33.6	29.1	24.4	36.7	20.7	Uvalde
908-3471	22.6	34.6	30.1	23.8	37.5	21	Uvalde
908-3971	20.4	34	30.1	23.6	37.9	20.2	Uvalde
908-153	22.4	34.5	31.5	24.7	37.9	21.3	Uvalde
908-492	22.4	36.2	31.6	24	38.6	21.2	Uvalde
908-357	17.9	30	26.4	20.7	32.8	18	Uvalde
908-2258	21.3	35.3	30.7	23.7	37	20.8	Uvalde
908-1601	21.2	34.7	30.7	22.1	37.6	21	Uvalde
43201-4	20.2	32.5	28.1	23.2	35.5	20	Coryell
41cm3-63	19.2	32.2	27.5	22.9	34.4	19.2	Comal
41cm3-69	20	32.3	27.7	22.8	35.2	19.7	Comal
41cm3-161	21.7	34.5	30.1	24.2	37.1	20.8	Comal
41cm3-134	21.9	No Data	29.3	24.2	37.9	20.9	Comal
41cm3-15	22.6	37.6	31.6	25.2	39.7	20.9	Comal
41cm3-140	20.6	33	28.6	23.8	35.2	20.9	Comal
41cm3-44	23.3	38	32.1	25.9	40.2	19.8	Comal
41cm3-165	19.4	32.4	28.2	22	35.3	19	Comal
41cm3-101	21.4	35.5	31.4	24.8	37.7	20.9	Comal
42198584	22.1	33.6	29.1	24.6	No Data	No Data	Val Verde

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