

THE INFLUENCE OF LOCAL FORAGE VARIABILITY ON WHITE-TAILED DEER

(Odocoileus virginianus) BODY SIZE AT FORT HOOD, TEXAS

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Nutritional quality and availability is thought to regulate geographic patterns of variability in animal body size due to phenotypic plasticity. The purpose of this study is to determine how vegetation quality, abundance and population density influence white-tailed deer (*Odocoileus virginianus*) body size on a subregional spatial scale at Fort Hood, Texas. Harvest and census records are used to test the hypothesis that white-tailed deer exhibit phenotypic plasticity (e.g. larger body size) in response to differences in vegetation quality and availability. Results from these analyses suggest that forage quality and abundance alone is not a main driver of white-tailed deer body size. Analysis of deer population density (generally) resulted in an inverse relationship with body size. Areas with high quality forage and low population density support larger deer while areas with low quality forage and high density support smaller than average deer. The few exceptions occur in areas exhibiting poor quality forage and low population density or high forage quality and high density. Results from this study suggest that continued overcrowding of deer within isolated areas may eventually lead to efficiency phenotypic conditions producing smaller sized deer. These results could prove useful in interpreting deer population responses to harvest management. For successful local management of deer, studies examining the combined influence of habitat variables (such as forage quality, abundance and population density) on deer health offer managers valuable information needed to establish annual harvest goals and understand deer-habitat relationships relative to carrying capacity.

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CHAPTER 1

INTRODUCTION AND BACKGROUND

White-tailed deer (*Odocoileus virginianus*, Zimmermann, 1780) is one of two species within the genus *Odocoileus* and is a medium sized deer with a wide distribution in North America. White-tailed deer is the most abundant and widespread of all the New World deer species with many genotypic and phenotypic variants throughout their geographic range (Heffelfinger 2011). There are 38 subspecies of *Odocoileus virginianus*, with many more being evaluated to distinguish between genetic, morphological and ecological characteristics. Most genotypic variants are due to isolation of deer populations, which resulted in genetic changes. However, many of the subspecies are considered unique due to phenotypic variations as separate deer populations adapt to local habitat, forage or climatic conditions (Strickland and Demarais 2000). White-tailed deer become smaller in body size towards the southern part of the United States and into Mexico.

White-tailed deer in Texas (*O. virginianus texanus*, Mearns, 1898) are famous for their large-antlered bucks but are smaller in body size compared to northern whitetails (Heffelfinger 2011). This is also the case at Fort Hood Army Base (FHAB) in central, Texas where deer have been managed through sport hunting since the mid-1900s. Deer management started at FHAB probably in response to an overabundant population due to reintroduction of native *O. virginianus texanus* in the mid-twentieth century (Wolverton 2008). High population density is thought to be the driving factor of diminutive deer body size within central Texas (Wolverton et al. 2007). Within Fort Hood, 1.5 year old white-tailed deer body size increased from 1971-2005, suggesting local populations became juvenile-dominated (Wolverton 2008). This coincides with

deer management strategies and has been shown to be closely correlated with a decrease in population density (Wolverton et al. 2007, Barr and Wolverton 2014). Those subregions with smaller deer indeed had higher population densities. However, other factors related to local habitat variation may influence deer body size at smaller spatial scales, such as between subregions at FHAB. Since local habitat quality varies across the landscape, some areas offer higher forage quality or availability to individual animals and may lead to higher growth and development, demographic rates and population density (Herfindal et al. 2006). Although variability in habitat and deer body size has been observed between two adjacent subregions of the fort (Wolverton et al. 2009a,b), variability among all subregions within the fort has yet to be evaluated.

This research summarizes quality, abundance, and distribution of forage for white tailed deer between subregions at FHAB and evaluates how body size relates to local vegetation. Since previous studies have shown differences in population density within the fort (Wolverton et al. 2007, Barr and Wolverton 2014), this research also evaluates how body size relates to deer density at the same subregional spatial scale. Based on these analyses, the research questions for this study are:

1. Does vegetation associated with white-tailed deer forage vary between subregions of FHAB?
2. How does deer body size relate to vegetation quality and abundance between subregions of FHAB?
3. How does deer body size relate to population density between subregions of FHAB?

Although broad landscape scale studies are important for understanding ecosystem dynamics, loss of resolution may overlook important population-specific influences at finer spatial scales

(Krausmann 1997:351). Spatial heterogeneity of habitat and animal populations within Fort Hood provides a unique opportunity to examine the influence of vegetation on deer body size and population dynamics at a smaller spatial scale. Analyses proposed here will provide wildlife managers with valuable information for management. For example, information concerning which areas support larger deer will help managers to decide where habitat and wildlife management strategies need to be implemented.

Factors Influencing Animal Body Size: A Literature Review

Many factors relate to variation in animal body size, including latitude, temperature, precipitation, home range, population density, and net primary productivity (NPP) (Davidson and Andrewartha 1948, Moran 1992, Pettoirelli et al. 2002, Toigo et al. 2006, Said et al. 2009, Wolverton et al. 2009a,b, Ramanzin and Sturaro 2014). One potential explanation for geographic patterns of variability in animal body size is based on observations that, for a particular species, body size increases with an increase in latitude. According to Bergmann's Rule, animals are larger in the colder climates or higher latitude of their geographic range than those of the same species in warmer climates or lower latitude. According to this rule, animal body size (growth rate) is regulated by temperature on the basis of conserving the animal's surface-to-volume ratio to prevent heat loss (Wolverton et al. 2009a). However, many species (e.g. arctic fox, coyote, black bear, jaguar, and white-tailed deer) do not fit this pattern (see Meiri et al. 2004, see Huston and Wolverton 2011).

Alternative hypotheses regarding these observed broad geographic patterns of animal body size have been developed. Valerius Geist (1987) showed that animal body size correlates

with latitudinal distribution of NPP and food availability during the growing season (referred to as “Geist’s Rule” (Huston and Wolverton 2011)). Wolf and cervid body sizes are larger in temperate regions with higher food availability and productive growing seasons compared to other regions (Geist 1978). Huston and Wolverton (2011) evaluate data (both modern and prehistoric) that support Geist’s Rule to suggest that animal body size is primarily regulated by “ecologically and evolutionarily relevant NPP” (eNPP) or the available food per individual animal during the growing season within a particular area. Further, their results indicate that the latitudinal geographic pattern of eNPP and animal body size is driven by both soil quality and the pulse of productivity within the growing season (Huston and Wolverton 2011). If the distribution of eNPP drives variability in animal body size, then the question remains if this is the case at different (smaller) spatial scales. Even between regions at approximately the same latitude (i.e., the United States), those regions with high plant productivity and available food support larger animals than regions with lower plant productivity (Huston and Wolverton 2011). Other factors (precipitation, topography and soil quality) relating to local habitat variability have been associated with differences in animal body size (Kie et al. 2005, Jones et al. 2010, Garner et al. 2011, Huston & Wolverton 2011, Lashley and Harper 2012, among others). First, it is important to review a fundamental mechanism by which size (or other phenotypic traits) can vary within a species, phenotypic plasticity.

Pfennig et al. (2010:1) define phenotypic plasticity as “the ability of a single genotype to produce multiple phenotypes in response to variation in the environment”. In 1904, R. Lauterborn first applied the concepts of phenotypic plasticity to describe the ‘seasonal polymorphism’ in plankton (which he coined cyclomorphosis) (Hutchinson 1967, Black and

Slobodkin 1987). Further, in 1909 R. Woltereck attributed cyclomorphosis in *Daphnia* primarily to changes in food resources (Whitman and Agrawal 2009). Variation in local environmental characteristics can cause differences in phenotypes between and among populations, influencing how individual organisms interact with the environment (Whitman and Agrawal 2009). Phenotypic plasticity is an evolutionary mechanism by which organisms are better able to respond (and adapt) to habitat, forage, or climatic conditions with beneficial phenotypic changes (DeWitt and Scheiner 2004:2). Such flexibility, or plasticity, is subject to (and influenced by) complex and dynamic environmental interactions. Geist (1978) not only linked ecomorphological traits (e.g. body size) to habitat variability, but also suggested that this variability caused epigenomic responses in individuals living in different habitats. Animals will exhibit a “maintenance”, or efficiency phenotype, when resources for maintenance and reproduction are sparse (Geist 1978). The idea is that less energy is used for body size (or low priority organs such as antlers) in order to maximize amount of resources for efficient reproduction. For example, does would select against mating with larger bucks (with larger antlers) because of the greater amount of resources needed to maintain these larger “luxury” characteristics. This can lead to higher deer population densities with diminutive sized deer. This is especially the case in small, isolated areas where dispersion to other habitats is unlikely or restricted. Alternatively, when resources are readily available due to limited competition (e.g. low population density) and offer adequate nutrition for growth, expression of a “dispersal” phenotype results in larger deer body and antler size. Environmentally mediated fluctuations that influence ontogenetic growth rates (e.g. body size) are “plastic” — the morphological characteristics may not be a permanent evolutionary change but instead a

response to environmental changes (Huston and Wolverton 2011). Specifically, local adaptation to a change in food productivity, quality and availability can directly affect phenotypic characteristics (such as body size), which is discussed in more detail below.

Plant productivity and availability

Ecologically and evolutionarily relevant NPP (eNPP) is an important environmental factor affecting animal growth rates during ontogeny and adult body size (Barr and Wolverton 2014). All living organisms require energy from food, which shapes their evolutionary biology and behavioral ecology (Southwood 1977). Energy availability is limited in environments by carrying capacity and/or population density (Huston and Wolverton 2011). It is thought that a major constraint on animal fitness (i.e. growth rate) results from a functional “trade-off” between the risk of predation and the energy required for foraging (Werner and Anholt 1993, Dmitriew 2011). When energy is limited, and any adaptive strategy leads to an energetic compromise (or “trade-off”), the expression of body size, growth rate, reproductive rate, and/or behavior can be affected (Southwood 1977). Differences in abiotic and biotic condition in an organisms’ habitat can result in variability in eNPP, which affects phenotypically plastic traits such as growth rate (Moran 1992, Ghilambor et al. 2007). Many habitat variables (e.g., temperature, precipitation, soil characteristics and elevation) determine the type and abundance of plant species (forage quality) available to animals and can be used as a measure of eNPP. However, it is important to determine how differences in diet (such as vegetation quality and availability) can affect animal body size (i.e. deer); these factors are discussed below. Once variables associated with diet are linked to body size, then further analysis of other variables associated with influence on vegetation (temperature, precipitation, soils and

elevation) can be evaluated to determine if eNPP is a main driver of body size at small spatial scales such as between subregions within FHAB.

Plant quality and abundance

An organisms' habitat is the area where it spends most of its life. A species' habitat is rarely continuous and is instead a mosaic related to different variables (Caughley 1977:57). Habitat variables that directly affect herbivore diets and nutrition are plant quality (nutrient content and digestibility) and plant abundance (quantity and accessibility). Since both plant quality and abundance vary seasonally, deer adjust their foraging behavior in order to meet nutritional needs. If a particular plant category is unavailable (or scarce) within the herbivores home range, then its diet will reflect higher than "normal" percentages of another plant category. If one or both of the above habitat variables are limiting, it can have a detrimental effect on deer nutrition resulting in smaller deer. Although no single plant species offers year-round nutrient levels for optimal deer growth and reproduction, some deciduous browse species provide higher levels of crude protein and digestibility (energy) for white-tailed deer than other plant species.

Many studies have evaluated how food availability affects animal growth rates. Meiri et al. (2004) found that brown bear body size is closely associated with proximity to food. Herczeg et al. (2012) found that food availability and predation were the two primary fitness traits affecting freshwater fish body size and growth rate, acting as important agents of both natural selection and phenotypic plasticity. Among ungulates, many studies have associated body size with habitat productivity. Bender et al. (2007) found that body condition of mule deer is linked to individual nutritional conditions in different habitats. Ramanzin and Sturaro (2014) found

that roe deer antler length and circumference (which were relative to both body mass and jaw length) are larger in regions with favorable climate and habitat conditions. Wolverton et al. (2009a) found that, even within a single region of the United States, body size of both modern and prehistoric deer is correlated with current agricultural productivity. Harmel et al. (1989) conducted a controlled experiment on managed whitetails in central Texas to determine the effect of genetics and nutrition on antler and body size. Those deer fed poor nutritional diets had lower body weights and smaller antlers. If the forage quality was later improved, antler development increased (however maximum body weight was never achieved). Their results indicate that body weight and antler characteristics respond in direct proportions to diet quality and are influenced by both genetics and nutrition.

Other factors

Some other habitat variables associated with vegetation thought to influence animal body size are soil characteristics and topography. Soil fertility, or soil nutrient content, has been closely linked with herbivore body condition, as it affects plant quality (Jacobson 1984, Jones et al. 2008, Jones et al. 2010, Garner et al. 2011, Huston & Wolverton 2011). Jones et al. (2010) used soil and forage quality as predictors of white-tailed deer fitness, such as body mass and antler score. Elevation, slope, aspect, distance to nearest water source, and direction of drainage also are thought to play roles in soil-nutrient flow, nutrient cycling, and successional trajectories of plant communities (Kie et al. 2005). As such, high quality soils may produce productive forage leading to rapid animal growth rate and large body size (Klein and Strandgaard 1972). Studies have shown that this is also the case in white-tailed deer (Jacobson 1984, Strickland and Demarais 2000). If results from this research suggest vegetation quality

and abundance influences deer body size at Fort Hood, then further analyses on other habitat variables (such as soil and elevation) can help determine if eNPP is a main driver of deer body size at finer (subregional) spatial scales. However, if results indicate that vegetation does not strongly influence deer body size at the scale observed in this study, other factors (such as population density) may be driving body size and will be further evaluated.

Population Density

Food availability and population density are interrelated. Animal population density affects the rate at which plant forage is available to individual animals (Kie et al. 1983, Wolverton et al. 2009a). Specifically, factors influencing herbivore population densities include intra- and interspecific competition, body condition and health, home range size, predation, sport hunting and anthropogenic disturbances (Klein and Strandgaard 1972, Kie et al. 1983, Pettoirelli et al. 2001, Nilsen et al. 2004, Keyser et al. 2005, Kjellander et al. 2006, Benhaïem et al. 2008, Simard et al. 2008, Wolverton 2008, Wolverton et al. 2012, Bonnot et al. 2013, Barr and Wolverton 2014, Garnick et al. 2014). Simard et al. (2008) evaluated feedback mechanisms in an insular population of introduced white-tailed deer. Their results suggest that hyperabundant population densities and over-browsing of quality forage led to modification of deer life history strategies to maintain reproduction at the expense of growth, leading to diminutive deer body size. Even at finer spatial scales, habitat patches (or areas) exhibiting spatial heterogeneity, such as variability in local habitat quality, can lead to differences in local animal population densities (Ye et al. 2013). Areas with higher habitat (or forage) quality and abundance may exhibit increased population densities on a local scale, particularly in fragmented landscapes. In areas with lower forage abundance, all available energy can be

channeled into growth such that as population increases, so too does the proportion of resource used for maintenance and growth (Caughley 1977:127). This results in over-browsing of available forage, leading to smaller body size. Population density spotlight surveys are done annually at Fort Hood, and this variable was examined to determine its effect on white-tailed deer body size among subregions of the fort. Wolverton et al. (2011) examined population density and deer body size between a managed population at FHAB and an unmanaged suburban population from west Austin, Texas. Those subregions with higher population density consisted of smaller white-tailed deer. Before evaluating how patterns of habitat variability can influence body size on a local (finer) spatial scale between subregions at Fort Hood, an understanding of the importance of scale in landscape ecology must first be established and is discussed below.

Landscape Ecology and the Importance of Scale

Interpreting how vegetation affects deer body size requires understanding the heterogeneity of the landscape (Turner et al. 1997). Landscape is defined as “an area in space that is heterogeneous” (Pickett and Rogers 1997:103) and is recognized at any scale. Studies in landscape ecology (and biogeography) regard spatial heterogeneity as an important causal factor in ecological processes (Pickett and Cadenasso 1995). Application of landscape ecological theories to management and conservation strategies is usually dependent on the spatial and hierarchical scale. *Scale* generally refers to “the resolution at which patterns are measured, perceived, or represented” (Milne 1998:33) and can be further divided into *grain* and *extent*. For example, vegetation type and deer density within a particular subregion (or

area) would represent the *grain* (“the finest level of spatial resolution available in a data set”, Wheatley and Johnson 2009). The individual subregion or deer home range within FHAB would describe the *extent* (width of the study area or duration of observation). These terms are also commonly used when applying fractal geometry to wildlife management strategies, which aims at describing patterns of observations across the landscape (Milne 1997, Ritchie 1997).

Wheatley and Johnson (2009) discuss how misconceptions of ecological processes occur when grain and extent are not clearly identified and used inconsistently across multiple scales, resulting in the inability to generalize processes across spatial scales. What is sometimes thought to be examination of processes at multiple scales is in actuality a multi-design study (observing phenomena in different ways within the same study) (Wheatley and Johnson 2009).

Examination of phenomena at different hierarchy scales (community versus population), as well as different spatial scales (coarse versus fine), is important for determining mechanisms responsible for observed patterns in wildlife (Milne 1997, Bissonette et al. 1997). A single mechanism may not explain patterns at every scale. Therefore, assimilating observations across many scales is important when developing predictive theories in ecology (Levin 1992). Simon Levin (1992) promoted the view that many ecological processes act at various spatial and temporal scales, thus generating patterns that may differ depending on the scale of the study. Further, clearly distinguishing between spatial and scalar observations is important as use of these two observational forms create ambiguity which may have unrealistic implications for wildlife management and conservation (Wheatley and Johnson 2009). This is especially important as current issues in ecology involve examining trends in global environmental change and its impact on populations and individual organisms (Chave 2013).

Theories in landscape ecology may offer wildlife and habitat managers compelling explanations when evaluating the influence of spatial heterogeneity on plant and animal interactions (Senft et al. 1987). Since forage quality and abundance often vary spatially across the landscape, large herbivores will forage on resources at several different spatial and temporal scales (Turner et al. 1997). In addition, animals make scale-dependent choices when it comes to habitat use and/or foraging (even down to selecting a specific portion of the plant to eat) (Turner et al. 1997), which varies seasonally. When evaluating how landscape variables are influencing animal growth and population densities, a fine scale approach may offer insights on how to successfully manage local populations. Petterroli et al. (2001) evaluated heterogeneity of habitat quality for roe deer (*Capreolus capreolus*) within a reserve in western France. Habitat with more abundant, higher quality forage correlated with higher densities and body weight of both fawn and adult deer. Fine-scaled spatial heterogeneity and available food affect life history traits within roe deer and are key factors in population dynamics (Petterroli et al. 2001, 2003). Similarly, White (1983) examined how reindeer foraging patterns influenced body mass. His results indicate that even small grazing patterns, such as preference of higher quality and availability of forage, can significantly affect ungulate performance and health (body mass). This study will examine the influence of habitat quality and population density on white-tailed deer body size within and among the subregions that serve as management units at Fort Hood. First, however, it is important to review the life history traits of white-tailed deer.

White-tailed Deer Life History Traits

White-tailed deer (*Odocoileus virginianus*) are ungulates found throughout North America. They exhibit various degrees of plasticity in response to local habitat conditions (Simard et al. 2008). An animal's body size is important to its physiology, ecology and life history and may exhibit various types of selection depending on its environment (Munoz et al. 2014). White-tailed deer anatomy and physiology generally correspond to degrees of local plant productivity and therefore can be highly predictable across regions (Heffelfinger 2011). Adult body size varies considerably according to region, habitat type and quality, subspecies, age, season and food productivity (Hesselton and Hesselton 1982, Sauer 1984, Geist 1998:268, Wolverton et al. 2009a, Ditchkoff 2011). As a paedomorphic species, white-tailed adults retain their juvenile physical characteristics (Ditchkoff 2011). White-tailed deer in Texas are sexually dimorphic; bucks contain antlers and are usually larger. Antlers are important sparring weapons necessary for rutting activity and, within Texas, reach maximum development around five years of age (Sims and Dillard 2013). Nutrition plays a major role in antler growth (Sauer 1984, Strickland and Demarais 2008) as mineral requirements (particularly for phosphorus) increase during antlerogenesis (antler development) (French et al. 1956, Grassman and Hellgren 1993). Studies also indicate that deer antler size decreases as population density and forage competition increases (Klein and Strandgaard 1972, Cook 1984).

Gestation in does lasts approximately 200 days (Hesselton and Hesselton 1982, Verme and Ullrey 1984, Ditchkoff 2011, Heffelfinger 2011). Younger does tend to have smaller litters due to competing demands of nutrients for growth and reproduction (Hesselton and Hesselton 1982, Verme and Ullrey 1984). While does usually reach maximum body size around two years

of age, bucks continue to increase in size until five years of age (Teer et al. 1965, Strickland and Demarais 2000, Ditchkoff 2011). Depending on habitat productivity, age of terminal growth in bucks is thought to relate to competition for mating opportunities (Hesselton and Hesselton 1982, Heffelfinger 2011). White-tailed deer have been found to live up to ten years, however in central Texas the average life span is five years.

Deer are ruminants with four chambered stomachs. As ruminants, they can digest complex carbohydrates with the help of symbiotic bacteria to aid in fermentation to obtain the energy they need for growth and survival (Verme and Ullrey 1998, Ditchkoff 2011, Heffelfinger 2011). White-tailed deer can modify the length of their gastrointestinal tract, which is influenced by body size, reproductive status, forage quality, and nutrient requirements (Ditchkoff 2011). Different plant species and parts of plants vary widely in nutritive value (Owen-Smith and Novellie 1982). Broadleaf herbaceous plants (forbs) and deciduous leaves and twigs (browse) contain a large portion of crude protein and digestible forage for whitetails (Armstrong and Young 2000). Mast consists of the fruit of the browsed plants (e.g. acorns, mesquite beans, prickly pear berries) and is an important source of nutrition for deer, especially during the fall season (Hesselton and Hesselton 1982). Secondly, graminoids (grasses, sedges and rushes; e.g., the “true grasses”) and forbs differ in palatability and nutritive value. Although deer will forage on both plant types, forbs have higher digestibility throughout the year than graminoids (Bellu et al. 2012).

White-tailed deer are concentrate-selector browsers; they are opportunistic generalists that are able to select the most nutritious foods available when the opportunity arises (Hesselton and Hesselton 1982). To be a successful opportunistic species requires 1) a high

reproductive rate, 2) early maturation, 3) rapid and effective long-distance dispersal, 4) hardiness to extremes in temperature and moisture, 5) plastic food habits, and 6) ability to deal with a great diversity of landscapes and predators (Geist 1998:266). Generalist foragers have highly flexible diet breadths (food types) that depend on the nutritional value of available browse (Sih 2004). Deer habitat within central Texas primarily comprises deciduous browse and secondarily forbs and most however the composition of their diet varies seasonally (Dillard et al. 2006). Browse consists of stems and leaves of perennial woody plants that are the preferred food for whitetails (Hesselton and Hesselton 1982, Armstrong and Young 2000). Woody plants are an important source of bedding, security and thermal cover for white-tailed deer (Fullbright 2011). Basic cover needs are 1) low growing vegetation to protect fawns from predators, 2) mid-level vegetation for escape cover from predators, and 3) over-story vegetation to protect deer from extreme weather (Armstrong and Young 2000).

Owen-Smith and Novellie (1982) propose a heuristic model to predict the optimal foraging behavior of ungulates. Depending on seasonal variability, they predict that the range of ungulate foraging behavior widens as food availability declines but when forage nutrient value falls below maintenance demands forage choice narrows. Within central Texas, white-tailed deer have been shown to be short-dispersers and are highly philopatric, staying near or returning to their home range (Wolverton et al. 2012). Except during breeding season, they generally live within a home range distance of approximately 2.5 km² (Dillard 2006). Landscape complexity (amount of edge) and productivity (habitat type) have a greater influence on size of home range and forage use than density (Walter et al. 2009). Dussault et al. (2005) found that during the summer, deer establish their home range in open habitat areas where accessibility

to forage abundance was higher. It is thought that this type of foraging behavior (or preference of habitat) may allow for reduced intra-specific competition for forage and can vary seasonally (Nilsen et al. 2004). Quinn et al. (2013) analyzed high-resolution GPS data to evaluate white-tailed deer habitat use within a fragmented landscape. Their results indicate that both sex and season influence home range of deer where bucks show a larger home range than does. This has also been shown to be the case for bucks within FHAB (Wolverton et al. 2012). Depending on habitat quality, bucks expand their home range in order to meet nutritional requirements to sustain larger body and antler size (Stewart et al. 2011).

White-tailed deer are considered mixed-browsed foragers and as such show resilience to habitat disturbances (Wemmer 1997:62), but studies show that within the array of available forage, white-tailed deer are able to feed selectively on browse of highest quality (Swift 1948, Klein 1965). Due to their small rumen they must feed every few hours (Ditchkoff 2011). Thus, as an opportunist animal, white-tailed deer will forage on plant species not widely recognized as deer food (e.g., cactus, fungus and lichen), especially during periods of food shortage (Hesselton and Hesselton 1982, Simard et al. 2008, Heffelfinger 2011). The quality of forage available influences white-tailed deer forage behavior (Hewitt 2001). As selective foragers, deer patch use decreases with a decrease in forage nutritional quality patches (Owen-Smith and Novellie 1982). White-tailed deer foraging behavior can have profound effects on local vegetation quality and availability. An understanding of deer life history traits, as well as factors that affect them, can aid in better management of deer populations while preserving important habitat for many other species, which is discussed in Chapter 2 below.

Summary

White-tailed deer exhibit substantial phenotypic plasticity in body size within and between populations. Understanding white-tailed deer life-history biology is necessary in order to determine how habitat variability affects traits such as reproduction, forage behavior and dispersal and, thus, overall deer health and survival. Foraging behavior has important implications on the quality and amount of nutrition and its effect on white-tailed deer body size. When large populations of deer occur in small areas over-browsing of available forage can result in body size diminution. Variability in white-tailed deer body size at FHAB has been studied at multiple spatial scales that relate to coarse-grained assessment of habitat (Wolverton et al. 2009a). Although there have been controlled studies of body mass and condition at smaller spatial scales (McCullough 1982, Kie et al. 1983, see summary in Huston and Wolverton 2011), particularly related to population density and harvest demographics, those studies that have been done on white-tailed deer focus on few general habitat variables (Kie et al. 1983, Jacobson 1984). Evaluating how local habitat variables affect deer life history traits, such as body size, can provide information to better manage deer populations at smaller spatial scales, translating to overall successful management strategies within FHAB.

The rest of this study is organized as follows. Chapter 2 examines how vegetation and deer body size varies across the fort and provides a summary of the quality and distribution of vegetation associated with deer forage within and among the management subregions of Fort Hood. In addition, deer population density across subregions of the fort is summarized. Data are analyzed to evaluate the influence of forage quality, abundance and deer population density on body size among subregions of the fort. Chapter 3 provides a conclusion based on

the results of this study as well as limitations, suggestions for further research and the implications for deer management at Fort Hood.

CHAPTER 2

FACTORS INFLUENCING DEER BODY SIZE AT FHAB

Environmental change, including climate change, can affect ecological and evolutionary processes (Ozgul et al. 2009). For example, changes in food availability can cause rapid phenotypic responses in animal populations, particularly in animal body size. Such changes in habitat (specifically in plant phenology) affect both phenotypic and demographic variability in animal populations (Ozgul et al. 2010). When there are large differences in forage quality and accessibility between regions, higher quality forage allows for less energy to be exerted on foraging and digestion, which can result in significant effects on body size in herbivores (Herfindal et al. 2006). Understanding how forage quality and availability affect white-tailed deer body size is important when implementing management decisions. For example, emphasis on habitat management to promote diversity of forage species year round becomes important in maintaining deer health. Habitat and management decisions are usually implemented at coarse scales due to the difficulty in managing forage quality (plant species) and availability (abundance). However, management decisions based on coarse scale analysis may not be successful at smaller spatial scales (Bissonette 1997).

Overabundant white-tailed deer populations have also been linked to diminutive body size (Teer et al. 1965, McCullough 1979, Kie et al. 1983, Geist 1998, Wolverton 2007, Barr and Wolverton 2014). Historically, white-tailed deer at FHAB have seen a decrease in population density with larger deer in some of the subregions as compared to other managed areas in central Texas, primarily due to heavy sustained harvest pressure (Wolverton et al. 2011). Previous research examined white-tailed deer body size and overabundance at FHAB

(Wolverton et al. 2009c, Barr and Wolverton 2014). They compared deer body size and density between the southern-most subregion (West Fort Hood) to the Northwest and Southwest subregions. West Fort Hood (WFH) had higher density and smaller deer when compared to the other two subregions. Therefore, further evaluation of density across all subregions of the fort and its influence on body size at a subregional scale is warranted.

The purpose of this chapter is to evaluate the variability of two variables known to influence white-tailed deer body size (vegetation associated with forage and deer population density) at a subregional spatial scale within FHAB. In order to determine how white-tailed deer body size is influenced by habitat; one must first assess the spatial patterns of vegetation associated with deer forage availability. Therefore, vegetation is summarized between subregions of the fort in order to assess the quality, abundance and distribution of forage available to white-tailed deer. Further analyses are performed to evaluate the influence of specific forage type and abundance on deer body size. If vegetation quality and abundance is an important driver of deer body size at FHAB, it is expected that those subregions with more abundant high quality forage will correlate with larger deer. Alternatively, other factors such as population density may have more of an influence on deer body size than vegetation. In order to determine how deer body size is influenced by population density at the same fine spatial scale, census data is summarized between subregions of Fort Hood. If results from this study indicate that those areas with higher population density contain smaller deer compared to lower density areas, then density may be the major driver of body size thus providing further support to previous studies at FHAB (Wolverton et al. 2007, Barr and Wolverton 2014). Since

forage availability and population density are interrelated, both factors together may contribute to the observed variability in body size at FHAB.

Study Area

The Fort Hood Army Base (FHAB) is part of an 87,890-ha (339 mi²) U.S. Army installation in Fort Hood, central Texas. FHAB is located in Bell and Coryell counties at the intersection of the Edwards Plateau and Cross Timbers ecoregions (Fig. 1). FHAB is located in Killeen, Texas approximately 97 kilometers south of Waco and north of Austin and encompasses three main military training (cantonment) areas. FHAB is divided into seven subregions consisting of 118 training areas that represent designated areas for military activity and field training (such as maneuver exercises, live weapons firing and aviation training). Two major airfields and several dirt landing strips are located within Fort Hood. For this study, a new subregional map further dividing three of the existing subregions (West Region, West Fort Hood and Live Fire) into separate north and south subregions was created to better assess relationships between habitat variability and deer body size at finer spatial scales (Fig. 2). The fort is open to public hunting and fishing as well as various outdoor recreation activities at Belton Lake Outdoor Recreation Area (BLORA). All areas within the fort have been managed for white-tailed deer since the mid-1900s, and harvest records have been kept since 1971 and include general location of kill, age, sex, field dressed body weight, and antler characteristics. US Highway 190 separates the northwestern and southwestern subregions of FHAB. The Cowhouse Creek runs west to east across the fort before emptying into Belton Lake.

A detailed description of the environmental setting at Fort Hood can be found in Teague and Reemts (2007), which is summarized here. Climate at Fort Hood consists of warm summers (July high 35.7 °C; low 21.4 °C) and mild winters (Jan high 16.2 °C; low 0.8 °C) with a majority of the precipitation occurring in July and December. Annual average precipitation at Fort Hood is approximately 84 cm with the wettest month of the year in May (approximately 11 cm). Soils consist primarily of mollisols and clay loam. Mollisols have dark, friable and thick A soil horizons that are high in organic humus and bases (such as calcium and magnesium), which are important for plant growth. These nutrients help to fertilize the soil making them the most productive of all soil groups (Bailey 1996:93). The landform topography in the FHAB consists of alternating flat valleys (elevation 175m) and limestone escarpments (elevation 370m). A prescribed fire program at Fort Hood aims to reduce encroachment of Ashe Juniper (*Juniperus ashei*) species in range areas, improve vegetation composition and improve wildlife habitats. Military training occurs over the entire fort except in those areas supporting two federally listed avian species where hunting and military training is prohibited. White-tailed deer populations at FHAB are managed in the context of conservation goals for these two federally listed birds: the black-capped vireo (*Vireo atricapilla*) and the golden-cheeked warbler (*Dendroica chrysoparia*). The Nature Conservancy currently lists Fort Hood as a priority conservation area and as such is managed to protect the habitat of those federally listed bird species (Cimprich and Kosteke 2006, Emrick et al. 2010). Over-browsing of important habitat by white-tailed deer is a concern for conservation efforts. Therefore, white-tailed deer management goals at Fort Hood are to produce high populations of deer with superior quality (in terms of body mass and

antler size for annual sport harvest) while maintaining optimal habitat to support deer populations and other species (Barr and Wolverton 2014).

Methods

In order to study white-tailed deer body size at FHAB, harvest data are summarized for each subregion to determine if size varies across the fort. To evaluate how habitat quality influences body size, vegetation data are summarized and classified according to forage type and abundance (proportion). Habitat indices are used as a proxy for measuring variability of poor quality habitat. All data were aggregated by training area and then summarized by subregion so that analyses were at a consistent spatial scale. The details of how vegetation and body size variability were analyzed are divided into three broad sections (white-tailed body size, vegetation quality and abundance, and habitat indices). Finally, census data are evaluated between subregions of the fort to determine the influence of population density on deer body size. A summary of results for each variable (vegetation or forage quality and abundance and population density) as well as deer body size are described below.

White-tailed deer body size

Subregions within FHAB are composed of smaller training areas. Deer harvest data are available for each of the training areas within the fort. Such data provide a unique opportunity to evaluate deer body and antler size on a fine spatial scale. Harvest data are collected annually during sport harvest season at designated check-in stations that correspond to the location (i.e. training area) where the deer was killed. Data used in this research was provided by the Fort Hood Directorate of Public Works, Natural Resource Management Branch (DPW-NRMB) and

consists of harvest date (season), location of kill (subregion and training area), sex, age (years), field dressed body weight (kg), and antler basal circumference (mm). Age is determined at check-in station using tooth wear and was categorized into specific age cohorts for this analysis. Field dressed body weight is the weight of the deer after being partially butchered (gutted) with all internal organs removed. Antler basal circumference (right antler, mm) is measured at check-in station and is the best representation of antler size for the available data. McCullough (1982) evaluated the relationship between antler characteristics to whole deer body weight and found a highly significant correlation of antler beam diameter with body weight. Field dressed weight and antler size are the most representative characteristics of deer body size in available harvest data and are used as proxies for white-tailed deer body size.

Harvest data were aggregated for the past 10 management years (2004 – 2013) in order to maximize sample size. Data collected for a particular harvest season (management year) are reported in the summer following the fall hunting season. For example, 2004 represents harvest season 2003-2004. White-tailed deer body size has been fairly consistent within age and sex cohorts over the past ten years at FHAB (Tab.1). Data from 1.5 year old bucks (yearlings), 2.5 year old bucks (adults), 1.5 year old does (yearlings) and 2.5 year old does (adults) are evaluated independently within and among the different subregions at FHAB. Since sample size for each age and sex cohort varies by subregion (less than 30 individuals in some subregions), normality is not assumed. Therefore, deer body size is assessed using non-parametric statistical analyses. Nonparametric descriptive statistics were utilized for weight and antler base to describe body size across subregions of FHAB. A Kruskal-Wallis (H) test is used to evaluate if white-tailed deer body size differs between subregions. In addition, Mann-

Whitney (U) pairwise comparisons with Bonferroni corrections were calculated to evaluate which of the subregions significantly differed in body size. Mann Whitney is the appropriate non-parametric test to compare differences between two independent samples when normality cannot be assumed (in this case, at least one sample size is smaller than 30).

Vegetation quality and abundance

Vegetation data for this analysis were obtained from the Fort Hood Vegetation Cover Map (The Nature Conservancy 2008) provided by the DPW-NRMB at Fort Hood, Texas. This vegetation map was originally hand-digitized from 2004 aerial imagery and later updated using 2008 and 2011 imagery. The cover map consists of a Geographic Information System (GIS) raster file where polygons (or parcels) of land were assigned to an association of vegetation based on both field data and imagery using the National Vegetation Classification System (Teague and Reemts 2007). Vegetation density is reported as the plant type (genus and species (when available)) per acre for each parcel. GIS (ArcGIS vs. 10.1) is then used to aggregate the parcels (patches) into forage types in order to calculate how much of each type of vegetation (acres) occurred in each training area. Relative abundance is used to summarize distribution of vegetation type (sum of vegetation type acreage/total acres) within each training area. After calculating vegetation abundance per training area (N = 118), vegetation is summarized by subregion (N = 9) so that the influence of each type of forage category on white-tailed deer body size could be further evaluated. For this thesis, vegetation data associated with white-tailed deer forage is based on vegetation type and abundance. A current vegetation map updating that of Teague and Reemts (2007) was created to illustrate the variability of habitat within and among the different subregions of FHAB (Fig.3).

In order to evaluate available forage for white-tailed deer among subregions at FHAB, vegetation is classified into four forage categories. Three of the categories represented the type of vegetation (i.e., forage quality) readily available to white-tailed deer: deciduous browse, shrubs and graminoids, respectively. The fourth category represents forage in disturbed or developed areas, which therefore provides poor quality forage for deer. Disturbed vegetation (bare ground) consists of <1% vegetation available to deer. Developed areas consist of all parcels labeled “developed,” including the main cantonment, recreational and airport landing strips. Since the main developed areas overlap subregions, these values were omitted from calculations of proportion of disturbed vegetation. The only parcel values used in analyses for this category are those identified in the Vegetation Cover Map as “disturbed vegetation” or “bare ground”. Table 2 provides a summary of the specific vegetation associated with white-tailed deer forage within FHAB as well as how they are classified for analysis. Nonparametric five points of data summary are utilized to obtain the relative abundance of each forage category to evaluate the distribution of vegetation among subregions at FHAB. A Chi Square (χ^2) test of contingency/independence is calculated to determine if vegetation significantly differs across subregions. Habitat (forage) type and subregion are used as the two categorical variables to evaluate if and how vegetation varies spatially across FHAB. A Spearman's rho (r_s) rank order correlation is calculated to determine the influence of proportion of forage type on deer body size.

Habitat indices

Habitat indices of white-tailed deer habitat are used as an ordinal measure of habitat variability in addition to proportion of vegetation (forage) type. Each index is used as a proxy of

forage quality representing the relative values of high and low quality vegetation: *Quercus*-dominated (QI), Graminoid-dominated (GI) and *Juniperus*-dominated (JI) and are calculated using the following formulas: (see Wolverton et al. 2009c).

$$\text{Juniperus Index (JI)} = \frac{\sum \text{Juniperus-dominated acreage}}{\sum (\text{Juniperus-dominated} + \text{Quercus-dominated})}$$

$$\text{Graminoid Index (GI)} = \frac{\sum \text{Graminoid-dominated acreage}}{\sum (\text{Graminoid-dominated} + \text{Quercus-dominated})}$$

A Spearman's rho (r_s) test is performed to determine the relationship between poor habitat (forage) quality and white-tailed deer body size (weight and antler size). In this way, the influence of poor quality forage (in relation to higher quality forage) on body size can be further evaluated. Since *Quercus* (oak) species are the preferred food for white-tailed deer and consist primarily of deciduous browse with some forbs and herbs, this category was considered the highest quality forage for white-tailed deer at FHAB. *Quercus* species are the most abundant forage at FHAB. *Juniperus* species are lower quality habitat for white-tailed deer and are found in lower abundance within FHAB. Graminoids (grasses) are foraged on primarily in the summer during drought conditions and are also associated with poor white-tailed deer habitat with limited availability within the fort. However, some vegetated areas classified as graminoid dominant are described as having a combination of more than fifty percent of graminoid, forbs and ferns. Forbs are flowering herbaceous plants that are not graminoids and may offer more digestible protein than deciduous browse during the summer season (Hewitt 2011).

Deer population density

Census data used in this research were provided by the DPW-NRMB, collected from annual spotlight surveys, daylight incidental reports, and harvest data. Data used for this study are averaged by subregion and consist of: acres per deer, does per buck, and fawns per doe. Does per buck and fawns per doe values relate to deer fertility. Census data are reported on a slightly coarser spatial scale than harvest data. West Fort Hood combines both the NWFH and SWFH subregions and Live Fire combines both the NLF and SLF subregions (see Fig. 2). Data encompassing all subregions studied in this research are only available for harvest seasons 2006 – 2014. Therefore analyses evaluating the relationship of vegetation to body size include data only from those reported harvest seasons. Spotlight data convey the number of deer seen and area surveyed (number of visible acres) (Shult et al. 1999). Spotlight surveys take place at night (to better see the reflection from a deer's eyes) with at least two observers using spotlights and binoculars taking visibility data at 1/10th mile intervals (Jester and Dillard TPWD). The same route is surveyed at least three times per year and before fall hunting season (mid-Aug to mid-September). One limitation of spotlight survey data consists of the chance occurrence of deer observations due to variability in habitat. For example, a high count of deer in areas with open grassland than in forested areas (thicker vegetation) may be due to deer are easier to spot in these habitats (DeYoung 2011). Since density estimates are ordinal scale at best, a Kruskal-Wallis (H) test is used to evaluate if white-tailed deer population density differs between subregions. In addition, Mann-Whitney (U) pairwise comparisons with Bonferroni corrections were calculated to evaluate which of the subregions significantly differed in population density.

Finally, a Spearman's rho (r_s) test was performed to determine the relationship between population density and white-tailed deer body size (weight and antler size) at FHAB.

Results

The results are divided into three broad sections: white-tailed body size, vegetation quality and abundance, and deer population density. The first section evaluates differences in white-tailed deer body size between subregions at FHAB. Bucks and does are reported separately and by age class (i.e. 1.5 year olds and 2.5 year olds) in order to eliminate any sex or age bias. The second section describes deer habitat foraging quality and abundance within FHAB. The distribution of vegetation type (deciduous browse, shrubs, graminoids, disturbed or developed) and abundance (proportion) is evaluated between subregions within the fort. Analyses examining the relationship between vegetation quality and abundance to deer body size are further assessed. The third section summarizes deer population density between subregions of FHAB and evaluates its relationship to body size.

White-tailed body size at FHAB

Descriptive statistics are reported for subregions of FHAB for white-tailed deer body size (field dressed weight and antler circumference) and are provided in Tables 3 and 4, respectively. Median field dressed weight (kg) and buck right antler basal circumference (mm) are used as proxies for body size and are reported separately for each cohort and by subregion. White-tailed deer body size varies among subregions for both bucks (Fig. 4) and does (Fig. 5). The Kruskal-Wallis H test indicates that there is a significant difference in the distribution of median deer body size (weight and antler size) among subregions of the fort ($\alpha = 0.05$). Body

size for all cohorts (1.5 and 2.5 bucks; 1.5 and 2.5 does) is significantly different between subregions of FHAB and is reported in Table 5. Mann-Whitney (U) pairwise comparisons with Bonferroni corrections were calculated to determine which pair of subregions significantly differed in body size ($\alpha = 0.05$). Each comparison tests the null hypothesis that the distributions in body size between those two subregions are the same. Significant differences between pairwise comparisons vary by subregion, age and sex. Therefore, pairwise comparisons between subregions with significant differences ($\alpha < 0.05$) are reported by cohort in Table 6 and summarized below.

Bucks (1.5 year old yearlings) — Results from the Mann-Whitney (U) pairwise comparisons test indicate that there are significant differences for 1.5 year old buck body weight between SWFH and two other subregions: SWR and SER. There was also a significant pairwise comparison between NWFH and SER. SWFH and NWFH have the smallest 1.5 year old bucks in the fort, while buck yearlings within SWR and SER are larger. Only two pairwise comparisons resulted in significant differences for 1.5 year old buck antler size (mm) between subregions. Both NWFH and SWFH median antler size were smaller when compared to SER.

Bucks (2.5 year old adults) — Results from the Mann-Whitney (U) pairwise comparisons test indicate that there are significant differences for 2.5 year old buck body weight between NWFH and six other subregions: SWR, NER, NFH, SER, NLF and SLF. NWFH have smaller deer compared to all of the above subregions. In addition, there is also a significant difference in weight between NWR and SLF. Within NWR, adult bucks are slightly below average size compared to the entire fort. NWFH deer have significantly smaller antlers compared to three other subregions: SER, NFH and SLF.

Does (1.5 year old yearlings) — Results from the Mann-Whitney (U) pairwise comparisons test indicate that there are significant differences for 1.5 year old doe body weight between NWFH and two other subregions: SER and SWR. Within NWFH, doe yearlings are smaller compared to those does in SER and SWR. Harvest data are not available for analysis within NWR and SLF.

Does (2.5 year old adults) — Results from the Mann-Whitney (U) pairwise comparisons test indicate that there is a significant difference for 2.5 year old doe body weight between NWFH and only one other subregion: SLF. NWFH have the smallest adult does in the fort, while SLF does are the largest. Harvest data are not available for analysis within NWR.

Results evaluating deer body size at FHAB indicate that size varies among many subregions of Fort Hood. Figures 4 and 5 illustrate the spatial distribution of median body size across FHAB for both bucks and does, respectively. In particular, NWFH deer are significantly smaller for all age and sex cohorts compared to other subregions. Examination of how vegetation and population density differ in NWFH compared to the rest of the fort may better explain why this particular area stands out, and is explored further in the discussion below.

Vegetation quality and abundance at FHAB

For this analysis, FHAB was divided into nine subregions covering 192,000 acres (77,700 hectares, 300 mi²) containing 89 military training areas. Table 7 provides a summary of the proportion (%) of available white-tailed deer forage classes and their distribution across the fort. Vegetation at FHAB associated with white-tailed deer forage primarily consists of deciduous browse (41%) and graminoids (39%). Shrubs make up less than a quarter of all vegetation within the fort (22%). Vegetation within disturbed and developed areas offers

limited forage availability to white-tailed deer and makes up only twelve percent (12%) of the fort. A Chi Square test of independence was performed to evaluate if vegetation associated with deer forage varies between subregions of the fort. The Chi Square test indicates that there is a significant association between the proportion of vegetation (forage) type and its distribution (or subregion) across FHAB ($X^2(24) = 37.75, p < 0.05$) with a small to moderate effect size ($\phi = 0.19$). The small effect size indicates that there is not a strong association between the frequencies of observed and expected distribution of median forage categories across the fort. The null hypothesis that the proportion and type of vegetation do not differ by subregion is rejected and is summarized below, but the differences are small.

The amount of deciduous browse was used as an indicator of high quality deer foraging habitat since many browse species offer adequate levels of crude protein, digestible energy and phosphorus year-round. Deciduous browse consists of stems and leaves of perennial woody plants and are the preferred forage for white-tailed deer (Hesselton and Hesselton 1982, Armstrong and Young 2000). Deciduous browse within FHAB consists primarily of *Quercus* species (oaks). Other plants classified as deciduous browse within the fort include *Carya illinoensis* (Pecan Hickory), *Ulmus* spp. (Texas Cedar and Slippery Elm), *Cephalanthus occidentalis* (Buttonbush), *Celtis laevigata* (Netleaf Sugarberry), *Platanus occidentalis* (American Sycamore), *Rhus lanceolata* (Prairie Sumac), *Juglans major* (Arizona Walnut), *Salix nigra* (Black Willow, and *Acer saccharum* (Sugar Maple) (Tab. 2). Five subregions within FHAB consist primarily of deciduous browse: SWFH (55%), SER (54%), NFH (40%), NLF (39%) and NWR (39%), and are all dominated with *Quercus* species (>50%). Forage within the NWR consists of almost an equal amount of deciduous browse and graminoid (Tab. 7). These five subregions are

considered the optimal subregions for white-tailed deer to forage. Therefore, it is expected that those subregions consisting primarily of deciduous browse, as high quality habitat, will support larger deer.

Shrubs are considered lower nutritional quality forage for white-tailed deer when compared to deciduous browse. *Juniperus* species (i.e. *J. ashei*) are the most common shrub species found at FHAB. NER and NWFH are the only two subregions consisting of higher than average *Juniperus*-dominated vegetation in proportion to high quality vegetation (*Quercus*-dominated) (Table 8). The only other plant species classified as shrub within the fort is *Prosopis glandulosa* (Honey Mesquite) (Tab. 2). Only one subregion consists primarily of shrubs, NER (45%), and those training areas with the highest amount of shrubs are all located within the far western part of the subregion. Therefore, it is expected that NER will have smaller deer compared to other subregions within the fort.

White-tailed deer at FHAB forage on graminoids (or grasses), primarily in the summer during drought conditions. Perennial grasses are relatively low in protein when compared to browse and forbs. Those plants within FHAB classified as graminoids include *Schizachyrium scoparium* (Little Bluestem), *Buchloe dactyloides* (Buffalograss), *Muhlenbergia reverchonii* (Seep Muhly) and other vegetation within the *Gramineae* family (which is identified as grassland with mulch and disturbed herbaceous vegetation (with some forbs)) (Tab. 2). Three subregions consist primarily of graminoids: NWFH (60%), SLF (49%), and SWR (46%) and have higher proportion of Graminoid-dominated vegetation compared to *Quercus*-dominated (Tab. 8). Again, NWR contains almost equal amounts of graminoid (39%) and deciduous browse (37%) (Tab. 7). Within SWR and NWR, over 95% of the graminoid vegetation consists of disturbed

herbaceous vegetation containing forbs whereas NWFH and SLF subregions consist of only 19% and 26%, respectively. Therefore, those areas with more abundant forbs may support larger deer compared to subregions with less forbs. Even though SWR primarily consists of disturbed herbaceous vegetation (46%), this subregion also has a fairly high amount of deciduous browse (40%) (Tab. 7). It is expected that those subregions consisting of primarily graminoids, as poor quality habitat, would have smaller deer.

The amount of disturbed or developed areas within each subregion can affect how much forage is available for white-tailed deer, which may indirectly influence deer body size. Disturbed areas within FHAB are generally classified as bare ground or developed. Disturbed and developed areas also include the main cantonments, recreational areas and landing strips/airports. FHAB is comprised of twelve percent (12%) disturbed or developed vegetation (forage) available to deer. NFH had the highest amount of disturbed and/or developed areas (17%) and has one of the smallest total areas within FHAB (6,917 acres) (Tab. 7). Only two other subregions consist of 10% or higher disturbed and/or developed areas: SWR (12%) and SLF (10%). Abundance and distribution of disturbed vegetation among subregions of the fort was evaluated to determine its influence on white-tailed deer body size.

Influence of habitat quality on deer body size

The Spearman's rho (r_s) rank order correlation test indicates that the proportion of disturbed and/or developed areas have a slight positive effect on body size at FHAB (Tab. 9). Disturbed and developed areas have a moderate positive effect on 2.5 year old doe field dressed weight ($r_s = 0.69$, $p = 0.04$) and only a weak (non-significant) positive effect on all other cohorts: 1.5 year old bucks ($r_s = 0.51$, $p = 0.16$), 2.5 year old bucks ($r_s = 0.47$, $p = 0.20$), and 1.5

year old does ($r_s = 0.43$, $p = 0.25$). None of the other forage categories are significantly correlated with deer body size. However, some forage categories exhibited a weak effect on body size (Tab.9) Proportion deciduous browse had a slight positive effect on 1.5 year old doe size and 2.5 year old buck antler size. NFH and SER have higher proportion of deciduous browse and *larger* than average adult buck antlers. In addition, these same two subregions have *larger* than average yearling does. In contrast, SWR and SWFH also have higher proportion of deciduous browse yet *smaller* than average deer (with the exception of NWR having no data reported for does). Proportion of graminoids had a slight negative effect on 1.5 year old does (Tab. 9). SLF and SWR have higher proportion of graminoids and larger deer (with the exception of SLF having no data reported for 1.5 year old does). NWFH also has higher proportion of graminoids and some of the smallest deer at FHAB. Although three subregions had higher than average proportion of shrubs (NER, NFH and NLF), none of the deer cohorts are significantly correlated to proportion shrubs. However, NER consists of 45% shrubs and has the highest JI index (indicating this subregion consists primarily of *Juniperus*-dominated vegetation (Tab. 8)) and smaller than average does, which is described in more detail below.

Although not significant at $\alpha = 0.05$, Spearman's rho rank order correlation test indicates that *Juniperus*-dominated habitat has a moderate negative effect on 1.5 year old doe body size ($r_s = -0.63$, $p = 0.07$) (Tab. 9). *Juniperus*-dominated habitat index (JI) was highest in NER and NWFH. These two subregions have *smaller* than average deer (with the exception of 2.5 year old bucks in NER, which are slightly larger than average but have smaller antlers). Graminoid-dominant habitat has a weak positive effect on 1.5 year old doe body size, although non-

significant. Graminoid-dominated habitat index (GI) was highest in NWFH and SLF followed by SWR, NLF and NWR, respectively.

Population Density at FHAB

Populations density at FHAB has been studied previously (Wolverton et al. 2011, Barr and Wolverton 2014), however not at a subregional scale. Table 10 provides a summary of the census data used in this study. WFH comprises NWFH and SWFH subregions. Similarly, LF comprises NLF and SLF subregions. The total population density at FHAB consists of one deer per 47 acres. Managers have known that WFH has some of the highest population density at FHAB (one deer per 30 acres), although NFH has an even higher population density (one deer per 14 acres). NER has slightly high population density (one deer per 44 acres) compared to total density. A Kruskal-Wallis test indicates that the distribution of population density ($N = 72$) significantly differs among subregions at FHAB (Table 11). A Mann-Whitney (U) pairwise comparison test with Bonferroni corrections was calculated to evaluate which of the subregions significantly differed in population density. Significant differences were observed for five pairwise comparisons and are reported in Table 12. Significant differences were observed between NFH and three other subregions: LF, SER and NWR. Again, NFH has the highest population density at FHAB and the other three subregions exhibit low population density. WFH population density was also significantly higher compared to LF. Fertility (does per buck and fawns per doe) did not significantly differ across subregions (Tab. 11). However, relative to the average across the fort, NER has more does per buck and SER, WFH and NFH have more fawns per doe (Tab. 10). Since population density significantly differs between subregions of

the fort, further analyses are examined to determine its influence on deer body size and are discussed below.

Influence of deer population density on body size

A Spearman's rho (r_s) test was performed to determine the relationship between population density and white-tailed deer field dressed weight at FHAB (Tab.13). Population density (deer/acre) has a weak, significant negative effect on 1.5 year old buck size ($r_s = -0.29$, $p = 0.02$). WFH (both NWFH and SWFH) have higher population density compared to most of the subregions and contain some of the smallest deer (i.e., 1.5 year old deer) in the fort. On the other hand, NFH exhibits the highest population density yet has larger than average deer. No other deer cohorts are significantly affected by population density (at $\alpha = 0.05$). Fertility (fawns/doe) has a strong negative effect on 1.5 year old buck size ($r_s = -0.44$, $p < 0.001$) and a small negative effect on 2.5 year old buck size ($r_s = -0.29$, $p = 0.02$). SER, WFH and NFH have the highest fawns per doe compared to other subregions (including the total) (Tab. 10). In addition, the number of does per buck has a weak negative effect on 1.5 year old does ($r_s = -0.36$, $p = 0.04$). NER has the highest number of does per buck compared to all other subregions and is the only subregion higher than the fort average (Tab.10).

There are a few significant results from this study to be addressed. In particular, there are stark differences between WFH and NFH compared to the other subregions at Fort Hood. The clear differences in vegetation, body size and population density at WFH and NFH provide the opportunity to compare extremes in habitat and population density on white-tailed deer body size at a finer spatial scale. Therefore, the results from these fine scaled comparisons

(including the analyses reported above) and the implications for deer and habitat management at FHAB are discussed below.

Discussion

White-tailed deer body size (i.e., field dressed weight and antler size) significantly differs between subregions within FHAB. The question is what drives (or has the most influence on) this localized spatial variability in body size? The discussion of the results from this study is divided into three sections. The first section discusses the influence of the proportion of forage quality on body size between subregions of FHAB. Habitat indices, as proxies of poor quality habitat, were used to determine the influence of relative forage quality and abundance on deer body size and are evaluated based on proportion of *Juniperus*-dominated (JI) and Graminoid-dominated (GI) habitat as compared to higher quality habitat: *Quercus*-dominated. The second section discusses the influence of deer population density on body size between subregions of the fort. Finally, the third section compares two subregions (NWFH and SWFH) within West Fort Hood as well as the northern most subregion of the fort (NFH). These three subregions represent the extremes of white-tailed deer body size, forage quality and population density at Fort Hood.

Influence of vegetation on deer body size

Even though pairwise comparisons between subregions resulted in some significant differences in body size (Table 8), there was not a clear relationship between habitat (forage) quality and white-tailed deer body size (Fig. 6). In fact, body size for all cohorts fluctuates considerably with the proportion of high quality forage (deciduous browse) (Fig. 7). As

expected, three of the four subregions consisting of higher quality forage (deciduous browse, *Quercus*-dominated) have larger than the average deer body size for all cohorts. In contrast, SWFH has some of the smallest deer in the fort yet the highest amount of deciduous browse (high quality forage) compared to all other subregions. Although the proportion of deciduous browse has a (weak) positive relationship with both 1.5 year old does and 2.5 buck antlers, a similar relationship with these two cohorts was also observed between poor quality (Graminoid-dominated, GI) vegetation (Tab. 9). Other discrepancies between forage quality and body size were also observed. For example, SER has one of the highest quality forage and abundance (deciduous browse) while SWR and SLF consists of primarily poor quality forage (graminoids), yet all three subregions have some of the largest deer in the fort. Based on these results, areas with higher quality and abundant forage do not support larger deer (on a subregional spatial scale) and therefore do not appear to be the main driver of white-tailed deer body size at FHAB. This is further supported when evaluating poor quality habitat's relationship with body size.

When available, high quality forage (particularly deciduous browse) comprises a majority of white-tailed deer diet. When unavailable (for example due to deer overabundance or extreme weather), low quality or palatability forage (shrubs and graminoids) make up a larger portion of deer diets (Tremblay et al. 2005). Two subregions with larger than average deer consist primarily of poor forage quality (herbaceous, Graminoid dominated vegetation): SWR and SLF. However, this trend is not consistent among subregions. Figure 8 illustrates how poor quality habitat is distributed among subregions of FHAB in relation to body size. Both NWR and SWR have higher Graminoid-dominated habitat compared to *Juniperus*-dominated

and fairly average sized deer. Similarly, both NWFH and SLF have higher Graminoid-dominated habitat yet have very different sizes of deer. NWFH has the smallest deer in the fort while SLF has the largest deer. This discrepancy may result from the fact that NWFH also has a high proportion of *Juniperus*-dominated habitat as compared to SLF, or that population density is influencing body size in this subregion (which is discussed in the next section). It is interesting to note that those subregions with a higher proportion of Graminoid-dominated habitat (compared to *Juniperus*-dominated) have substantially larger deer than those subregions with higher *Juniperus* (i.e. SWR, SLF, and NWFH), and is discussed in more detail below.

Forbs are herbaceous flowering plants that are not graminoids, however the data provided for this analysis generally listed disturbed herbaceous vegetation as those areas containing at least fifty percent of graminoids, *forbs* and ferns and was not plant specific. Forbs may offer additional nutrient quality for deer, are readily available throughout the year (particularly in the southwest United States such as Texas) and are foraged on during the winter (Hewitt 2011). Forbs generally comprise a higher proportion of seasonal diets in areas with more availability, such as in mesic rangelands near the coast (Hewitt 2011). If forbs have a strong influence on deer body size at FHAB, then those subregions (e.g. SWR and NWR) with a high proportion of herbaceous vegetation containing forbs would expect to support larger deer compared to areas without many forbs. Although SWR has larger than average deer for all cohorts, NWR has slightly smaller than average bucks with considerably smaller than average antler size (for both age cohorts). The results from this study indicate that forage consisting of higher proportion of forbs is probably not influencing deer body size compared to subregions with lower quality forage (i.e. *Juniperus* or Graminoid-dominated). However, forb data for this

study are generally categorized and may not offer adequate resolution to determine its effect on white tailed deer body size between subregions at Fort Hood.

The proportion of disturbed and developed habitat positively and significantly relates to 2.5 year old doe body size more strongly than any other vegetation type. However, this type of habitat is uncommon. Only twelve percent (12%) of the fort available to white-tailed deer consists of disturbed/developed vegetation. For example, only NFH consists of above average areas of disturbed/developed vegetation (17%) and has one of the lowest proportions of available forage (total acreage) for white-tailed deer (6,917 acres) (Tab.3). Since disturbed forage is not common, habitat associated with disturbed or developed vegetation is probably not having a substantial effect on overall deer body size within FHAB.

The proportion of forage type (deciduous browse, shrub, graminoid) does not appear to be a good predictor of deer body size between subregions of Fort Hood (Fig. 6). The results suggest that forage quality alone may not have a substantial influence on deer body size at a smaller spatial scale (such as the subregion) at FHAB, or data examined at this scale may not capture vegetation variability in order to determine its influence on body size. Previous studies suggest small deer body size at FHAB is density-dependent (Wolverton et al. 2011, Barr and Wolverton 2014). Results from this study indicate some clear patterns between deer population density and body size, which is discussed in more detail below.

Influence of population density on deer body size

Variability in white-tailed deer body size at FHAB may be primarily density dependent. Animal populations fluctuate between density dependent and density independent over time and can be influenced by scale of landscape, environmental heterogeneity, and the quality and

distribution of forage (McCullough 1999). Population density is significantly different between some subregions of the fort, particularly in WFH and NFH (which have considerably higher density compared to other subregions). An examination of the relationship between total population density and field dressed weight for each cohort indicate some clear patterns (Tab. 13). Similar to previous studies, population density appears to influence body size in bucks more than does (McCullough 1979, Palmer et al. 1997, Lesage et al. 2001, Wolverton 2008). Although not statistically significant, population density at FHAB has a small negative influence on both 1.5 and 2.5 year old bucks.

The number of fawns per doe (as a measure of fertility) has a significant negative relationship on both 1.5 and 2.5 year old bucks. SER, WFH and NFH have more fawns per doe compared to other subregions within FHAB (Tab. 10). Although WFH and NFH exhibit high population density, SER has considerably lower density compared to the rest of the Fort. These results suggest sexual segregation may occur within SER. Does in SER are average sized (compared to the larger than average bucks) and even though there is not a high doe per buck ratio, greater vulnerability of smaller does and fawns may lead to differences in habitat use between sexes (Bowyer 2004, Stewart et al. 2011). For example, SER has one of the highest proportions of deciduous browse at FHAB and, as such, may offer more protection from predators and optimal bedding for fawns (Hirth 1977, Fullbright 2011). It is thought that a tradeoff exists in areas with high population density where females are more likely to forage on poor quality vegetation as long as reproductive requirements are met (Bowyer 2004, Stewart et al. 2011). Areas with high population density can negatively impact female nutrition more than males (McCullough 1979, Kie and Bowyer 1999). Results suggest this may be the case at FHAB;

NER has the highest proportion of shrubs compared to other subregions and considerably smaller than average does.

Although there are some clear relationships between white-tailed deer body size and population density between subregions of FHAB, body size fluctuates considerably in relationship to density (Fig. 9) and closely resembles the pattern of proportion deciduous browse described previously (Fig. 7). In general, as population density increases deer body size (weight) decreases. NFH appears to be the exception when considering an expected inverse relationship between population density and deer body size (Fig. 10). Even though NFH has the highest population density, this subregion has a high proportion of deciduous browse as well as larger than average deer. Once NFH is removed from the analysis, there is a clear negative (although not significant) trend between density and body size (Fig. 11). Specifically, WFH has high population density and smaller than average deer. A closer examination of these two variables at WFH (i.e. NWFH, SWFH) and NFH reveals some stark differences compared to other subregions (see *West Fort Hood and North Fort Hood: a comparison of extremes* section below).

Population density also exhibits some clear relationships with proportion vegetation and habitat quality and is reported in Table 14. As food availability and population density are interrelated, it is expected that those regions with higher density and poor forage quality would exhibit smaller deer (compared to overabundant populations with higher quality forage). Deciduous browse has a strong positive correlation with the number of fawns per doe. This would make sense as woody vegetation provides optimal cover for fawns (as previously discussed) and is considered higher forage quality. The proportion of shrubs (poor forage quality) has a strong positive relationship with the number of does per buck. Again, this

supports previous discussion regarding sexual segregation of white-tailed deer with females utilizing poor quality habitat more than males. White-tailed deer overabundance and its effect on vegetation has been widely studied (DeCalesta 1997, Jones et al. 1993, Cote et al. 2004). As keystone species, overabundant white-tailed deer populations can damage or destroy habitat (Waller and Alverson 1997). Although there are some inconsistencies between the correlations of the proportion of vegetation (i.e. shrubs and graminoids) compared to the habitat index values (JI and GI), some clear relationships are worth mentioning. Although not significant (at $\alpha = 0.05$), the proportion of graminoids has a weak negative correlation with population density and moderate negative correlation with fertility across subregions of FHAB (Tab. 14). However, the proportion of Graminoid-dominated vegetation (GI) relative to high quality vegetation (*Quercus*-dominated) has a strong positive correlation with the number of fawns per doe. Perhaps areas with higher proportion of graminoids and high population density (such as NFH) are responsible for this observed relationship, further supporting the predator avoidance hypothesis. Does will exhibit a reproductive strategy by foraging with fawns in open, grass habitats consisting of primarily graminoids (Kie and Bowyer 1999), which simply relates to the idea that there is “safety in numbers”. Most likely other factors (or a combination of factors) are contributing to this pattern since subregions with high Graminoid-dominated vegetation and lower population density (SLF and SWR) do not show any significant differences from other subregions in regards to the number of fawns per doe.

West Fort Hood and North Fort Hood: a comparison of extremes

Within West Fort Hood (WFH), the southern-most area of FHAB, are two smaller areas: NWFH (5,460 acres) and SWFH (10,170 acres). Even though both of these subregions have

relatively smaller than average deer compared to the rest of the fort, there are substantial differences in vegetation and deer body size between them. Therefore, this area offers an even finer spatial scale analysis of the influence of vegetation on white-tailed deer body size at FHAB. These two subregions are separated from the rest of the fort by US Highway 190 and are located on either side of a main cantonment area (16 acres), which contains a major airport (Fig. 12). In addition, substantial suburban development surrounds the southern portions of WFH. These two subregions represent the extremes of vegetation quality. SWFH is twice as large as NWFH and has the highest amount of deciduous browse within the fort (55%), while NWFH has the lowest deciduous browse (21%) and highest proportion graminoids (60%). In addition, NWFH has considerably more poor quality habitat (*Juniperus* and Graminoid dominated vegetation) compared to SWFH (Fig. 13). These stark differences in vegetation, yet similar small sized deer and high population densities, between these subregions suggest forage quality and abundance is not substantially influencing deer body size as expected. Rather, population density would seem to have more of an influence on body size within WFH. However, examination of these same variables at NFH does not support population density as the main driver of body size at FHAB and is discussed in detail below.

NFH has larger deer (especially compared to SWFH and NWFH), smaller land area (after NWFH), high proportion of deciduous browse (high quality forage) and the highest amount of disturbed vegetation (17%) at Fort Hood. Although NFH primarily consists of deciduous browse (lower than SWFH and higher than NWFH), it has almost twice the amount of shrubs compared to the two WFH subregions (Fig. 13). In addition, NFH has the highest population density at FHAB (one deer per 14 acres). As would be expected, most of the significant pairwise

comparisons of density occur between NFH and other subregions (Tab. 11). Why is NFH so different from the rest of the fort? Even though there is a high amount of disturbed vegetation, this small subregion is fairly isolated from the rest of the fort and is not surrounded by as much suburban development as WFH. Figure 12 illustrates how NFH differs in regards to geography as well as spatial distribution of vegetation within this subregion. NFH is divided by a fairly large cantonment area (and two landing strips) which makes up 14% of the entire subregion. The proportion of vegetation is unevenly distributed across NFH (Fig. 12). The northern part of this subregion consists primarily of shrubs while the southeastern part of the subregion consists primarily of deciduous browse. The southeastern part of NFH is geographically closer to NLF and NER in relation to the northern part of the subregion. Perhaps deer within NLF and NER are dispersing into the southeastern part of NFH, thus influencing this analysis. Since there are not any obvious boundaries (fencing) separating the subregions of FHAB (other than natural or developed barriers), deer home ranges are most likely overlapping adjacent subregions. Perhaps NFH, which contains a “balance” of diverse vegetation, offer deer the variety of forage needed for optimal growth throughout the season.

Summary

Managers and hunters at FHAB have noticed for many years that West Fort Hood (NWFH and SWFH) consists of substantially smaller deer compared to other areas of the fort. The purpose of Chapter 2 was to determine if white-tailed deer body size significantly differed between subregions of FHAB. If so, what is influencing these differences? This chapter evaluated two factors thought to influence white-tailed deer body size: vegetation quality (and

abundance) and deer population density. Variability of vegetation quality and abundance associated with deer forage was demonstrated to differ among subregions. It was expected that if vegetation was a major driver of deer body size, those subregions with higher quality forage would support larger deer compared to subregions with lower quality forage. Although some subregions exhibited this expected pattern (SER, SWR and SLF) other subregions with high quality forage had smaller than average deer (SWFH and NWR). In addition, NFH consisted of low quality forage yet had larger than average deer. Even between the two isolated subregions within West Fort Hood, vegetation differed. NWFH has poorer quality vegetation (graminoids) compared to SWFH, which had the most abundant high quality vegetation (deciduous browse) in FHAB (Fig. 13). However, deer within both of these subregions are among the smallest in the fort. According to the results from this analysis, there is not a clear association between proportion of vegetation type (quality) or abundance and deer body size at a subregional scale within FHAB (Fig. 6). Differences in vegetation at Fort Hood may not be substantial enough to influence white-tailed deer body size in a density-independent manner. Therefore, the influence on population density on deer body size was evaluated.

White-tailed deer population density significantly differed among subregions. It was expected that those subregions with higher density would have smaller than average deer due to intraspecific competition of resources. A direct subregional comparison of population density relative to deer body size (for specific cohorts) is confounded by incomplete demographic census data. However, some clear patterns were apparent. First, deer population density generally appears to have an inverse relationship with body size (Fig. 11). Figure 14 summarizes how habitat variables (vegetation quality and deer population density) relate to

body size among subregions of FHAB and illustrates some clear patterns, as well as exceptions (i.e. NFH). Subregions with *high vegetation quality and low density* tend to have larger than average deer (SER, SWR and SLF) and are represented in Quadrant A. Deer in subregions with *medium vegetation quality and low density* (such as NLF) also were larger, however bucks in NWR were slightly smaller than average (Quadrant C). In contrast, SWFH has *high vegetation quality and high population density* with smaller than average deer, which is represented in Quadrant B. Finally, subregions with *low vegetation quality and high population density* have smaller than average deer (NER, NWFH), with the exception of NFH (which has larger deer and do not follow the general trend compared to other subregions) (Quadrant D). These results, in general, support previous studies that population density and body size exhibit an inverse relationship (Teer et al. 1965, Keyser et al. 2005, Wolverton 2008, Barr and Wolverton 2014). Although vegetation quality and abundance did not significantly correlate with body size as expected, there are some clear associations with body size when vegetation and population density are considered together. These results support previous observations that, even on a fine spatial scale such as between subregions at FHAB, white-tailed deer exhibit phenotypic plasticity in response to complex and dynamic environmental interactions such as vegetation quality (as a measure of eNPP) and population density (Wolverton et al. 2009a).

CHAPTER 3

CONCLUSION

The purpose of this study was to determine whether the spatial distribution of forage quality and abundance for white-tailed deer influenced body size at a localized scale within Fort Hood Army Base (FHAB). In addition, the distribution of white-tailed deer population density was also examined to determine its effect on body size at the same spatial scale. In order to determine if deer body size is influenced in a density-independent or density-dependent way, the following research questions were framed in order to evaluate these habitat variables at a subregional scale:

1. Does vegetation associated with white-tailed deer forage vary between subregions of FHAB?
2. How does deer body size relate to vegetation quality and abundance between subregions of FHAB?
3. How does deer body size relate to population density between subregions of FHAB?

Chapter 2 analyzed the distribution of vegetation associated with deer forage quality and abundance as well as deer population density within each subregion at Fort Hood to determine how variability in deer forage and density relate to variability in body size. The first two questions evaluate the influence of deer body size independent of population density. High quality vegetation was expected to correlate with larger, healthier deer and those areas with lower quality vegetation were expected to correlate with smaller deer. Question three further analyzed how deer body size related to subregional population density. If population density was influencing body size, it was expected that those areas with high population density would correlate with smaller deer due to intraspecific competition.

Results from these analyses suggest that, at least on a subregional spatial scale, forage quality and abundance alone is not a main driver of white-tailed deer body size within FHAB. Since forage quality and abundance, which is thought to represent ecologically relevant net primary productivity (eNPP), was not found to influence body size at FHAB, other environmental factors (such as topography and soil quality) were not examined. Analysis of deer population density (generally) resulted in an inverse relationship with body size. Results from this study indicate that (on a localized spatial scale) vegetation quality and abundance along with deer population density drive white-tailed deer body size. Within subregions of FHAB, areas with high quality forage and low population density support larger deer while areas with low quality forage and high density support smaller than average deer. The few exceptions occur in subregions exhibiting poor quality forage and low population density or high forage quality and high density areas.

Limitations

The population density data provided for this study are averaged by subregion on a coarser scale than that examined for vegetation. Even fine-scaled differences in habitat use by deer could lead to differences in spotting deer during spotlight surveys used to determine regional population density (Stewart et al. 2011). The quality, abundance and availability of vegetation in a particular region and its effect on white-tailed deer body size may simply be measuring selection or preference of forage by deer at a particular time. Selection or preference means the deer actually choose that forage type disproportionately or independently to its availability (Johnson 1980). Specifically, selection is where the animal

chooses a resource and preference and is based on the likelihood that a resource will be selected if offered on an equal basis with other types of forage (Johnson 1980).

Even though previous observations of white-tailed deer at FHAB indicate they are highly philopatric and have a small home range (2.5 km²), spatial analyses for this study were based on data categorized within “human-designated” subregions (military training areas). Deer may (and probably do) forage outside these subregions, which exhibit variability in forage quality, abundance, and population densities. Therefore, these subregions may not be a realistic indicator of white-tailed deer home range (and forage behavior) within the Fort Hood study area.

Examination of habitat variables at too fine a spatial scale may overlook landscape patterns and species characteristics appropriate for successful population management of deer. The vegetation data used in this study may oversimplify plant species associated with deer forage into broad categories, preventing the evidence of patterns of selectivity. Vegetation type and amount is affected by weather and soil quality, thus can vary seasonally and annually. Environmental variables (such as topography, climate and soil characteristics) are known to influence plant phenological stages and nutritional value (Jacobson 1984, Mysterud et al. 2001, Marshall et al. 2005, Jones et al. 2008, Jones et al. 2010, Lashley and Harper 2012). Evaluating environmental variables together with population density may greatly enhance our understanding of their effect on white-tailed deer body size.

Further Research

Distribution of forage quality is unique to a particular habitat, such that further evaluation of environmental influences (such as precipitation, extreme seasonal weather, soil quality) on forage can help to better understand and predict local deer population dynamics (DeYoung 2011). Increased white-tailed deer populations may be in response to resource pulses, especially during years with above-average rainfall (Holt 2008, DeYoung 2011). Fort Hood averages 32 inches of rain annually and as of June, 2015; Fort Hood has received 24 inches of rainfall making this year one of the wettest in history. Future research evaluating white-tailed deer habitat, body size and population density among subregions of FHAB in response to this increased rainfall may provide evidence to support effects of such resource pulses. In addition, examining the same variables used in this study at a larger spatial scale (such as within the different climatic zones of Texas) may provide evidence that vegetation quality and abundance alone influence white-tailed deer body size. If this is the case, additional analyses examining other habitat factors (such as topography and soil quality) associated with eNPP would be warranted.

A recent study examining white-tailed deer within suburban environments suggest that deer avoid high density residential areas yet prefer moderately disturbed habitat patches exhibiting ongoing plant succession (Potapov et al. 2014). White-tailed deer within FHAB have been shown to have small home ranges (Wolverton et al. 2012) and may vary seasonally and between sexes. Suburban areas (like those around West Fort Hood) may offer protected areas for deer, providing high quality foraging opportunities with low risk of predation or harvest

(Bowman 2011). Further studies examining deer body size and density in relation to disturbed or developed areas may provide useful information in management at Fort Hood.

Finally, the results from this study have shown that white-tailed deer body size significantly varies between subregions of FHAB. WFH, in particular, is isolated from other subregions of the fort and has overabundant deer populations in both of the smaller subregions (NWFH and SWFH). Results from this study suggest that continued overcrowding of deer within such isolated areas may eventually lead to efficiency conditions (Geist 1998) producing smaller sized deer. Further research examining genetic differences between these subpopulations can elucidate alternative theories supporting the occurrence of efficiency over dispersal conditions.

Implications for Management

The scale of habitat management must be matched to the species of interest since species have their own spatial scale at which they respond to the environment (Ritchie 1997). Studying ecological processes using multi-scalar analyses at more than one observational scale is important since different patterns at multiple scales (such as landscape and micro-habitat) have been reported (see summary in Wheatley and Johnson 2009). The importance of long term studies and use of large datasets to use in both empirical and theoretical research at multiple spatial scales can provide knowledge useful for ecosystem and wildlife management. The results from this study could prove useful in interpreting deer population responses to harvest management. Overabundant deer populations can affect the diversity and structure of local plant communities, impacting many other species (McShea 2012). Overabundant white-tailed deer populations and diminutive body size within central Texas have been observed by

managers for some time. Management goals at FHAB are currently being challenged to minimize conflicts of overabundant white-tailed deer populations with other natural resources. Especially in relation to conservation of habitat for two threatened bird species. For successful management of deer at FHAB, studies examining the combined influence of habitat variables (such as deer forage quality, forage abundance and population density) on deer health offer managers valuable information needed to establish annual harvest goals and understand deer-habitat relationships relative to carrying capacity. This translates to more effective deer management and species conservation on a local spatial scale with varying vegetation and deer body size, such as between subregions at Fort Hood.

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Table 1

Descriptive statistics of white-tailed body size over the past ten harvest seasons (2004 – 2013) at Fort Hood Army Base (FHAB). Field dressed weight (kg) and right antler basal circumference (RBC) (mm) are used as proxies for deer body size.

Body Size Cohort	Mean	Standard Deviation	Coefficient of Variation	n
Weight				
1.5 Bucks	72	9	0.1	287
2.5 Bucks	96	13	0.1	420
1.5 Does	61	7	0.1	144
2.5 Does	70	8	0.1	194
RBC				
1.5 Bucks	63	32	0.5	278
2.5 Bucks	91	31	0.3	417

Table 2

Summary of white-tailed deer forage at Fort Hood Army Base (FHAB). Vegetation was classified into three forage categories: Deciduous Browse, Shrub (evergreen) and Graminoid (herbaceous).*

Deciduous Browse		Shrub (Evergreen)		Graminoid (Herbaceous)	
Scientific Name	Common Name	Scientific Name	Common Name	Scientific Name	Common Name
<i>Quercus spp.</i>	Oak	<i>Juniperus ashei</i>	Ashe juniper	<i>Schizachyrium scoparium</i>	Little bluestem
<i>Q. buckleyi</i>	Texas red oak				
<i>Q. fusiformis</i>	Texas live oak				
<i>Q. marilandica</i>	Blackjack oak				
<i>Q. muehlenbergii</i>	Chinkapin oak				
<i>Q. sinuata var. breviloba</i>	White shin oak				
<i>Q. stellata</i>	Post oak				
<i>Carya illinoensis</i>	Pecan hickory	<i>Prosopis glandulosa</i>	Honey mesquite	<i>Buchloe dactyloides</i>	Buffalograss
<i>Ulmus spp.</i>	Elm			<i>Muhlenbergia reverchonii</i>	Seep muhly bunchgrass
<i>Ulmus crassifolia</i>	Texas cedar elm				
<i>Ulmus rubra</i>	Slippery elm				
<i>Cephalanthus occidentalis var. occidentalis</i>	Buttonbush			<i>Gramineae</i> ⁺	Grassland with mulch Disturbed herbaceous ⁺⁺
<i>Celtis laevigata</i>	Netleaf sugarberry			<i>Sorghastrum nutans</i>	Indian grass
<i>Platanus occidentalis</i>	American sycamore				
<i>Rhus lanceolata</i>	Prairie sumac				
<i>Juglans major</i>	Arizona walnut				
<i>Salix nigra</i>	Black willow				
<i>Acer saccharum</i>	Sugar maple				

* Data obtained from Fort Hood Vegetation Cover Map (The Nature Conservancy 2007) and described in Teague and Reemts (2007).

⁺ Vegetation >50% herbaceous dominant (graminoids, forbs and ferns)

⁺⁺ Herbs dominant (graminoids, forbs and ferns) with at least 25% canopy cover

Table 3

Descriptive statistics of white-tailed deer field dressed weight (kg) for subregions at Fort Hood Army Base (FHAB) for harvest seasons 2003—2014. Higher than average weights are bold.

Subregion/Cohort	Median	Range	IQR ^a	n
NER				
1.5 Bucks	70	25	10	26
2.5 Bucks	96	40	15	35
1.5 Does	58	32	9	19
2.5 Does	67	31	9	31
NFH				
1.5 Bucks	74	41	17	32
2.5 Bucks	98	74	19	49
1.5 Does	62	38	9	51
2.5 Does	72	40	10	45
NLF				
1.5 Bucks	77	11	15	12
2.5 Bucks	99	72	12	38
1.5 Does	61	5	4	4
2.5 Does	75	17	9	11
NWFH				
1.5 Bucks	69	20	15	68
2.5 Bucks	88	62	13	59
1.5 Does	57	30	7	25
2.5 Does	65	19	7	20
NWR				
1.5 Bucks	71	26	8	17
2.5 Bucks	94	50	10	44
1.5 Does
2.5 Does
SER				
1.5 Bucks	74	26	9	40
2.5 Bucks	98	60	17	54
1.5 Does	62	23	7	24
2.5 Does	70	33	12	36
SLF				
1.5 Bucks	75	12	7	8
2.5 Bucks	107	61	21	30
1.5 Does
2.5 Does	78	33	19	5
SWFH				
1.5 Bucks	67	45	10	29
2.5 Bucks	94	42	18	28
1.5 Does	59	9	5	8
2.5 Does	67	33	7	23
SWR				
1.5 Bucks	74	40	13	55
2.5 Bucks	97	59	18	83
1.5 Does	66	25	12	13
2.5 Does	72	28	15	23
TOTAL (N of all 9 regions)				
1.5 Bucks	72	52	12	287
2.5 Bucks	95	80	18	420
1.5 Does	61	38	8	143
2.5 Does	70	54	10	194

Table 4

Descriptive statistics of white-tailed deer right antler basal circumference (mm) for subregions at Fort Hood Army Base (FHAB) for harvest seasons 2003–2014. Higher than average weights are bold.

Region	Median	Range	IQR^a	n
NER				
Cohort				
1.5 Bucks	57	194	14	26
2.5 Bucks	89	64	14	35
NFH				
1.5 Bucks	59	160	12	29
2.5 Bucks	95	72	16	48
NLF				
1.5 Bucks	59	203	22	11
2.5 Bucks	86	71	15	37
NWFH				
1.5 Bucks	55	213	9	65
2.5 Bucks	82	310	16	58
NWR				
1.5 Bucks	55	35	11	17
2.5 Bucks	88	68	19	44
SER				
1.5 Bucks	62	259	13	38
2.5 Bucks	92	270	18	54
SLF				
1.5 Bucks	64	21	11	8
2.5 Bucks	92	56	11	30
SWFH				
1.5 Bucks	53	61	12	29
2.5 Bucks	90	308	21	28
SWR				
1.5 Bucks	60	255	16	55
2.5 Bucks	88	79	18	83
TOTAL (N of all 9 regions)				
1.5 Bucks	58	290	14	278
2.5 Bucks	90	315	16	417

"n" and "N" indicate sample and population size

^a IQR = Interquartile range

Table 5

Kruskal-Wallis test results of white-tailed deer body size between subregions at FHAB for harvest seasons 2004—2013. Field dressed weight (kg) and right antler basal circumference (RBC) (mm) are used as proxies for deer body size.

Test Variable	Test Stat	p value ^a	Sig. Difference (Subregions)	N
Weight				
1.5 Bucks	30.38	<0.001	SWFH-SER; NWFH-SER	287
2.5 Bucks	43.50	<0.001	NWFH-SWR; NWFH-NER; NWFH-NFH; NWFH-SER; NWFH-NLF; NWFH-SLF; NWR-SLF	420
1.5 Does	20.27	0.002	NWFH-SER; NWFH-SWR	144
2.5 Does	26.86	<0.001	NWFH-SLF	194
RBC				
1.5 Bucks	22.48	0.004	SWFH-SER; NWFH-SER	287
2.5 Bucks	29.04	<0.001	NWFH-SER;NWFH-NFH;NWFH-SLF	420

^a Significant at $\alpha = 0.05$

Table 6

Mann-Whitney pairwise comparison^a test results between subregions with significant differences in deer body size at FHAB for harvest seasons 2004—2013. Deer are considerably smaller in NWFH and SWFH subregions; deer are slightly smaller in NWR.

Test Variable	Subregion Comparisons ^b	Test Stat	p value ^c
Weight			
1.5 Bucks	SWFH-SER	78.09	0.004
	NWFH-SER	-60.64	0.009
2.5 Bucks	NWFH-SWR	-90.64	<0.001
	NWFH-NER	90.80	0.016
	NWFH-NFH	94.34	0.002
	NWFH-SER	-95.14	0.001
	NWFH-NLF	102.10	0.002
	NWFH-SLF	-157.60	<0.001
	NWR-SLF	-94.46	0.036
1.5 Does	NWFH-SER	-37.04	0.039
	NWFH-SWR	-50.54	0.008
2.5 Does	NWFH-SLF	-87.85	0.049
RBC			
1.5 Bucks	SWFH-SER	69.09	.023
	NWFH-SER	-60.60	.009
2.5 Bucks	NWFH-SER	-83.14	0.01
	NWFH-NFH	102.48	<0.001
	NWFH-SLF	-106.34	0.003

^a With Bonferroni corrections

^b Subregion comparison represents smaller-larger size deer

^c Significant at $\alpha = 0.05$.

Table 7

Descriptive statistics of vegetation classes (%), training areas (n) and acreage between subregions of FHAB for harvest seasons 2003—2014. Highest percentages are bold.

Subregion	Deciduous Browse	Shrub	Graminoid	Disturbed Developed	Training Areas	Total Acres
NER	37	45	16	1	9	29,651
NFH	40	29	14	17	9	6,917
NLF	39	24	31	6	13	31,985
NWFH	21	13	60	6	8	5,462
NWR	39	20	37	5	11	36,391
SER	54	20	20	5	13	21,457
SLF	27	13	49	10	6	18,266
SWFH	55	15	25	5	6	10,170
SWR	38	4	46	12	14	31,759
TOTAL	41	22	39	12	89	192,059

Table 8

Descriptive statistics of habitat indices for each subregion of FHAB. *Juniperus*-dominated and Graminoid-dominated represent those subregions with poor quality habitat. Highest values (greater than average) are bold.

Subregion	<i>Juniperus</i> -dominated	Graminoid-dominated
NER	0.6	0.4
NFH	0.2	0.4
NLF	0.4	0.5
NWFH	0.5	0.8
NWR	0.4	0.5
SER	0.3	0.3
SLF	0.4	0.7
SWFH	0.2	0.3
SWR	0.1	0.6
TOTAL	0.4	0.5

Table 9

Spearman's rho (r_s) test results^a of the relationship between vegetation type (%) and habitat index^b (JI, GI) to white-tailed deer body size for each cohort. Field dressed weight (kg) and right antler basal circumference (RBC) (mm) are used as proxies for deer body size. Values in bold indicate a relationship.

Body Size Cohort	Deciduous			Disturbed		
	Browse	Shrub	Graminoid	Developed	JI	GI
Weight						
1.5 Bucks	-0.10	0.12	0.03	0.51	-0.17	-0.13
2.5 Bucks	0.02	0.24	-0.17	0.47	-0.23	0.10
1.5 Does	0.43	0.08	-0.44	0.43	-0.63	0.44
2.5 Does	-0.09	0.02	-0.02	0.69c	0.35	-0.06
RBC						
1.5 Bucks	-0.17	0.00	-0.03	0.29	-0.22	0.34
2.5 Bucks	0.43	0.20	-0.32	0.23	-0.34	0.46

^a Perfect correlation = +1 or -1

^b JI: *Juniperus*-dominated, GI: Graminoid-dominated

^c Only relationship significant at $\alpha = 0.05$; $p = 0.04$.

Table 10

Average deer population density^a at FHAB for 2006—2014. Subregions with high density^b are bold.

Subregion	Deer/Acre	Doe/Buck ^c	Fawn/Doe ^c
WFH (NWFH, SWFH)	1/30	2.00	0.41
Northeast (NER)	1/44	2.86	0.32
Northwest (SWR)	1/52	2.05	0.27
Southeast (SER)	1/96	2.05	0.42
Southwest (SWR)	1/49	1.90	0.29
Live Fire (NLF, SLF)	1/107	1.64	0.22
NFH	1/14	2.09	0.41
Total	1/47	2.18	0.34

^a Population density based on spotlight surveys during Aug – Sep of that particular harvest season.

^b Density higher than total average population density.

^c Relates to fertility.

Table 11

Kruskal-Wallis test results for between subregion analyses of population density at FHAB (2006—2014^a). WFH and NFH have higher population densities compared to other subregions; NFH has highest population density at FHAB.

Test Variable	Test Stat	p value ^c	Sig. Difference (Subregions)
Deer/Acre	43.26	< 0.001	LF-WFH; LF-NFH; SER-NFH; NWR-NFH, TOTAL-NFH
Doe/Buck ^b	9.48	0.22 ^d	-
Fawn/Doe ^b	6.989	0.43 ^d	-

^a Population density based on spotlight surveys during Aug – Sep of that particular harvest season.

^b Relates to fertility.

^c Significant at $\alpha = 0.05$; N = 72

^d Fertility is not significantly different between subregions.

Table 12

Mann-Whitney pairwise comparison^a test results between subregions with significant differences of population density (Deer/Acre) at FHAB (2006—2014^b). WFH and NFH have higher population densities compared to other subregions.

Subregion Comparisons	Test Stat	p value ^c
LF-WFH	-36.44	0.004
LF-NFH	-54.83	< 0.001
SER-NFH	47.17	< 0.001
NWR-NFH	33.67	0.01
TOTAL-NFH	31.11	0.03

^a With Bonferroni corrections

^b Population density based on spotlight surveys during Aug – Sep of that particular harvest season.

^c Significant at $\alpha = 0.05$.

Table 13

Spearman's rho (r_s) test results^a of significant relationship between white-tailed deer population density and field dressed weight at FHAB (2006–2014^b). Values in bold indicate a significant relationship ($\alpha = 0.05$).

Weight	Deer/Acre	Doe/Buck ^c	Fawn/Doe ^c
1.5 Bucks	-0.29^d	-0.08	-0.44^e
2.5 Bucks	-0.14	-0.07	-0.29 ^d
1.5 Does	-0.01	-0.36^d	-0.08
2.5 Does	0.06	-0.05	-0.23

^a Perfect correlation = +1 or -1

^b Population density based on spotlight surveys during Aug – Sep of that particular harvest season.

^c Relates to fertility.

^d $p < 0.05$

^e $p < 0.001$

Table 14

Spearman's rho (r_s) test results^a of the relationship of vegetation type (%) and habitat index^b (JI, GI) to white-tailed deer population density. Values in bold indicate a relationship.

Test	Deciduous		Graminoid	Disturbed		JI	GI
	Browse	Shrub		Developed			
Deer/Acre	0.10	0.44	-0.42	0.42	-0.32	0.03	
Doe/Buck	0.31	0.92^{cd}	-0.67	-0.09	0.25	0.62	
Fawn/Doe	0.82^c	0.57	-0.61	0.29	-0.43	0.83^c	

^a Perfect correlation = +1 or -1

^b JI: *Juniperus*-dominated and GI: Graminoid-dominated are indicators of poor quality habitat.

^c Significant at $\alpha = 0.05$

^d $p < 0.01$

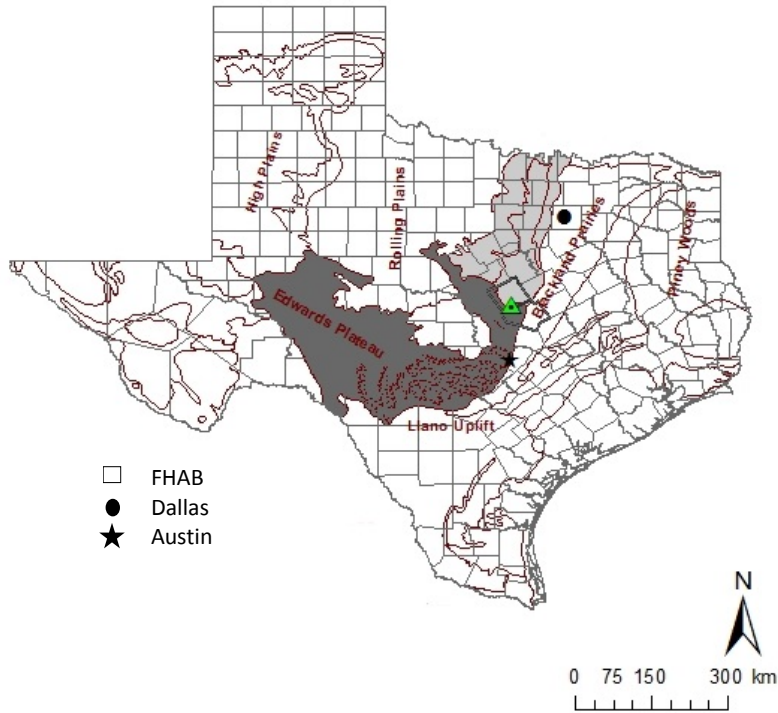


Figure 1. Texas map showing location of FHAB located in Bell and Coryell counties at the intersection of the Edwards Plateau (dark gray) and Cross Timbers (light gray) natural ecoregions in central Texas.

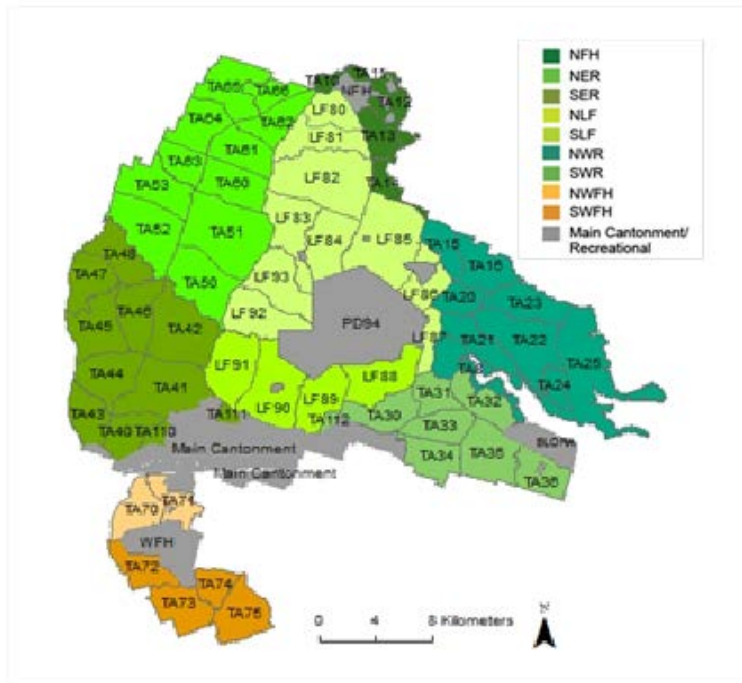


Figure 2. Subregional map of FHAB dividing the FHAB into 9 subregions* consisting of 83 training areas and 3 main cantonment areas: “Main Cantonment”, “WFH” and “NFH”. PD94 is a permanent duded area designated for live fire military training. Belton Lake Outdoor Recreation Area (BLORA) is open to public fishing and other recreational activities.
 *NFH (North Fort Hood), NER (Northeast Region), SER (Southeast Region), NLF (North Live Fire), SLF (South Live Fire), NWR (Northwest Region), SWR (Southwest Region), NWFH (North West Fort Hood), SWFH (South West Fort Hood)

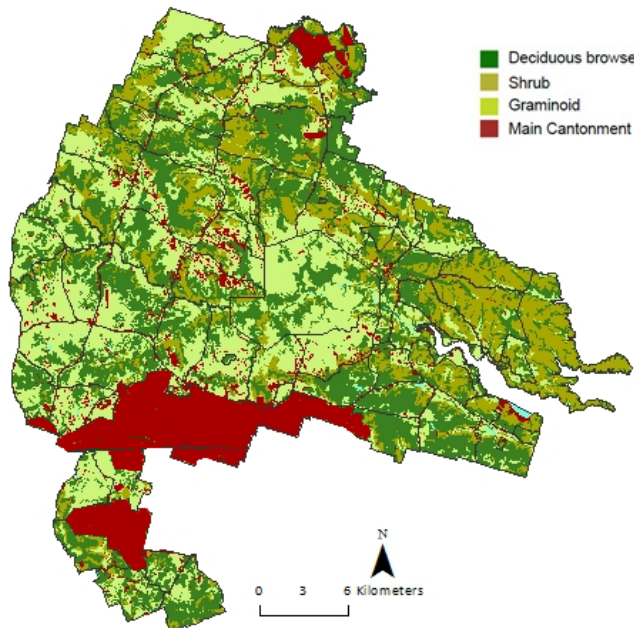


Figure 3. Vegetation map of FHAB illustrating the distribution of vegetation categories (deciduous browse, shrub and graminoids) used in analysis of white-tailed deer forage quality.

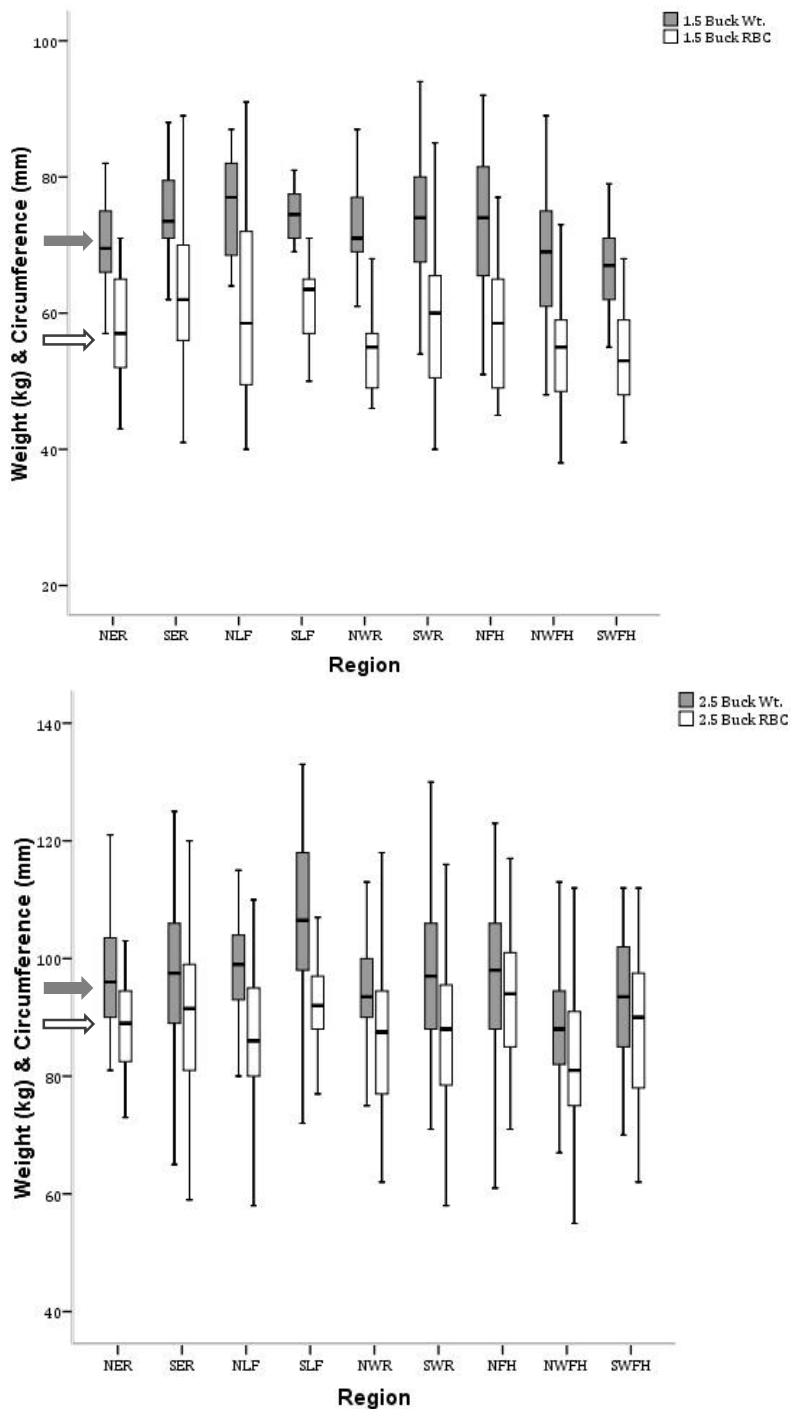


Figure 4. Boxplots of 1.5 (top) and 2.5 (bottom) year old white-tailed deer buck body size between subregions (“Regions”) of FHAB. Plots depict the median, the interquartile range (IQR) and the range (data reported in Tables 3 and 4). Differences in body size among regions is indicated where the interquartile ranges and ranges do not overlap. Field dressed weight (“wt.” in kg) and right antler basal circumference (“RBC” in mm) are used as proxies for body size. Outliers were omitted in order to better illustrate the differences in median body size across regions of the fort. Arrows on y-axes represent average body size in the fort (weight in gray, RBC in white).

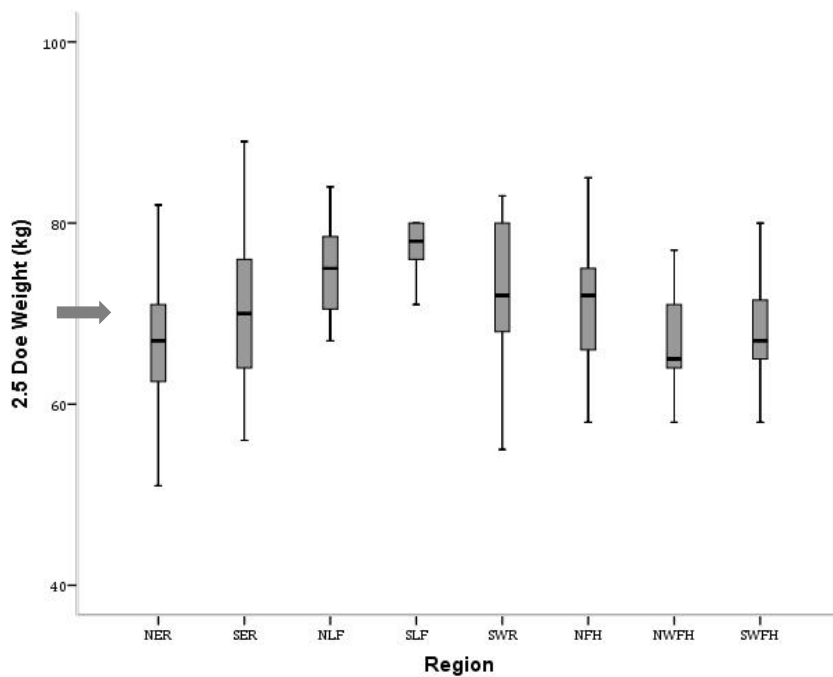
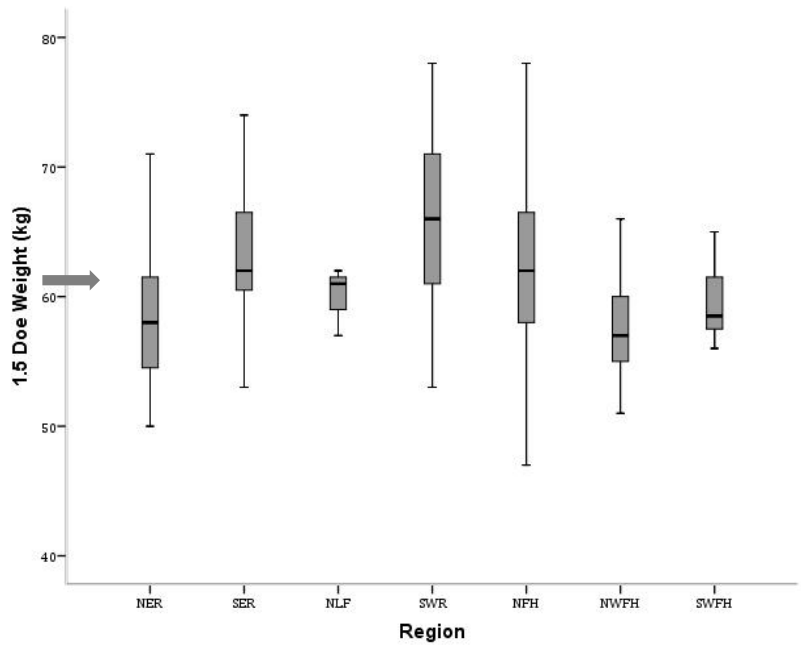


Figure 5. Boxplots of 1.5 and 2.5 year old white-tailed deer doe body size between subregions (“Regions”) of FHAB. Plots depict the median, the interquartile range (IQR) and the range (data reported in Tables 3 and 4). Differences in body size among subregions is indicated where the interquartile ranges and ranges do not overlap. Field dressed weight (“wt.” in kg) is used as proxy for body size. Outliers were omitted in order to better illustrate the differences in median body size across regions of the fort. Gray arrows on y-axes represent average body size in the fort.

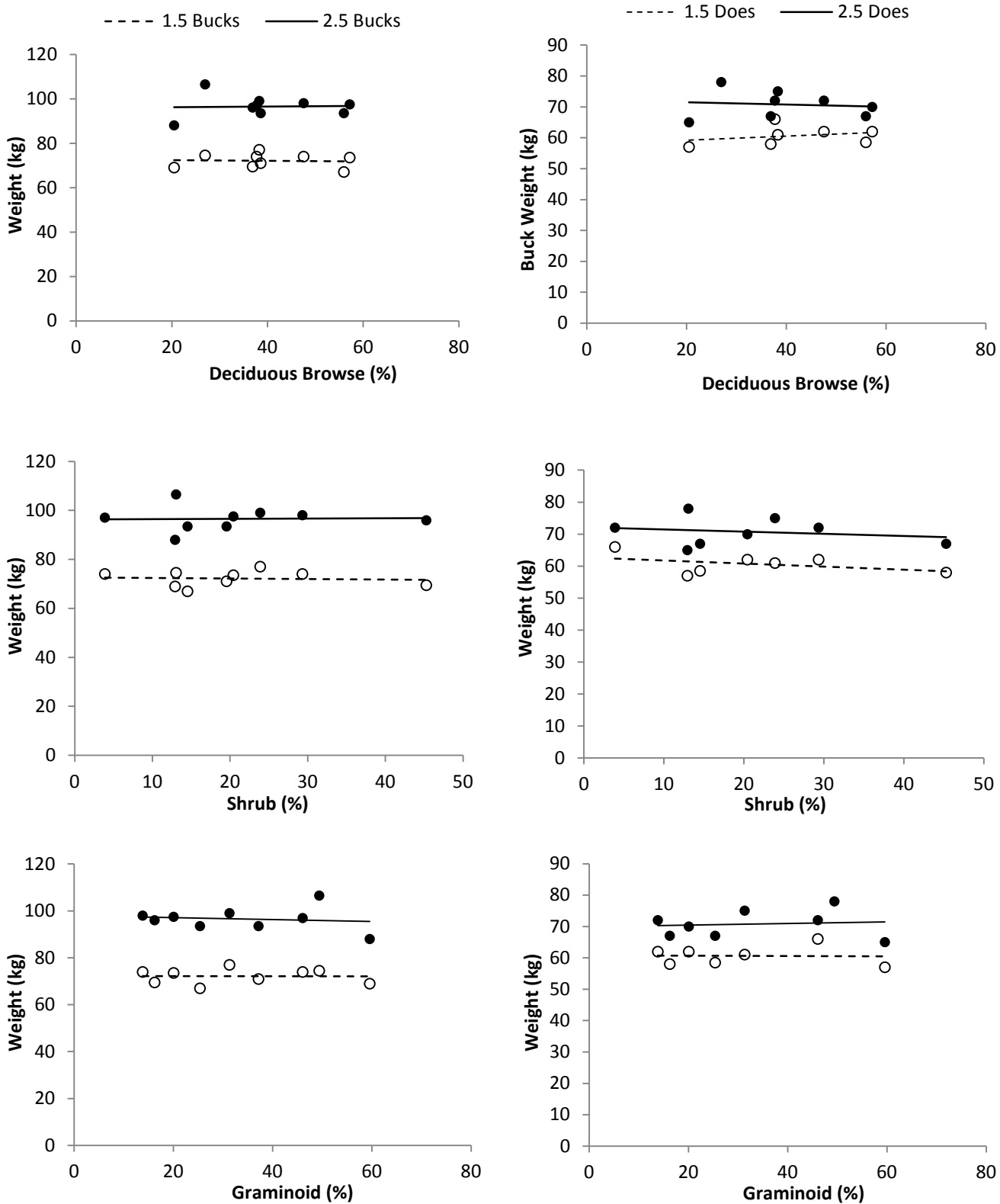


Figure 6. Bivariate plot illustrating relationship between median proportion of forage quality (deciduous browse, shrubs and graminoids) and median white-tailed deer buck (*left*) and doe (*right*) field dressed weight (kg) among subregions at FHAB during harvest seasons 2003-2014. R^2 values (which measure the goodness of fit of the trendline to the data) are all ≤ 0.1 , indicating that forage quality and abundance are not good predictors of deer body size.

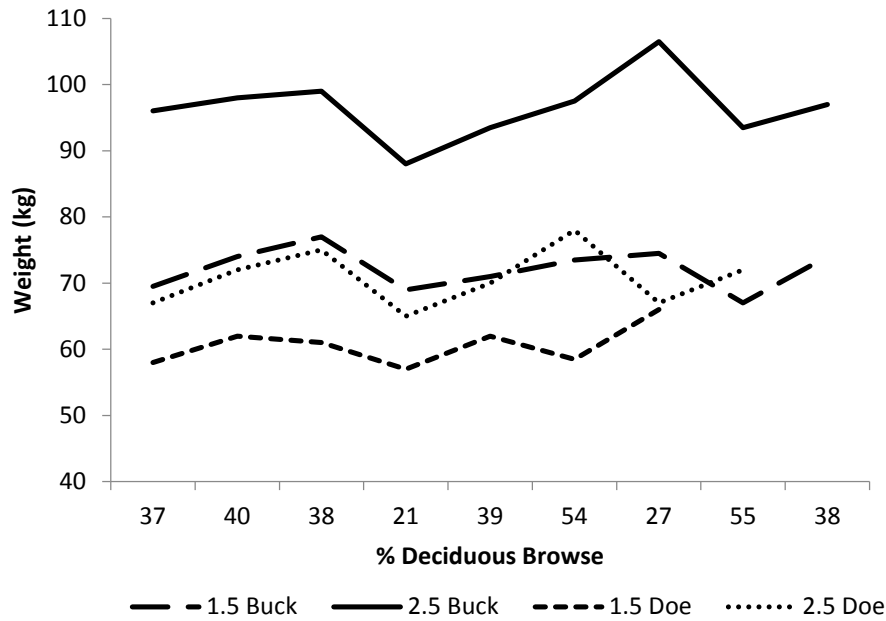


Figure 7. Line graph illustrating fluctuations in median deer body size with median proportion high quality forage (deciduous browse) between subregions of FHAB. Fluctuations may be due to changes in deer population density.

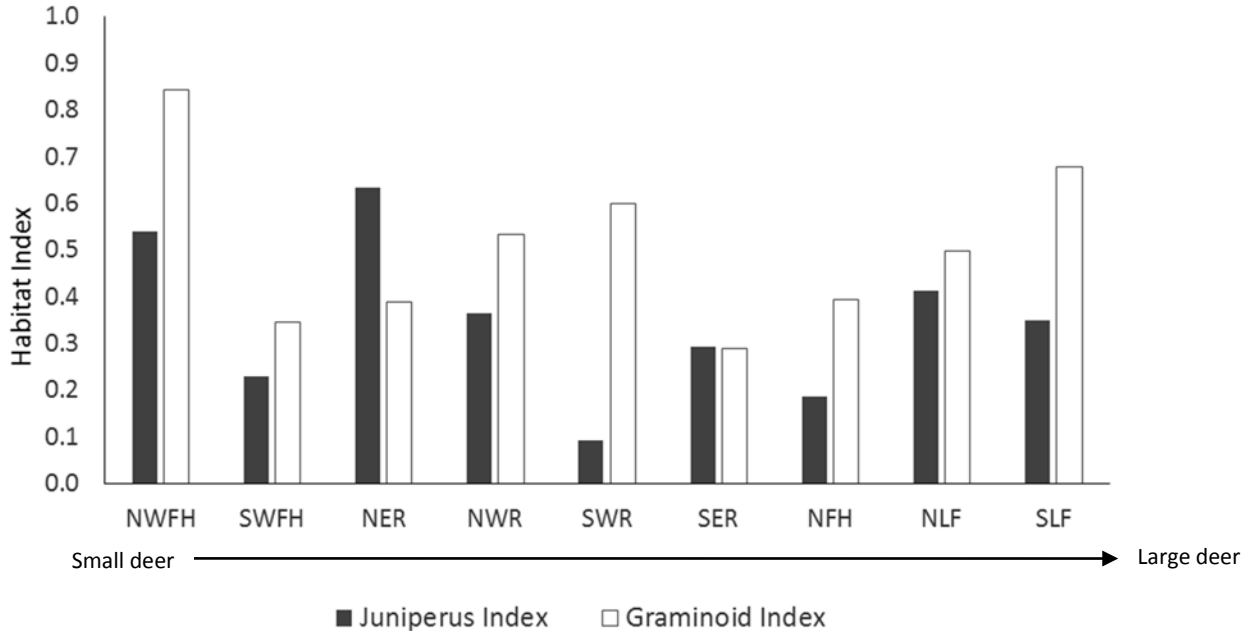


Figure 8. Bar graph illustrating how poor quality habitat is distributed among subregions of FHAB. Habitat quality index is used to measure amount of vegetation associated with poor quality habitat: *Juniperus*-dominated and Graminoid-dominated. Subregions are listed in rank order (left to right) according to deer body size: NWFH have the smallest average deer and SLF have the largest average deer.

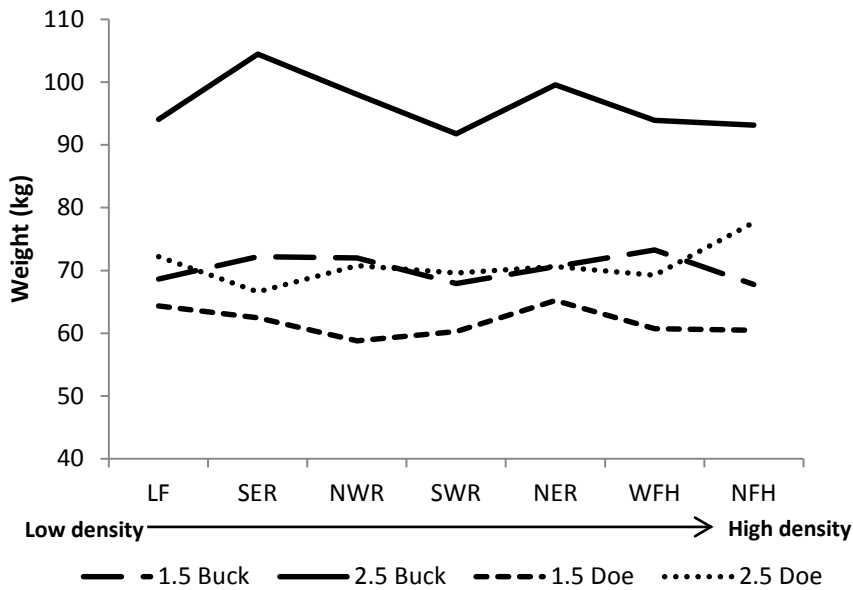


Figure 9. Line graph illustrating fluctuations in median deer body size with rank order population density between subregions of FHAB. Subregions are listed in rank order (*left to right*) according to density: LF has the lowest deer population density and NFH has the highest density. Population density represents total density per subregion (not cohort specific).

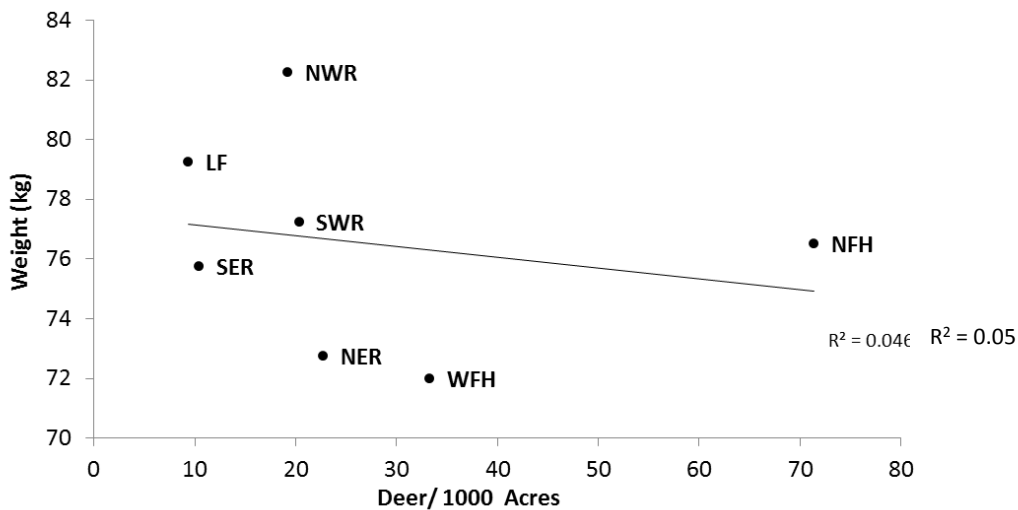


Figure 10. Bivariate plot illustrating the relationship between deer population density and body size among subregions of FHAB. There is a slight negative (non-significant) trend (or inverse relationship); as population density increases, deer weight decreases.

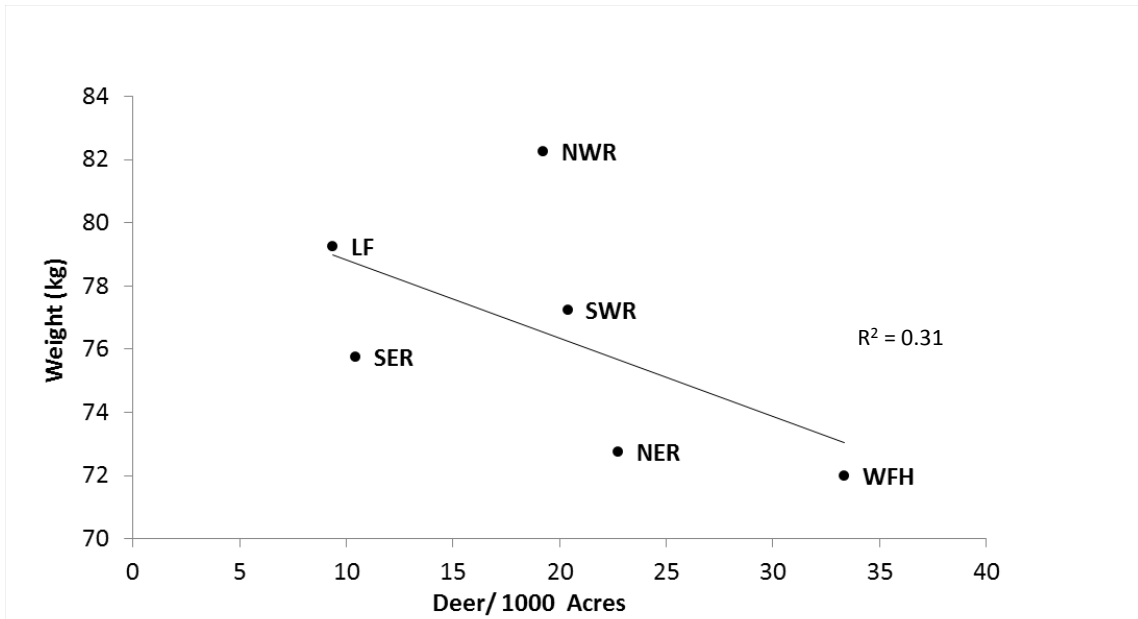


Figure 11. Bivariate plot illustrating the relationship between deer population density and body size among subregions of FHAB. NFH has been omitted from analysis to better illustrate a stronger inverse relationship, although still non-significant (at $\alpha = 0.05$).

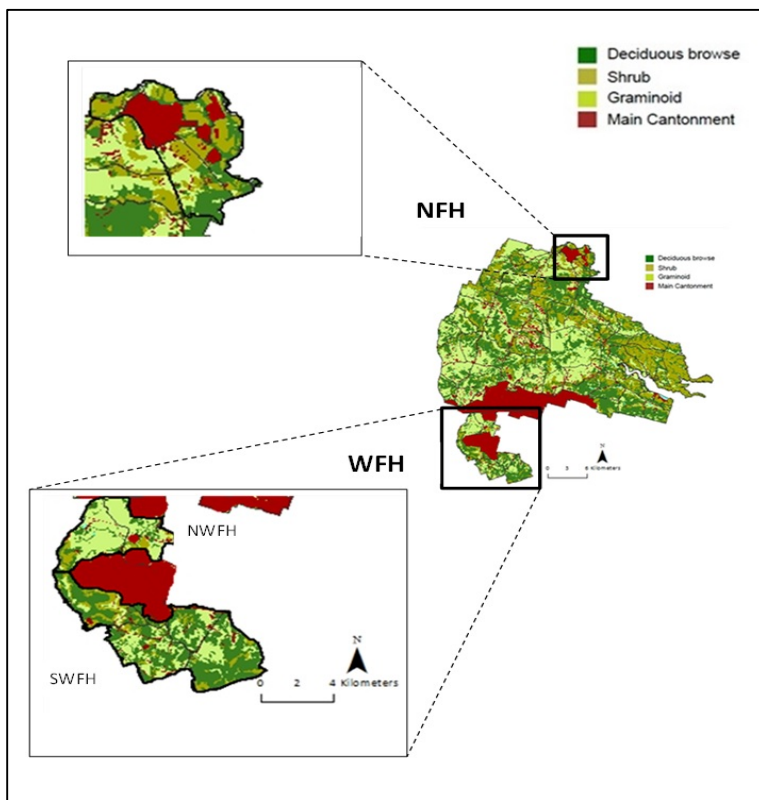


Figure 12. Map illustrating distribution of vegetation (forage) categories between NFH and WFH (NWFH and SWFH). NFH has unevenly distributed vegetation and is fairly isolated from the rest of the fort. WFH (NWFH and SWFH) is surrounded by suburban development and are separated from each other by a large cantonment. Vegetation is significantly different between these two subregions of WFH.

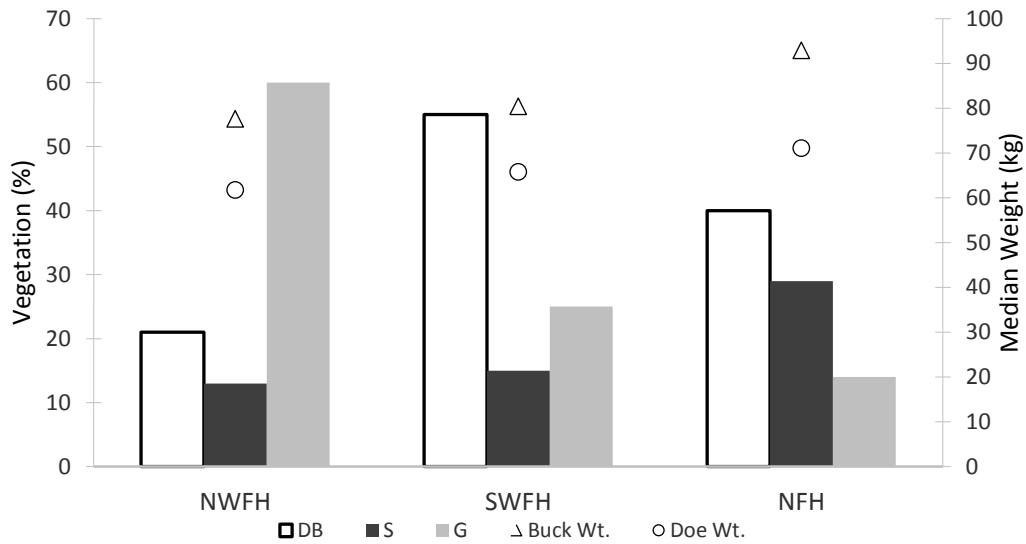


Figure 13. Graph illustrating the differences in vegetation (%) and deer body size (kg) within WFH (NWFH and SWFH) and NFH. SWFH has the more high quality forage (Deciduous Browse “DB”) yet smaller than average deer. NWFH has more low quality forage (Graminoids “G”) and smaller than average deer. NFH has more Deciduous Browse (yet substantial amount of Shrubs “S”), and some of the largest deer in the fort. All three subregions contain the highest population density in the fort (NFH and WFH, respectively).

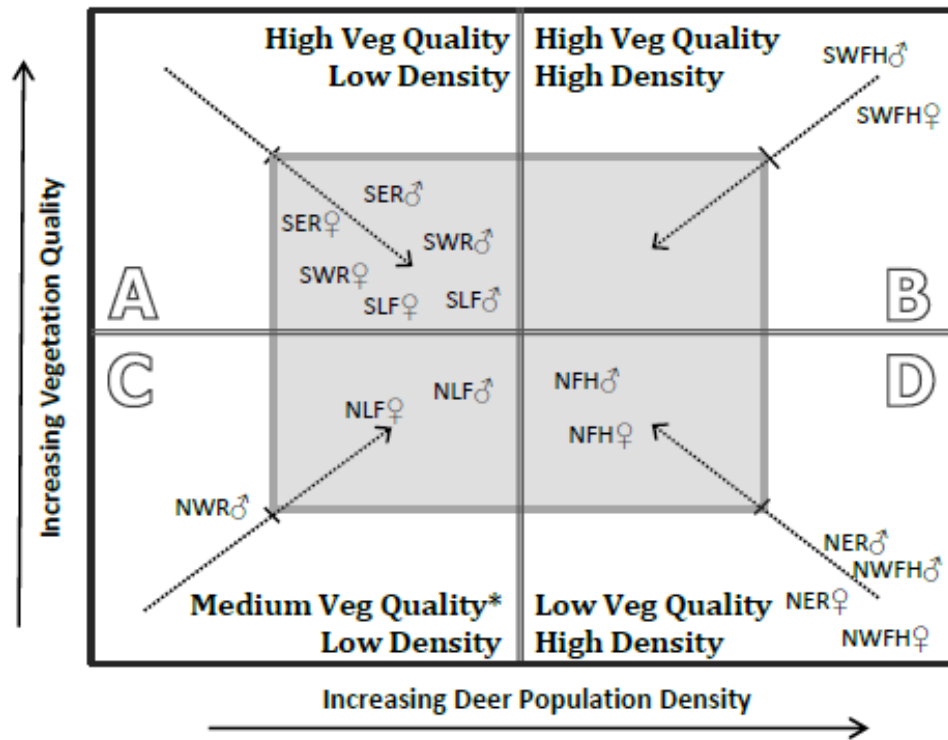


Figure 14. Summary of results illustrating the relationship between vegetation quality (y-axis), deer population density (x-axis), and deer body size (weight) among subregions of FHAB. Dotted arrows represent an increase in deer body size where those subregions within the gray box have larger than average deer (hash marks at the corners of the box represent average body size). Quadrants (A,B,C,D) represent trends and are discussed in Chapter 2. *Medium vegetation quality represents those subregions with almost an equal amount of high quality forage and low quality forage (see Table 7). Does = ♀, Bucks = ♂