To the Graduate Council:

I am submitting herewith a thesis written by Jared Tyler Beaver entitled "An Evaluation of Population Estimators and Forage Availability and Quality for White-tailed Deer in Tennessee." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Wildlife and Fisheries Science.

Craig A. Harper, Major Professor

We have read this thesis
and recommend its acceptance:

Lisa I. Muller

Frank T. van Manen

John C. Waller

Accepted for the Council

Carolyn R. Hodges
Vice Provost and Dean of the Graduate School

An evaluation of population estimators and forage availability and quality for white-tailed deer in Tennessee

A thesis presented for the
Master of Science Degree
The University of Tennessee, Knoxville

Jared Tyler Beaver
August 2011

DEDICATION

I dedicate this work to the memory of my oldest brother, Yorke Brown Beaver Jr., and to my late grandfather Ray "Pop" Wood. In life, "Little" Yorke was a loving son and brother who loved the outdoors; Pop taught me the value of an honest day's work and the value of staying close to Christ. Both have left lasting impressions and instilled in me a love for Christ, a respect for hard work, and a passion for the outdoors and all its critters. While their passing was hard to bear, their memory provides me with daily inspiration.

ACKNOWLEDGMENTS

There are many people who I would like to recognize who have helped make this project possible. First and foremost, I would like to thank God for providing me with the opportunity and ability to work in a field that I'm passionate about and for the countless blessings he has provided in my life.

Thanks to the various funding sources including the University of Tennessee, Department of Forestry, Wildlife and Fisheries, the US Department of Defense, Arnold Air Force Base (AAFB), Arnold Engineering Development Center (AEDC), and the US Fish and Wildlife Service. A special thanks to AAFB Natural Resource Manager, Rick McWhite, who without, this project would not have been possible. Thanks to the Tennessee Wildlife Resources Agency personnel for all their technical support. In particular, I would like to thank Wes Winton, AEDC WMA Manager, for all of his assistance and allowing me to use his equipment and storage facilities.

A special thanks to my major professor, Dr. Craig Harper, who saw enough in me to take a chance and provide me with the opportunity to work with white-tailed deer. The experience and knowledge gained in habitat management and population ecology is greatly appreciated. I truly appreciate your guidance, support, and remarkable ability to read me and keep me motivated, but most of all your friendship. I would also like to give a special thanks to Dr. Lisa Muller and Dr. Frank T van Manen, who always went out of their way to assist me and provide guidance. Thanks for your friendships and allowing me to constantly nag you. I would also like to thank Dr. John Waller, and Dr. Robert Kissell Jr., for all their assistance and support throughout my project. Thanks to Dr. Arnold Saxton for all his statistical assistance. I would also like to thank Dr. Miles Silman from Wake Forest University who has served as a mentor and role model in science, conservation, and life.

Logistical support was provided by countless individuals. In particular, Mike Black provided valuable data from previous years at AAFB; and Susan Finger and Stephen Farrington provided tremendous GIS and GPS support.

I would like to express my appreciation to fellow graduate students Matt Goode and Seth Basinger, and to my first friend in Knoxville, Austin Keene, for all of their help with field work and everything else. Thanks for the shared hunting experiences and friendships. I couldn't have done it without you. Additional thanks to the many technicians who have helped with field work. Also, thanks to all my friends "back home" who have also supported me and shared in various hunting and fishing experiences. In particular, Daniel Cauble, who has shared the majority of my childhood memories. Thanks for always being there and for all the memories from baseball, to hunting and fishing, to just plain being mischievous, and hopefully to many more to come. Also, thanks to his parents, Danny and Betsy Cauble, for also being there when I needed it and keeping me in line when I needed it most.

Finally, I would like to express my deep appreciation to my family for their support and encouragement. To my loving parents, Yorke and Jane Beaver, who without their constant wisdom, guidance, and support I would not be the man I am today. Thanks to my mother for always pushing me and striving to make me a better person; and thanks to my father for "lessons" in humility and instilling in me the love and passion I have for the outdoors. You both have made tremendous sacrifices to provide me with my every need and more; thank you. Thanks to my brothers and wonderful sister-in-laws, Britt and Lori Beaver, and Ryan and Emily Beaver, who have served as incredible role models and encouraged me to be a better person.

Thanks for always being there, words are not enough. I would also like to thank Tim Burns who has also been like a brother to me and helped me get my first elusive white-tailed buck. That is certainly a memory I will always cherish. Lastly, thanks to my amazing fiancée and soul mate Kristen Banks, who has endured a stressful long-distance relationship while constantly providing unconditional love and encouragement. I owe you so much. Thanks is not enough.

ABSTRACT

Given the white-tailed deer's (*Odocoileus virginianus*; deer) popularity and potentially negative impact on forested systems; Arnold Air Force Base (AAFB) in Tullahoma, Tennessee, USA has made minimizing negative deer impacts on biodiversity a priority. To address these management issues, I initiated a study on AAFB to investigate deer survey techniques and the effects of deer density on forage availability across vegetative communities.

Current use of infrared-triggered cameras (camera) for estimating deer populations does not provide a measure of precision critical for density estimation. I conducted a camera survey for deer in Wildlife Management Area (WMA) Units 1 and 2 at AAFB, August 2010 and used Program DENSITY to fit a spatial detection function of capture-recapture (spatial modeling) data from the camera surveys of bucks. Spatial modeling can provide reliable estimates of buck density and facilitate our understanding of biases associated with camera surveys for deer.

I compared population and precision estimates from spotlight, ground thermal infrared imaging (ground imaging), and aerial vertical-looking infrared (aerial imaging) surveys in the Security Area (SA) of AAFB, January–February 2010. All 3 techniques provided a precise estimate of deer density. However, the high cost of ground imaging does not justify its use. I also found the potential of road bias in distance sampling to invalidate the technique, unless random transects representative of the study area can be applied. Aerial imaging is less susceptible to road bias, but use should be restricted to large areas where high cost can be justified.

I evaluated the effects of 2 deer densities on forage availability and quality within 4 vegetative communities on WMA Units 1 and 2, and the SA of AAFB 2010. Forage availability was consistently greater during summer verses winter and within middle-aged and young pine stands at the low deer density site versus the high deer density site. Both crude protein and total

digestible nutrient values were similar regardless of deer density. I recommend managers consider implementing management practices that would reduce deer density and increase forage availability when forage availability beings to decline and deer density estimates approach levels seen detrimental in literature.

PREFACE

Data presented here were collected in cooperation with Arnold Air Force Base, The University of Tennessee, Tennessee Wildlife Resources Agency, and the US Fish and Wildlife Service. The study was initiated to address various local concerns and management issues regarding white-tailed deer populations.

The primary focus of my research was to evaluate density estimation techniques, forage availability, and nutritional quality for 2 areas of differing white-tailed deer densities. These data have been broken into 3 chapters formatted to meet requirements specified by the Journal of Wildlife Management and will be submitted individually to peer-reviewed journals.

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INTRODUCTION

In 1994, Department of Defense lands adopted ecosystem management guidelines for use in natural resources management. These guidelines incorporated considerations for all species and vegetation communities. They also encouraged collaboration with other federal, state, and local agencies, incorporating regional approaches to management. Under these guidelines, all species are considered, and provisions for outdoor recreation, including hunting, and recreational opportunities are consistent with goals in natural resources management.

White-tailed deer are considered a keystone species in the eastern United States (Miller et al. 2003). Deer density influences the structure and composition of the forest understory (Tilghman 1989, Rossell et al. 2005). Elevated deer density and chronic overbrowsing limit the availability of food and cover for many wildlife species in the eastern deciduous forest (Casey and Hein 1983, de Calesta 1994) and impact both faunal and floral species diversity (Anderson and Katz 1993, Rossell et al. 2005, Webster et al. 2005, Rossell et al. 2007). Deer overbrowsing also negatively affects the overall health of the deer population (Johnson et al. 1995).

The white-tailed deer is the most popular game animal in the country. The number of days spent hunting deer and the expenditures for deer hunting exceed that from all other species combined (U.S. Fish and Wildlife Service et al. 2006). The deer population on Arnold Air Force Base is managed jointly by Department of Defense and the Tennessee Wildlife Resources Agency. Whereas the Security Area is managed through Arnold Engineering Development Center and is open to hunting only by their employees, surrounding area on Arnold Air Force Base is open to public hunting and is managed as a Wildlife Management Area through Tennessee Wildlife Resource Agency. The Security Area is bordered by a 2-m tall fence, which is suspected to influence deer movement, but not necessarily contain deer movement.

Preliminary data collected using infrared triggered camera surveys by Arnold Air Force Base personnel suggest there are > 20 deer/km^2 within the Security Area (J. T. Beaver, University of Tennessee, unpublished work).

Given the potential impact deer can have on forested systems and the popularity of deer hunting on Arnold Air Force Base, information is needed to help meet management goals and objectives indicated in the Integrated Natural Resource Plan. Managing the deer population to minimize negative impacts on biodiversity is a priority management concern for Arnold Air Force Base. To address these concerns and management issues, the University of Tennessee initiated a study to investigate deer survey techniques, forage availability, and effects on vegetation communities in 2 areas of differing deer densities.

I used these data to formulate 3 manuscript chapters formatted under the requirements specified by the Journal of Wildlife Management, which will be submitted individually to either the *Journal of Wildlife Management* or the *Wildlife Society Bulletin*. Chapters 1 and 2 evaluate white-tailed deer population estimators, including an evaluation of the potential biases associated with traditional analysis of infrared-triggered camera surveys using spatial detection probability modeling, and the examination of potential road bias associated with distance sampling techniques by use of aerial vertical-looking infrared. Chapter 3 evaluates deer density effects on forage availability and quality of the vegetative community.

I. EVALUATION OF REMOTE CAMERA SURVEYS

TO ESTIMATE POPULATION DENSITY

ABSTRACT

Use of infrared-triggered camera (hereafter; camera) surveys for white-tailed deer (*Odocoileus virginianus*; deer) population estimation is popular among landowners. However, current use of camera surveys does not provide detection probability critical for accurate density estimation. Also, it is not known if the camera surveys provide an unbiased sample of the population. I conducted camera surveys for deer in Units 1 (1,385 ha) and 2 (1,488 ha) at Arnold Air Force Base, August 2010, using 1 camera per 53 and 62 ha in Units 1 and 2, respectively. I used Program DENSITY to fit a spatial detection function of capture-recapture data (spatial modeling) from the camera surveys of antlered bucks. Camera survey buck density estimates differed by calculation method (traditional sampling, spatial modeling). However, spatial modeling strengthens camera surveys by including the spatial distribution of captured deer, a means to model for behavioral biases and a measure of precision. Mean antlered buck density estimates (buck/km^2) obtained via traditional sampling for Units 1 and 2 were 1.95 and 2.56, respectively. Density estimates of bucks obtained via spatial modeling and susceptibility to capture ($g0$) were 1.59 bucks/km^2 (SE = 0.32, $g0$ = 0.32; Unit 1) and 2.45 bucks/km^2 (SE = 0.60, $g0$ = 0.24; Unit 2). There was a higher detection probability with higher camera density. Both estimation methods indicated lower deer density in Unit 1 versus 2. Deer movement data indicated potential changes in behavior associated with baiting. Analysis of camera surveys using spatial modeling takes full advantage of the data and adds the flexibility to evaluate concerns with equal detectability, which provides more precise estimates of buck density. Use of spatial modeling can provide reliable estimates of buck density and facilitate my understanding of biases associated with camera surveys for deer.

KEY WORDS baiting, density estimates, equal detectability, infrared-triggered cameras, mark-recapture, *Odocoileus virginianus*, spatial modeling, white-tailed deer.

INTRODUCTION

Population monitoring is a critical component in wildlife ecology and management (Gibbs 2000). White-tailed deer (*Odocoileus virginianus*; hereafter deer) are an important big game species in North America (Miller et al. 2003). Deer are also keystone herbivores in the eastern United States and elevated density levels can alter the structure and composition of the forest understory (Tilghman 1989, Waller and Alverson 1997, Miller et al. 2003, Rossell et al. 2005). Chronic overbrowsing limits the availability of food and cover for many wildlife species in the eastern deciduous forest (Casey and Hein 1983, de Calesta 1994) and impacts both faunal and floral species diversity, affecting the overall health of the deer population (Anderson and Katz 1993, Johnson et al. 1995, Rossell et al. 2005, Webster et al. 2005, Rossell et al. 2007).

Given the their economic importance and potential impacts deer can have on forest ecosystems, managers need reliable but cost-effective tools for population monitoring (Jenkins and Marchinton 1969, Jacobson et al. 1997, McKinley et al. 2006, Heilbrun et al. 2006). Techniques that not only estimate density (Lancia et al. 1994) but also allow detection of changes in density over time are needed (Gibbs 2000, Murray and Fuller 2000, Peterson et al. 2003).

Remote photography surveys have a long history in wildlife research and have surged in popularity since the advancement and commercialization of infrared-triggered camera (hereafter; camera) systems (Jacobson et al. 1997, Cutler and Swann 1999, Koerth and Kroll 2000). Camera surveys have been used to as a population technique for many wildlife species and have been shown to be an effective deer tool for taking inventories and creating trend data (Jacobson et al.

1997, Koerth and Kroll 2000, Heilbrun et al. 2006, Rowcliffe et al. 2008). They can be more cost-effective (Kucera and Barrett 1993, Rowcliffe et al. 2008), less invasive (Franzreb and Hanula 1995, van Schaik and Griffiths 1996, Cutler and Swann 1999, Rowcliffe et al. 2008), and less labor intensive (Seydack 1984, Cutler and Swann 1999, Rowcliffe et al. 2008) compared with other techniques, such as direct observations or mark-recapture studies (Cutler and Swann 1999, Larrucea et al. 2007). They are also capable of providing continuous detection by providing data 24 hrs a day in a variety of vegetation types and during various weather and light conditions with limited human attention, which can reduce human influence and observer bias (Cutler and Swann 1999, Larrucea et al. 2007, Rowcliffe et al. 2008).

However, as with other survey techniques, camera surveys have limitations. Studies have evaluated potential sources of bias, including camera density and survey duration (Jacobson et al. 1997, McKinley et al. 2006, Larrucea et al. 2007), human activity, scent, and presence of equipment possibly altering behavior (Hunt and Ogden 1991, Laurance and Grant 1994, Picman and Schriml 1994, Whelan et al. 1994). Furthermore, behavioral biases, timing of the survey, spatial movement, and responses to baiting may influence which animals are photographed, violating the assumption of equal detectability (Jacobson et al. 1997, Kilpatick and Stober 2002, Larrucea et al. 2007, McCoy et al. 2011).

Traditional approaches to camera surveys estimate abundance (N) based on recaptures of recognizable individuals from camera images (Karanth and Nichols 1998, Rowcliffe et al. 2008). The capture-recapture of known-antlered adult males is assumed the same for adult females and fawns (Jacobson et al. 1997, McKinley et al. 2006) and equal detectability among all individuals and locations is assumed; however this assumption has not been investigated in detail (Jacobson et al. 1997, Karanth and Nichols 1998, Cutler and Swann 1999). Also, traditional approaches to camera surveys and other conventional capture-recapture techniques ignore the spatial component of such data (Efford et al. 2004, Borchers and Efford 2008, Efford et al. 2009).

The effective trapping area for capture-recapture studies is difficult to estimate (Efford et al. 2004, Borchers and Efford 2008). However, spatially explicit capture-recapture (spatial modeling techniques have been developed in recent years that address these concerns by applying spatial detection functions to capture-recapture data (Efford 2004, Borchers and Efford 2008). Thus, my primary objective was to determine if spatially explicit capture-recapture models can provide reliable density estimates with levels of precision sufficient for making long-term management recommendations. I also evaluated the assumption of equal detectability associated with bait and capture heterogeneity at camera sites.

STUDY AREA

Arnold Air Force Base encompasses 15,816 ha in Coffee and Franklin Counties, Tennessee. The base is approximately 113 km southeast of Nashville and positioned between Manchester, Tullahoma, and Winchester. Arnold Air Force Base is within the Duck River and Elk River watersheds. It is located within the Interior Low Plateau geomorphic province. The Interior Low Plateau is composed of 2 physiographic provinces, the Central Basin and the Highland Rim. Arnold Air Force Base is within the Eastern Highland Rim physiographic province (U.S. Department of Defense 2006).

Most of Arnold Air Force Base is composed of either cultivated loblolly pine (*Pinus taeda*) plantations (2,223 ha) or continuous hardwood forest (9,329 ha), which consisted mostly of southern red oak (*Quercus falcata*), scarlet oak (*Quercus coccinea*), post oak (*Quercus stellata*), black oak (*Quercus velutina),* white oak (*Quercus alba*), willow oak (*Quercus phellos*), water oak (*Quercus nigra*), and blackjack oak (*Quercus marilandica*). The forest understory included dogwoods (*Cornus* spp.), maples (*Acer* spp.), sassafras (*Sassafras albidum*), sourwood (*Oxydendrum arboretum),* blueberries (*Vaccinium* spp.), hickories (*Carya* spp.), and blackgum (*Nyssa sylvatica*). Grasslands and early successional vegetation in utility rights-of-way occupied 898 ha. The remaining 1,895 ha were occupied by buildings and structures, mowed areas, and other open areas (including landfills and roads; U.S. Department of Defense 2006).

Arnold Air Force Base commander and his staff of military personnel and civil service employees are responsible for the overall planning, direction, scheduling, assignment, and funding associated with mission requirements. The US Fish and Wildlife Services and Tennessee Wildlife Resource Agency are cooperating agencies with the base. Arnold Air Force Base is managed jointly by Department of Defense and Tennessee Wildlife Resource Agency, while the Security Area is managed through Arnold Engineering Development Center the area outside the Security Area is open to public hunting and is managed as a Wildlife Management Area (WMA) through Tennessee Wildlife Resource Agency. The WMA is divided into 6 units (U.S. Department of Defense 2006).

METHODS

Camera design.—I established camera sites based on guidelines provided by Jacobson et al. (1997). I used Cuddeback Expert digital cameras (Non Typical, Inc., Green Bay, WI), and followed Tennessee Wildlife Resource Agency baiting regulations. I conducted camera surveys in approximately 2,900 ha of deer habitat in WMA Units 1 (1,385 ha) and 2 (1,488 ha). I defined deer habitat as any area other than reservoirs, buildings, parking lots, or roads. I overlaid these 2 tracts with 48.6-ha grid cells in GIS and placed cameras near the center of each grid. However, exact placement varied based on topography, likelihood of visitation by deer, and ease of access (Jacobson et al. 1997).

I recorded a GPS location for each camera site and placed a numbered tag in view of the camera lens. I removed debris and vegetation and oriented the lens north to eliminate backlighting caused by sunrise or sunset. I pre-baited each camera site for 7 days using 23 kg of shelled corn approximately 3 to 6 m from each camera. I activated cameras for 10 days on a 24-hr capture setting with a 2-minute delay. I checked cameras every other day and refreshed batteries, memory cards, and bait as needed. At the end of the 10-day period, I collected each camera and compiled images by site for analysis. I conducted the camera survey over 2 sessions because of a limited number of cameras. I began the first 10 day sampling period on 3 August 2010 with 28 camera sites. I started the second 10 day sampling period on 13 August 2010 with 26 sites. I maximized time and resources by overlapping the pre-bait of the second sample period and active phase of the first sample period, which allowed me to remove cameras from 1 sample period and place them immediately onto another.

Traditional camera analysis.—I analyzed camera images using methods described by Jacobson et al. (1997). I identified individual bucks based on antler configuration and body characteristics. I determined total number of bucks, does, and fawns. Total counts included known repeats of individuals. I divided total number of unique bucks by total number of buck images to get a ratio (unique-to-total bucks) and I multiplied this ratio by total does and fawns to get an estimated number of unique does and fawns for the entire survey area. I used these numbers and combined with my effective trapping area, which was determined by administrative boundaries (Unit 1 1,385 ha, Unit 2 1,488 ha), to obtain traditional camera survey estimates of deer density (deer/km^2) and other population ratios (i.e., buck:doe, fawn:doe ratios). However, I only used antlered buck density estimates for comparison with spatial modeling because they were individually identified and all other estimates are dependent upon the assumption of equal detectability.

Spatial analysis.—I also analyzed camera data of individual bucks and their capture locations using spatial modeling with program DENSITY (version 4.4, http://www.otago.ac.nz/density, accessed 11 Nov 2010). Spatial modeling used maximum-likelihood methods to estimate adult buck density, measure of precision (coefficient of variance; CV), detection probability (g_0), and spatial scale (σ; Efford et al. 2004, Borchers and Efford 2008). I fit half-normal detection functions to the data. I generated 6 models a priori based on biological relevance for both WMA Unit 1 and 2. I modeled for both heterogeneity (*h2*) and behavioral (*b*) effects on capture detection probabilities (*g0*) and for behavioral effects on spatial detection probability (σ). I applied a habitat mask to better specify which areas should be included for density estimation. I identified the city of Tullahoma adjacent to both WMA Units 1 and 2 as non-habitat area so that it would not be included in the spatial analysis as it served as a functional barrier to deer movement. I used minimum Akaike Information Criterion corrected for small sample size (AIC_c; Hurvich and Tsai 1989) for model selection of each site. I ranked models according to $\Delta_i AIC_c$ ($\Delta_i AIC = AIC_{ci} - AIC_c min$) and AIC_c weights (w_i) and used the weights to determine the relative importance of potential sources of variance within the models (Posada and Buckley 2004). I used model averaging to estimate population density (Buckland et al. 2001).

RESULTS

I had to remove 4 camera sites from WMA Unit 2 analysis because of camera malfunctions. Consequently, Unit 1 contained 26 usable camera sites and WMA Unit 2 contained 24 sites, creating a systematic spacing of a camera site for every 53 ha and 62 ha, respectively (Fig. 1). I obtained 5,827 and 7,906 total photographed deer and identified 27 and 38 individual antlered bucks for WMA Units 1 and 2, respectively (Table 1). I calculated density and parameter ratios for all bucks, does, and fawns (Table 1). I obtained an antlered buck density estimate of 1.95 and 2.56 buck/km^2 for WMA Units 1 and 2, respectively (Table 1).

I observed from the traditional camera analysis that there was no crossover of individually identified bucks from WMA Units 1 and 2. Therefore, I applied a habitat mask to account for the major highway between WMA Units 1 and 2 serving as a functional barrier to deer movement. When models for WMA Unit 1 were run, Unit 2 was masked as non-habitat area and therefore not included in the spatial calculations. When running Unit 2, I masked Unit 1.

I found from spatial modeling of individually identified bucks (Table 1) that half-normal models that included behavioral effects for the spatial scale and detection parameters were consistently supported, with both parameters receiving 57% and 74% of the Akaike weights for WMA Units 1 and 2, respectively (Table 2). Model-averaged density estimates and precision were 1.59 buck/km^2 (SE = 0.32) and 2.45 buck/km^2 (SE = 0.60) for WMA Units 1 and 2, respectively (Table 2). Model-averaged detection probability (*g0*) was 0.32 for WMA Unit 1 and 0.24 for WMA Unit 2 (Table 2).

DISCUSSION

Although I obtained similar density estimates for the traditional camera method (WMA Unit 1: 1.95 bucks/km^2; WMA Unit 2: 2.56 deer/km^2; Table 1) and spatial modeling (WMA Unit 1: 1.59 deer/km^2; WMA Unit 2: 2.45 bucks/km^2; Table 2), my study was based on an open population of an unknown number of deer. Therefore, I do not know which technique provides a more accurate density estimate. However, my results suggested spatially explicit capture recapture can be used with camera survey data to obtain antlered buck density estimates, detection probability, and a measure of precision sufficient for making management decisions. This is critical for biologist because traditional camera surveys do not provide a measure of precision. According to White et al. (1982), an estimate without a measure of precision (the sampling variance) and an assessment of related assumptions is not reliable.

Confidence intervals of density estimates using spatial modeling analysis overlapped those of estimates obtained with traditional methods (WMA Unit 1: 0.95–2.23 deer/km^2; WMA Unit 2: 1.25–3.65 bucks/km^2). The SECR analysis incorporates spatial encounter history and location of each capture, creating an explicit account of the spatial nature of the sampling process (Efford et al. 2004, Borchers and Efford 2008). With traditional analysis, the effective trapping area for each camera survey must be determined, which can lead to biased estimates (Efford et al. 2004, Borchers and Efford 2008). A number of individuals are identified during a survey period but they may not all be found within the effective trapping area at any given time. Thus, density estimates using traditional camera surveys may be biased high. However, with SECR the effective trapping area can be estimated using maximum-likelihood methods based on capture-recapture data of individual bucks. Moreover, habitat areas that were not used by the animals were excluded, ultimately yielding more robust and reliable estimates compared with traditional methods (Pledger 2000, Efford et al. 2009, Clark et al. 2010).

Detection probability (*g0*) for WMA Units 1 and 2 were 32% and 24%, respectively. Detection probability was higher for Unit 1, which had a higher camera density. McKinley et al. (2006) reported a 90% detection probability of marked individuals at a density of 1 camera/41 ha and 61% at a density of 1 camera/81 ha. Based on previous studies, I expected detection probabilities for the WMA Units to be between 60 and 90%, with a slightly higher detection probability in Unit 1. I contribute the lower than expected detection probability obtained from

SECR analysis to the additional spatial component accounting for individual movement on and off the study area and potential sources of variance due to the use of bait considered in the analysis.

The assumption of equal detectability is essential to all parameter ratios and density estimates because they are calculated from estimates of antlered bucks. Jacobson et al. (1997) recognized bias by gender could be problematic for unbiased estimates of deer populations. Other studies have indicated behavioral biases influence which animals are captured on camera (Jacobson et al. 1997, Cutler and Swann 1999, Larrucea et al. 2007). Behavioral responses to baiting violate the assumption of equal detectability (Cutler and Swann 1999, Kilpatrick and Stober 2002, Campbell et al. 2006, Roberts et al. 2006). McCoy et al. (2011) found sex ratio and recruitment data from randomly placed cameras differed from cameras at feed stations during all time periods evaluated. However, unlike traditional camera surveys, spatial modeling does not rely on equal detectability and can model heterogeneous mixtures, individual covariates, and behavioral responses (Pledger 2000, Efford et al. 2009, Clark et al. 2010).

Spatial modeling for both WMA Units 1 and 2, suggested a behavioral response to both the capture and movement parameters. Behavioral bias in my models may have resulted from bait used as an attractant and was supported by data from the 3 GPS-collared deer captured on camera during the survey (P. S. Basinger, University of Tennessee, unpublished data). Average distance of GPS locations to the closest bait site within each individual's minimal convex polygon home range increased for the 3 deer captured on camera during the survey (580–627, 300–361, 304–375 m; respectively) for the 7-day lag period immediately following the survey and baiting period. Mean distance to bait sites for the 3 GPS-collared deer also increased from the 7 days while bait was present (358 m) to the 7-day lag period (474 m) and then decreased again for the following 7 days period (303 m). This behavior is similar to that reported by Kilpatrick and Stober (2002) where temporary bait sites caused a shift in activity within each individual's range that was exposed to bait. Campbell et al. (2006) found high variability among radio-collared female deer in response to baiting, shifting their center of activity closer to bait sites during baiting periods. These responses to bait violate assumptions important for traditional camera surveys.

Traditional camera survey methods involve identification of individual bucks. Thus, additional parameter estimates and ratios must be achieved based on the assumption of equal detectability, which is potentially susceptible to behavioral bias. The assumption of equal detectability should be examined with a marked population where sex and age could be included in the modeling analysis as covariates. This should be repeated at higher camera densities. A complete understanding of biases involved with camera surveys will enhance this tool as a density estimation technique for managing white-tailed deer.

MANAGEMENT IMPLICATIONS

Spatially explicit capture recapture models strengthen camera surveys by including the spatial distribution of captured deer, by incorporating capture heterogeneity and behavioral responses, and by providing a measure of precision. Managers should be aware of potential biases in their data and how they may affect their management decisions.

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APPENDIX

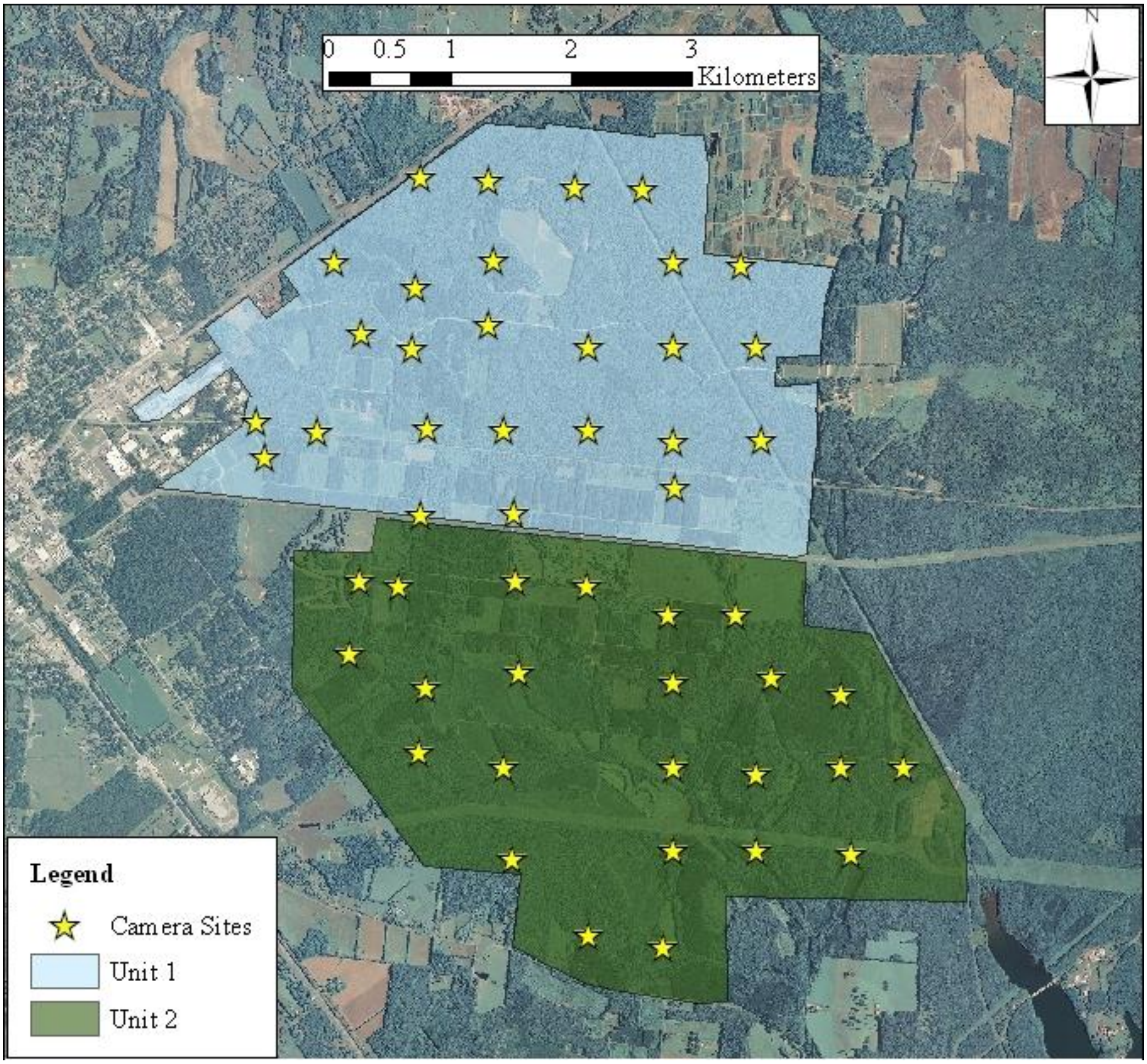

Figure 1. Infrared-triggered camera site locations for Wildlife Management Area Units 1 and 2 at Arnold Air Force Base in Tullahoma, Tennessee, USA, July–August 2010. Wildlife Management Area Unit 1 contained 26 usable camera sites and Wildlife Management Area Unit 2 contained 24, creating a systematic spacing of an infrared-triggered camera for every 53 ha and 62 ha, respectively.

Table 1. Number of white-tailed deer photos, population abundance and density, and ratios based on traditional camera survey analysis for Wildlife Management Area Units 1 and 2, Arnold Air Force Base, Tullahoma, Tennessee, USA, July–August 2010.

	Unit 1	Unit 2
Picture tally		
Bucks	1,605	2,193
Does	3,373	4,424
Fawns	521	840
Unknown	328	449
Ratios		
Doe:buck	2.10	2.02
Antlerless:antlered	2.43	2.40
Fawn:doe	0.15	0.19
Individual abundance estimates		
Antlered bucks[a]	27.00	38.00
Does	56.74	76.66
Fawns	8.76	14.56
Density estimates		
Deer/km^2	6.68	8.69
Antlered bucks/km^2	1.95	2.56

[a] Individually identified based on antler characteristics

Table 2. Spatially explicit capture-recapture models and antlered white-tailed deer density for Units 1 and 2 at Arnold Air Force Base, Tullahoma, Tennessee, USA, July–August 2010. I used the half-normal detection function and modeled detection probability (*g0*) as a constant [.] or a function of behavioral (*b*) and heterogeneity (*h2*) effects and spatial scale (σ) as a constant or a behavioral effect.

Model and Unit	AIC_c[a]	ΔAIC_c	w_i[b]	D[c]	SE	g0[d]	SE	σ[e]	SE
Unit - 1									
Half-normal g0[*b*] σ[.]	993.06	0.00	0.22	1.68	0.34	0.27	0.08	351.43	15.99
Half-normal g0[*b*] σ[*b*]	993.17	0.11	0.22	1.58	0.33	0.20	0.07	410.53	42.36
Half-normal g0[*h2*] σ[.]	997.61	4.55	0.18	1.55	0.31	0.30	0.06	347.78	14.06
Half-normal g0[.] σ[*b*]	1004.30	11.24	0.13	1.63	0.33	0.55	0.07	314.27	21.17
Half-normal g0[*h2*] σ[*b*]	1004.31	11.25	0.13	1.53	0.32	0.18	0.08	360.38	26.78
Half-normal g0[.] σ[.]	1005.86	12.80	0.12	1.50	0.29	0.56	0.07	350.24	15.83
Model average				1.59	0.32	0.32	0.07	360.21	23.55
Unit - 2									
Half-normal g0[*b*] σ[.]	963.80	0.00	0.33	2.56	0.56	0.15	0.05	334.93	14.44
Half-normal g0[*b*] σ[*b*]	965.14	1.34	0.30	2.47	0.57	0.12	0.05	372.50	38.44
Half-normal g0[.] σ[*b*]	986.22	22.42	0.11	2.26	0.40	0.45	0.05	269.13	19.26
Half-normal g0[*h2*] σ[*b*]	986.74	22.94	0.10	2.21	0.40	0.30	0.07	281.37	16.87
Half-normal g0[*h2*] σ[.]	987.37	23.57	0.10	2.80	1.38	0.50	0.05	342.42	15.52
Half-normal g0[.] σ[.]	997.76	33.96	0.06	1.84	0.31	0.45	0.05	333.91	14.75
Model average				2.45	0.60	0.24	0.05	334.24	22.64

[a] Akaike's Information Criterion adjusted for small *n*
[b] Akaike wt.
[c] Density (no. antlered deer/km^2)
[d] Detection probability of the capture function (g0)
[e] Spatial scale parameter of the capture function (σ)

II. AERIAL VERTICAL-LOOKING INFRARED IMAGERY TO EVALUATE BIAS OF DISTANCE SAMPLING TECHNIQUES FOR WHITE-TAILED DEER

ABSTRACT

Population monitoring is an important component when managing white-tailed deer (*Odocoileus virginianus*; deer), and a method without a measure of precision and an assessment of the relevant assumptions may be regarded scientifically invalid. Distance sampling can be applied to ground thermal infrared imaging (ground imaging) and spotlight surveys to overcome limitations with these conventional deer survey techniques. Aerial vertical-looking infrared imagery (aerial imaging) is a relatively new technique designed to overcome the burdens of both current aerial and traditional distance surveys. I compared population and precision estimates and evaluated assumptions for each technique on the Security Area of Arnold Air Force Base in Tennessee, USA during January-February 2010. Deer density (deer/km^2) and precision for spotlight, ground, and aerial imaging were 21.4 (CV = 15.2), 10.9 (CV = 10.1), and 5.41 (CV = 23.1), respectively. All precision estimates were within acceptable standards for making management recommendations. A 1-tailed *t*-test of aerial imaging found observed deer distances were closer to roads than randomly generated distances, suggesting a road-bias selection by deer, which would bias spotlight and ground imaging estimates high. All 3 techniques provided a precise estimate of deer density. However, the high cost of ground imaging does not justify its use over spotlight surveys. I also found the potential of road bias in distance sampling to invalidate the technique, unless random transects representative of the study area can be applied. Aerial imaging is less susceptible to road bias, but its use should be restricted to large areas where high cost can be justified.

KEY WORDS aerial imaging, deer density, distance sampling, ground imaging, *Odocoileus virginianus*, road bias, spotlight surveys, thermal imaging, white-tailed deer.

INTRODUCTION

White-tailed deer (*Odocoileus virginianus*; hereafter deer) are considered a keystone species in the eastern United States (Waller and Alverson 1997). Elevated deer density levels overtime can alter the structure and composition of the forest understory (Tilghman 1989, Miller et al. 2003, Rossell et al. 2005) and eventually negatively affect the overall health of the deer population (Anderson and Katz 1993, Johnson et al. 1995, Rossell et al. 2005, Webster et al. 2005). Given the potential impact deer can have on forested systems and their economic impact, additional information is needed to help provide managers and researchers with accurate, reliable, and cost-effective estimates of deer population characteristics (Jenkins and Marchinton 1969, Jacobson et al. 1997, McKinley et al. 2006).

In order for a population estimator to be effective, it must provide robust density estimates that are precise and have minimal bias (White et al. 1982, Diefenbach 2005, Mills 2007). According to White et al. (1982), an estimate without a measure of precision (the sampling variance) and an assessment of related assumptions is not reliable. Evaluating whether a population estimation technique provides unbiased estimations is difficult because the true population size is unknown and all estimators have some combination of bias and imprecision. However, estimators can still be useful if they are quantified (White et al. 1982, Diefenbach 2005). Even though estimates may not accurately represent the true population size, they could detect small relative changes in the population over time if bias is constant (White et al. 1982, Diefenbach 2005). Evaluating the precision, or repeatability, of a population estimator can be accomplished regardless if the true population size is known by conducting repeated surveys during a period in which the population is not expected to change, and assuming bias is constant (White et al. 1982, Diefenbach 2005).

Historically, deer population estimates have been derived from a variety of survey techniques (Lancia et al. 1994, Gill et al. 1997, Drake et al. 2005). Distance sampling is a popular technique used for estimation of wildlife densities and was developed specifically to address some of the limitations of conventional deer survey techniques (Gill et al. 1997, Buckland et al. 2001, Ward et al. 2004). Distance sampling has proven more efficient than most conventional methods (Burnham et al. 1985, Gill et al. 1997, Buckland et al. 2001) and does not require all animals within a predetermined area be detected (Gill et al. 1997, Buckland et al. 2001). Distance sampling techniques are potentially well-suited to monitor deer in forested areas, where detection or visibility varies continuously (Gill et al. 1997, Buckland et al. 2001, Focardi et al. 2001). Ground thermal infrared imaging (ground imaging) has grown in popularity as a technique to which distance sampling can be applied (Gill et al. 1997, Belant and Seamans 2000, Focardi et al. 2001, Ward et al. 2004). However, spotlight surveys are the most popular and commonly used method to apply distance sampling because of low cost and simplicity (Fafarman and DeYoung 1986, Whipple et al. 1994, Collier et al. 2005). Ground imaging increases detection and reduces observer bias compared with spotlight surveys by reducing animal disturbance (Belant and Seamans 2000). However, high cost of the device must be justified by an increase in accuracy and precision of density estimates (Belant and Seamans 2000, Focardi et al. 2001).

Distance sampling requires relatively large sample sizes and randomly placed lines or transects (Buckland et al. 2001). Random line placement helps ensures a representative sample of the mean relevant distance, which is required for a valid density estimate. However, it is common practice to use established tracks and roads as transects from which to survey for practicality and safety reasons (Gill et al. 1997, Heydon et al. 2000, Ward et al. 2004). Aerial imaging is a relatively new technique believed to provide more reliable estimates of wildlife population density (Naugle et al. 1996) because recent approaches have used non-overlapping, random transect placement to obtain a more representative sampling (Naugle et al. 1996, Kissell and Tappe 2004, Kissell and Nimmo 2011).

Aerial imagery has primarily been based on forward-looking infrared (Naugle et al. 1996, Bernatas and Nelson 2004, Gregory 2005) but results have been varied (Naugle et al. 1996, Dunn et al. 2002, Haroldson et al. 2003) because detection may be affected by vegetation type (Dunn et al. 2002), and flying height (Wiggers and Beckerman 1993). However, recent modifications allow use of a vertical position for the infrared imager (aerial imaging; Kissell and Nimmo 2011) along with improved thermal imaging resolution and temperature differentiation, which have improved detection rates and have reduced differences in visibility and blind spots from deciduous vegetation (Gill et al. 1997, Kissell and Nimmo 2011). A probability of detection must be provided or a complete census for the area sampled must be assumed (White et al. 1982) and, as with ground imaging the high initial cost must be justified by a significant increase in accuracy and precision of density estimates (Naugle et al. 1996, Focardi et al. 2001).

As wildlife managers continue to use spotlight, ground imaging, and aerial imaging surveys to estimate deer density, each sampling method's assumptions should be evaluated and comparisons made with alternative estimation techniques required to evaluate accuracy and precision (Anderson 2001, Collier et al. 2005). However, my study was based on an open population of an unknown number of deer I do not know which technique provides the more accurate density estimate. Therefore, because the success of the spotlight, ground imaging, and aerial imaging surveys has been variable (Wiggers and Beckerman 1993, Naugle et al. 1996, Dunn et al. 2002, Belant and Seamans 2000), I compared density (no. of deer/km2), detection probability, and precision for each of the 3 techniques. I also evaluated assumptions associated with each technique.

STUDY AREA

Arnold Air Force Base encompasses 15,816 ha in Coffee and Franklin Counties, Tennessee. The base is approximately 113 km southeast of Nashville and positioned between Manchester, Tullahoma, and Winchester. Arnold Air Force Base is within the Duck River and Elk River watersheds. It is located within the Interior Low Plateau geomorphic province. The Interior Low Plateau is composed of 2 physiographic provinces, the Central Basin and the Highland Rim. Arnold Air Force Base is within the Eastern Highland Rim physiographic province (U.S. Department of Defense 2006).

Most of Arnold Air Force Base is composed of either cultivated loblolly pine (*Pinus taeda*) plantations (2,223 ha) or continuous hardwood forest (9,329 ha), which consisted mostly of southern red oak (*Quercus falcata*), scarlet oak (*Quercus coccinea*), post oak (*Quercus stellata*), black oak (*Quercus velutina)*, white oak (*Quercus alba*), willow oak (*Quercus phellos*), water oak (*Quercus nigra*), and blackjack oak (*Quercus marilandica*). The forest understory included dogwoods (*Cornus* spp.), maples (*Acer* spp.), sassafras (*Sassafras albidum*), sourwood (*Oxydendrum arboretum),* blueberries (*Vaccinium* spp.), hickories (*Carya* spp.), and blackgum (*Nyssa sylvatica*). Grasslands and early successional vegetation in utility rights-of-way occupied 898 ha. The remaining 1,895 ha were occupied by buildings and structures, mowed areas, and other open areas (including landfills and roads; U.S. Department of Defense 2006).

Arnold Air Force Base commander and his staff of military personnel and civil service employees are responsible for the overall planning, direction, scheduling, assignment, and funding associated with mission requirements. The US Fish and Wildlife Services and Tennessee

Wildlife Resource Agency are cooperating agencies with the base. Arnold Air Force Base is managed jointly by Department of Defense and Tennessee Wildlife Resource Agency, while the Security Area is managed through Arnold Engineering Development Center and is open to hunting only by its employees. The Security Area is surrounded by a wire fence 2-m in height. The area outside the Security Area is open to public hunting and is managed as a Wildlife Management Area (WMA) through Tennessee Wildlife Resource Agency. The WMA is divided into 6 units (U.S. Department of Defense 2006).

METHODS

Ground imaging.—I collected ground imaging data from a vehicle with the assistance of experienced Tennessee Wildlife Resource Agency biologists. I equipped the vehicle with a thermal imager (ProTech©, Thermal-Eye 250D, Berea, OH), video recorder (Sony Walkman©, GV-HD700, Park Ridge, NJ), hand-held weather unit (Kestral©, 4500, Sylvan Lake, MI), GPS unit (Garmin Nuvi©, 650, Chicago, IL), 2 spotlights ($\geq$ 1 million candle power), and a laser rangefinder (accurate to within 0.5 m). The video recorder was powered by an in-cab inverter to maintain full power and clarity on monitors throughout sampling.

I established 1 continuous, non-overlapping transect across the Security Area designed to prevent double-counting (Anderson et al. 1979) and provide representative coverage of the area (Fig. 2; Buckland et al. 2001). I used a transect length of 42.6 km for the Security Area. I drove each transect on 4 separate occasions over 2 nights between 1800 and 2300 hrs on 26 and again on 27 January 2010, and between 0200 and 0700 hrs on 27 and again on 28 January 2010. I considered each time the transect was driven a trial and treated each trial as an individual event. Each trial averaged 3 hours with 6 hours between trials. I surveyed only the right side of the transect for safety reasons, creating a sampling fraction = 0.5. I instructed drivers not to exceed 16 kph.

Deer, or clusters of deer, were recorded when they were perpendicular to the vehicle. I defined a cluster as all deer within a 20-m radius of initial sighting. I recorded the direction and distance from the perpendicular position to the individual or cluster center to the nearest meter with aid of spotlight and rangefinder. I also recorded the number of individuals within each cluster along with GPS location of vehicle. In cases where flushing occurred before a perpendicular position was acquired, I used the straight-line distance from where the animal was initially spotted, direction, observer location, and trigonometry to calculate perpendicular distance (Mills 2007).

I used Program DISTANCE 6.0, version 2 (Buckland et al. 2001, Thomas et al. 2002) to calculate detection probability across all perpendicular distances. I obtained insufficient data from open and forested areas to justify separation (Gill et al. 1997). As recommended by Buckland et al. (2001), I fit 8 a priori models to the data by using the uniform and half-normal key functions with no adjustments or cosine, simple polynomial, and hermite polynomial adjustments. I used minimum Akaike Information Criterion corrected for small sample size (AIC_c; Hurvich and Tsai 1989) for model selection of each site. I ranked models according to $\Delta_i AIC_c$ ($\Delta_i AIC = AIC_{ci} - AIC_c min$) and AIC_c weights (w_i) and used the weights to determine the relative importance of potential sources of variance within the models (Posada and Buckley 2004). I used model averaging to estimate population density (Buckland et al. 2001).

Spotlight Surveys.—I performed 4 spotlight surveys for the Security Area (8–10, 12 February 2010), 2 weeks following aerial imaging and ground imaging surveys. I began each spotlight survey at 1900 hrs and duration was 4–5.5 hrs, depending on number of deer sightings.

I conducted spotlight surveys under similar weather conditions to those during the imaging and ground imaging surveys and followed standard protocol used by Mitchell (1986) for road spotlight surveys of white-tailed deer. I used a driver, recorder, and 2 observers in an equipped vehicle to perform spotlight surveys. I equipped the vehicle used for spotlight surveys with the same hand-held weather unit, GPS unit, spotlights, and range finders used during the ground imaging surveys.

I used the same continuous, non-overlapping transect used during ground imaging sampling of the Security Area for spotlight surveys (Fig. 2). As with ground imaging surveys, I only surveyed the right side of the transect, creating a sampling fraction = 0.5 and again instructed drivers not to exceed 16 kph during the survey. I performed spotlight counting procedure and density analysis identical to the ground imaging surveys. As with ground imaging, I fit the same 8 a priori models to the data.

Aerial imaging.—For aerial vertical-looking infrared imagery (aerial imaging) sampling, I used equipment and methodology for detection consistent with Kissell and Tappe (2004), and Kissell and Nimmo (2011). I used a Mitsubishi IR-M500 thermal infrared imager (Mitsubishi Electric Corporation, Canada) equipped with a 50-mm lens mounted in the belly of a Cessna 182 fixed-wing aircraft. The camera remained stationary for the entire flight, with the head perpendicular to the flight path. I used mid-infrared and far-infrared wavelengths (1.2–5.9 µm) and I sent output to a digital video cassette recorder (Sony GV-D1000; Sony Electronic Inc., Park Ridge, NJ). I routed the GPS signal through a video encoder-decoder (VED) and it was recorded on the audio portion of the tape. This labeled the video with a continuous stream of positions, time, date, speed, and altitude data (Fig. 3). I reviewed and analyzed recorded video using a video-editing program (Avid Xpress DV, Version 3.0; Burlington, MA) and a 1000-line, 33-cm black-and-white monitor (Sony PVM-137; Sony Electronic Inc., Park Ridge, NJ). I identified thermal signatures of deer by unique shape and brightness relative to the background, and then exported them as 8-bit tagged information file format (TIFF) images (Fig. 3). I geo-referenced TIFF images using the encoded GPS data and then transferred them into GIS (ArcView GIS, Version 9.3, Redlands, CA). I converted GPS locations to Universal Transverse Mercator (UTM) coordinates to calculate area and distances (Kissell and Tappe 2004, Change 2006, Kissell and Nimmo 2011).

I conducted 4 separate flights to coincide with each trial for ground sampling. I treated each flight as an independent event. Non-overlapping, parallel transects (*n* = 14) were established for the Security Area totaling 39.3 km (Fig. 4). I randomly placed the first transect for each flight. All others were systematically placed parallel and spaced approximately 400 m apart. Flight-line spacing and GPS information minimized the potential for double counting. I established 10 locations outside the perimeter where personnel on the ground observed the number of deer using hand-held thermal imaging immediately after flyover as an independent measure of detection. Transects were flown in a north-south direction. Flights were conducted at 457-m aboveground level (AGL) and approximately 120 km/hr. I conducted all flights when conditions were suitable for flying and detectability of deer was not hampered (Gregory 2005, Kissell and Nimmo 2011).

I used known area and the number of deer per transect area to determine a raw deer density estimate (deer/km^2). I treated density of each transect (*n* = 14) per flight trial as an observation and calculated sample means using the 14 observations of strip transect density. I used a Proc Mixed model analysis of variance in SAS 9.2 (SAS Institute Inc., Cary, NC) to compare density means and variance across flight trials. I used the coefficient of variation (CV), a measure of sampling variance, as my measure of precision. I also calculated detection probability using comparisons with the number of deer observed during the ground observations (Kissell and Nimmo 2011). For the 10 ground locations, I determined the minimum detection probability by dividing the number of deer observed from the ground by the number seen from aerial imaging for those locations.

RESULTS

I observed deer from 0–521 and 0–415 m for ground imaging and spotlight surveys, respectively. However, as recommended by Buckland et al. (2001) I truncated lower distances of the distribution by 20 m to offset the detection line because there were few detections near the transect line creating a ‘shoulder’ on the frequency distribution. I also truncated 5% of the ground imaging and 10% of the spotlight data from the upper portion of detection distances because observations at extreme distances would only confound information used for estimating the detection function and add sampling variance to the density estimate (Buckland et al. 2001). I obtained 62 observations from 20–125 m (Ground imaging; Fig. 5) and 68 deer observations from 20–134 m (Spotlight; Fig. 6) after truncating the data. Average cluster size was 2.25 (SE = 0.16) and 2.10 (SE = 0.15) for ground imaging and spotlight, respectively. Based on model averaging, the estimated deer density (no. of deer/km^2) for ground imaging and spotlight was 10.9 (CV = 10.1 %) and 21.4 (CV = 15.2 %), respectively (Table 3 and 4).

I observed 39 clusters of deer during the 4 aerial imaging trials (Fig. 4). Deer densities ranging from 4.13 to 6.77 deer/km^2 were observed during the 4 flight trials with an average deer density of 5.53 deer/km^2 (CV = 23.8 %). Probability of observing deer in the imagery was $\geq$88.9 %. I also observed deer cluster distribution by aerial imaging revealed a tendency for deer to affiliate with roads (Fig. 4). Therefore, I conducted a post-hoc analysis and tested for potential road bias using a 1-sample, 1-sided *t*-test to determine if observed distances were at least as far away from roads as random distances. I used my aerial imagery in GIS to calculate the mean distance to roads (observed sample). I then calculated the mean and standard deviation (SD) of distances from roads for the random locations and used the SD to calculate the standard error (SE) for the *t*-test. I repeated this procedure 1,000 times to obtain a mean random distance and SD and used my iterations as the number of observations for the *t*-test to find the critical *t*-value. The mean distance to roads calculated from aerial imaging observations was 110 m and the mean distance to roads calculated from the random observations was 145 m (SE = 0.57). The corresponding critical $t_{\alpha=0.05,\ df=999} = 1.65$ (Zar 2010) and calculated a $t = -61.05$.

DISCUSSION

Technique comparison.—My results indicated spotlight and ground imaging provided greater precision than aerial imaging. However, all 3 techniques provided sufficient precision for management (CV < 25%; Skalski et al. 2005). Density estimates for the Security Area differed among the 3 techniques. Spotlight and ground imaging yielded density estimates 2 to 4 times greater than aerial imaging. However, aerial imaging revealed a tendency for deer to be closer to roads, indicating potential bias for spotlight and ground imaging techniques (Fig. 4).

During spotlight and ground imaging sampling, I noticed a peak in deer detections occurred >20 m from the transect line (Fig. 7). There may be 2 explanations for this finding. First, deer may use that area next to the road but showed a response to the vehicle by moving away prior to being detected, thus violating a key assumption of distance sampling (Buckland et al. 2001, Ward et al. 2004). Second, deer on the Security Area may have avoided areas near the road, regardless of the disturbance, thus creating a ‘shoulder’ on the frequency distribution. However, it is difficult to discern which of the 2 possibilities is most likely. If deer are moving away from the road because of disturbance and being counted further away from transects, truncation of the data would result in overestimation of density because an area of higher density was effectively used as zero distance (Ward et al. 2004).

Deer cluster distribution by aerial imaging revealed a tendency for deer to affiliate with roads (Fig. 4). Observed deer distances from roads were less than random distances. Association between transect and animal is a violation of another important assumption of distance sampling (Buckland et al. 2001, Ward et al. 2004) and can lead to overestimation of density by distance sampling techniques (Gill et al. 1997, Buckland et al. 2001). Random transect placement ensures density estimates are representative of the entire area and not just the transect areas (Buckland et al. 2001). However, Ward et al. (2004) found a common practice was to use established tracks, especially roads, because vegetation, topography, and funding may not allow for random line transect establishment (Gill et al. 1997). Not having transects representative of the entire study area will bias the detection curve and thus the density estimate. It is possible that deer are selecting for the margin between roads and forest because food resources are potentially greater (Case 1978), as open fields and edge vegetation are commonly associated with areas adjacent to roads. Thus, my data suggest that use of established roads for spotlight and ground imaging sampling can lead to overestimation of deer density.

I found similar detection ranges with spotlight and ground imaging. Focardi et al. (2001) made similar observations and observed no difference in the performance between spotlight and thermal imaging in other species containing a tapetum lucidum. However, they did notice a difference between the 2 techniques in species lacking a tapetum lucidum, which they associated with a reduction in detection because of a lack of visibility with spotlight. Because of similar performance, the high initial cost of a thermal camera for ground imaging ($4,000–15,000) may not be justified compared with spotlight surveys to determine white-tailed deer density. My results also indicated all 3 techniques can provide levels of precision sufficient for making long-term management recommendations (<25%; Skalski et al. 2005). However, of the 3 techniques, aerial imaging is least likely to violate assumptions and is not susceptible to road bias. Robustness to road bias may justify high initial cost ($10,000 for my study) of aerial imaging, depending on species, study scale, and site composition. I note the cost of aerial imaging is a fee charge and any additional surveys would require another cost.

Evaluation of assumptions.—A large sample size is important for the success of distance sampling. Lower sample sizes provide lower. Generally > 60 observations are needed for reliable density estimates (Buckland et al. 2001). On the Security Area, I barely met this requirement over 4 different sampling sessions.

Advancement in technology and methodology for aerial imaging has reduced personnel time (Dunn et al 2002, Focardi et al. 2001, Gregory 2005) and labor intensity compared with previous aerial imaging studies that required circular plots (Wiggers and Beckerman 1993, Haroldson et al. 2003, Bernatas and Nelson 2004). It also provides adequate cover over a short period of time to ensure population closure (White et al. 1982). Use of GPS-placed transects reduce deviation from the transect line, thus enhancing density estimation (Leptich et al. 1994, Naugle et al. 1996). The ability to cover large areas over short periods of time also helps offset high initial cost because similar distance sampling techniques require increased sampling efforts or multiple teams to cover the same area over a similar period.

Aerial imaging minimized animal disturbance and improved detection rates compared with traditional visual surveys (Naugle et al. 1996, Havens and Sharp 1998, Focardi et al. 2001). Historically, probability of detection has been an area of concern in the development and use of aerial infrared imagery. High probability of detection (>85%) should be expected where vegetation cover is limited (Parker and Driscoll 1972, Naugle et al. 1996). Of the 36 deer seen at the 10 ground verification sites, 32 of them were confirmed by a ground crew. However, it is not known if aerial imaging misclassified thermal signatures as deer, if the ground crew missed deer, or a combination, resulting in a minimum detection probability of ≥88.9 %. Ground verification occurred in a mixture of open fields and deciduous hardwood stands comprising >80% of the vegetation. Tree foliage can obstruct thermal radiation and interfere with detection of animals (Wiggers and Beckerman 1993). Conducting surveys in deciduous forest during winter increases visibility (Naugle et al. 1996, Gill et al. 1997, Kissell and Nimmo 2011). However, a dense pine canopy can make detection difficult (Dunn et al. 2002, Gregory 2005). I did not have any ground verification sites in dense pine vegetation on the Security Area (<10%) and acknowledge deer could have been missed in this vegetation type because detection probability varies based on site composition. Site composition is important to detection probability and aerial imaging can be limited in areas with considerable pine cover. Future research should stratify study areas to create a detection curve for distance sampling techniques and a detection probability for aerial imaging by vegetation type.

MANAGEMENT IMPLICATIONS

My data suggest truncation of lower extremes of the detection curve for distance sampling techniques will overestimate deer populations if transects are not representative of the study area. Therefore, although spotlight and ground imaging surveys can provide managers with a precise estimate of deer density, I do not recommend their use unless random transects can be applied or existing tracks provide representative coverage of the study area. Aerial imaging is less likely to violate distance sampling assumptions. However, because of its high initial cost aerial imaging is probably most applicable for study areas with a similar or greater extent as in my study and random transect placement is not possible. If distance sampling is going to be used, I do not recommend ground imaging because of the greater cost. I recommend managers carefully examine the limitations with each survey technique and use those only appropriate.

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APPENDIX

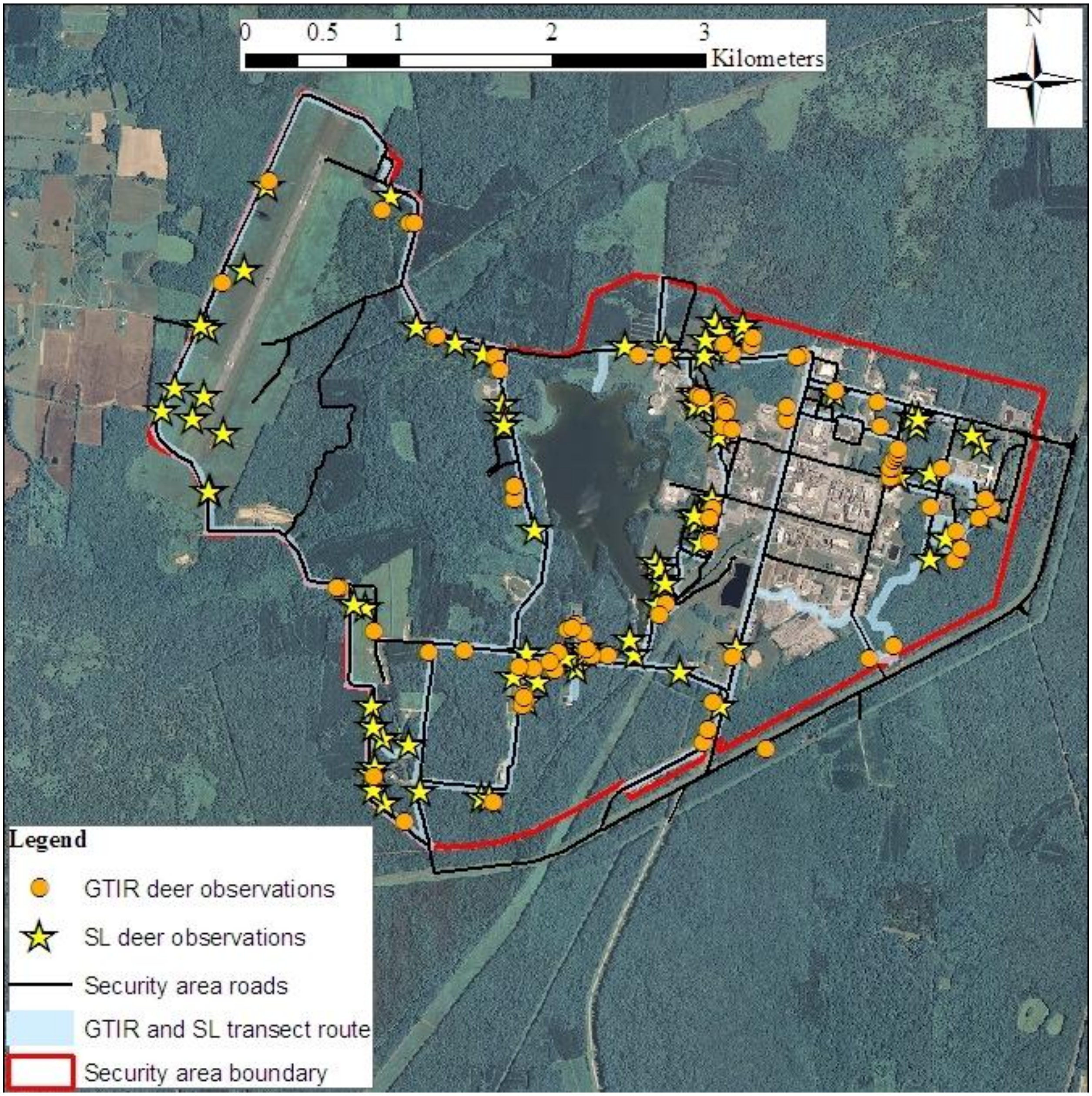

Figure 2. Transect driven for each ground thermal infrared (ground imaging) and spotlight survey (SL) trial and all clusters of white-tailed deer observed within the Security Area of Arnold Air Force Base, Tullahoma, Tennessee, USA, 26–28 January, 2010 for ground imaging surveys, and 8–12, February 2010 for spotlight surveys.

Figure 3. Aerial vertical-looking infrared (imaging) image of white-tailed deer within the Security Area of Arnold Air Force Base in Tullahoma, Tennessee, USA, 27 January, 2010. The bottom of the image contains the labeled portion of the video that provided continuous stream of positions, time, date, speed, and altitude data.

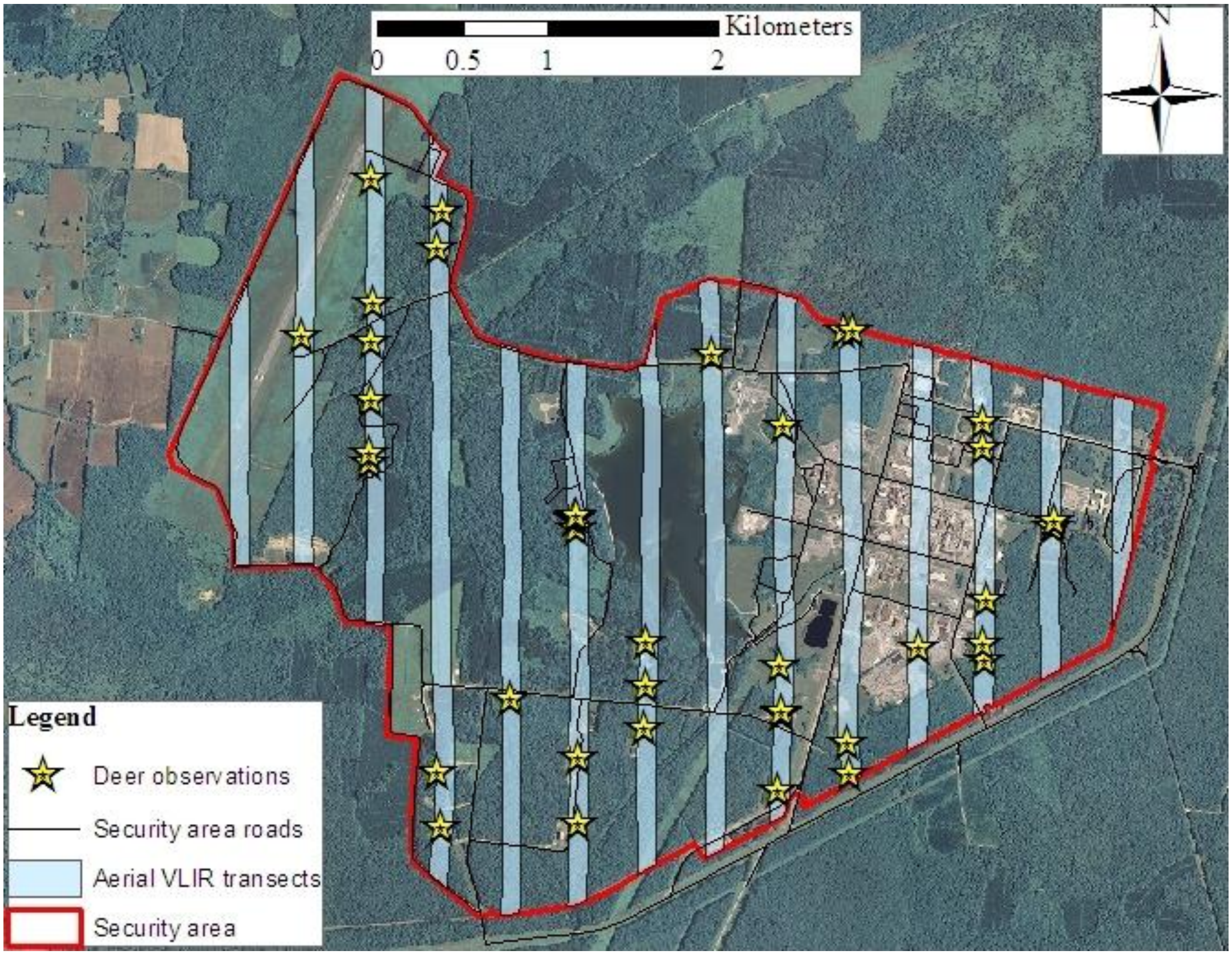

Figure 4. Aerial vertical-looking infrared (imaging) transects flown during each trial and all individual or clusters of white-tailed deer observed within the Security Area of Arnold Air Force Base in Tullahoma, Tennessee, USA, 26–28 January, 2010.

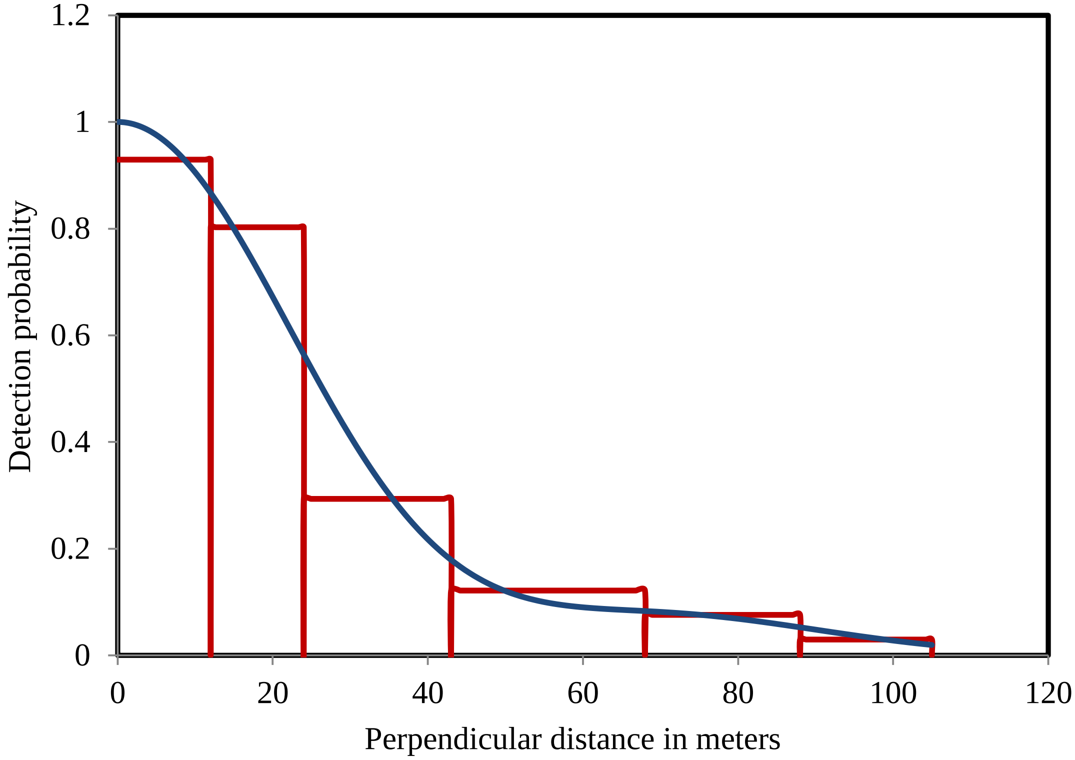

Figure 5. Detection probability curve of the ground thermal infrared (ground imaging) dataset for the Security Area of Arnold Air Force Base, Tullahoma, Tennessee, USA, 26–28 January, 2010. We truncated observations on the upper (5%) and lower (offset 20 m) extremes of the distribution.

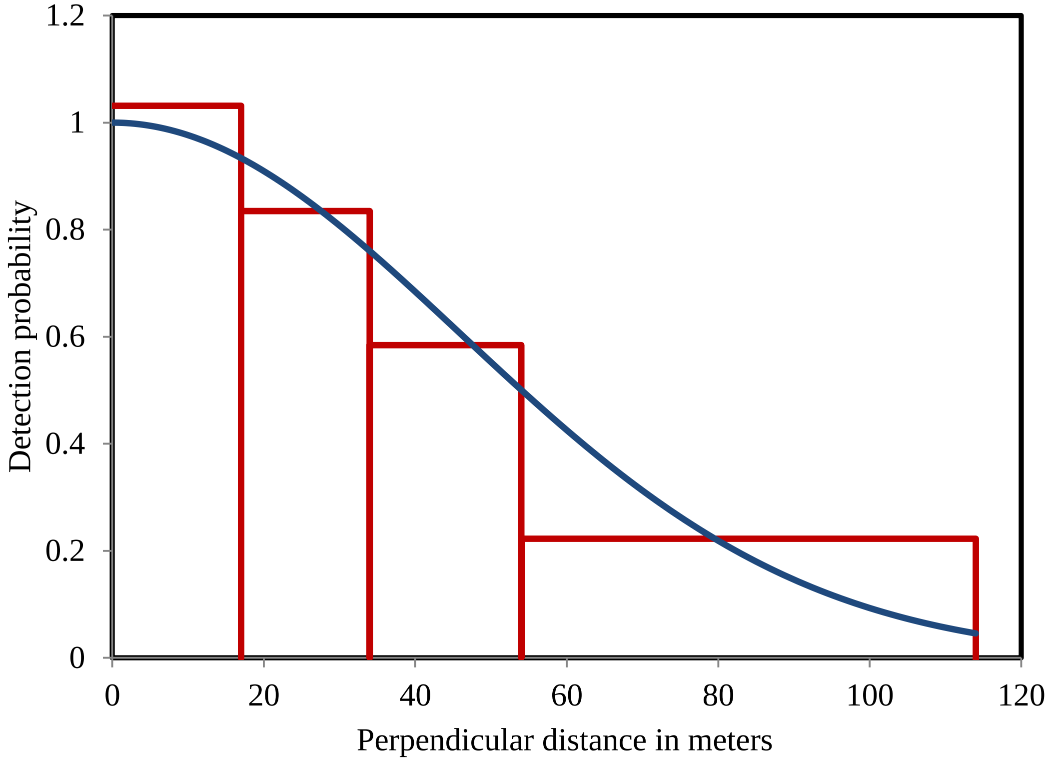

Figure 6. Detection probability curve of the spotlight dataset, for the Security Area of Arnold Air Force Base, Tullahoma, Tennessee, USA, 8–12 February, 2010. We truncated observations on the upper (10%) and lower (offset 20 m) extremes of the distribution.

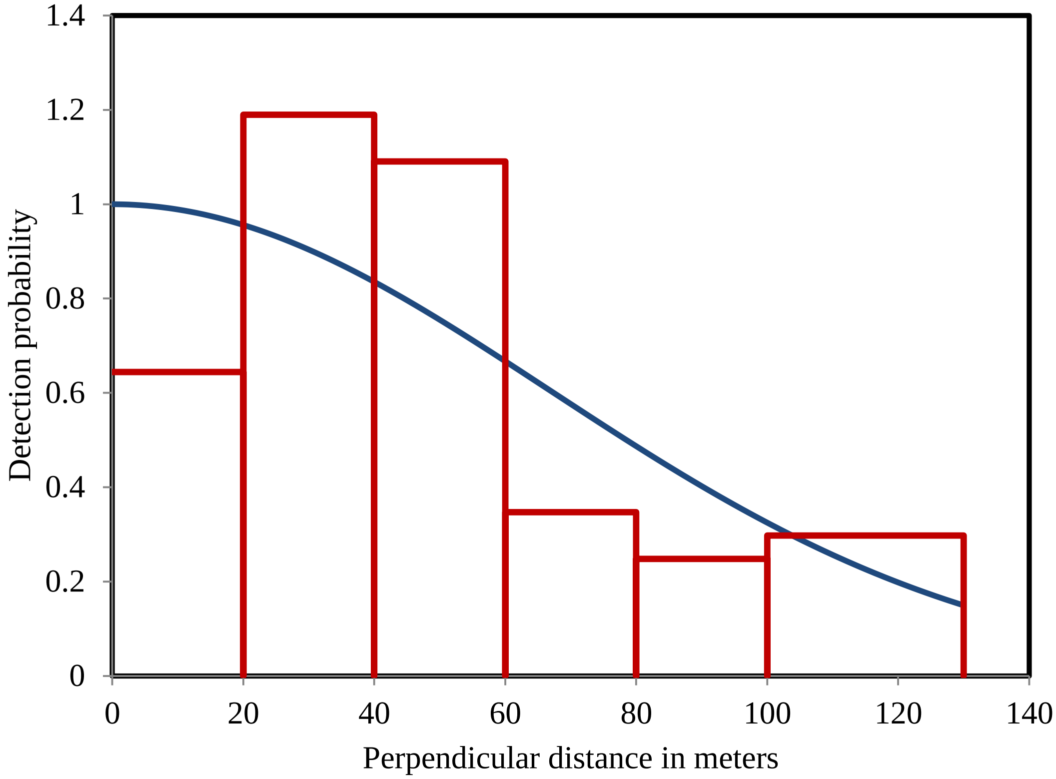

Figure 7. Detection probability curve of the spotlight dataset, for the Security Area of Arnold Air Force Base, Tullahoma, Tennessee, USA, 8–12 February, 2010. Observations show evidence of road avoidance before the lower extremes of the distribution were truncated (offset to 20 m).

Table 3. All models used in distance sampling analysis of ground thermal infrared surveys with truncation of the upper portion of detection distances to a distance of 125 m, with truncation of lower distances of the distribution by 20 m for white-tailed deer in the Security Area, Arnold Air Force Base, Tullahoma, Tennessee, USA, 8–12 February, 2010.

Model	AIC_c[a]	ΔAIC_c	ω_i[b]	D[c]	CV[d]
Left and right truncation (20-125 m)					
Half-normal cosine adjustment	187.87	0.00	0.14	17.05	0.13
Uniform cosine adjustment	190.11	2.23	0.12	16.64	0.13
Half-normal no adjustment	191.83	3.95	0.11	13.10	0.12
Half-normal simple polynomial adjustment	192.07	4.20	0.11	13.98	0.16
Uniform simple polynomial adjustment	192.43	4.56	0.11	14.00	0.12
Half-normal hermite adjustment	193.94	6.07	0.10	13.11	0.14
Uniform hermite adjustment	202.05	14.18	0.07	9.56	0.11
Uniform no adjustment	246.28	58.41	0.01	4.75	0.07
Model average				10.89	0.10

[a] Akaike's Information Criterion adjusted for small n

[b] Akaike wt.

[c] Density (no. of deer/km^2)

[d] Coefficient of variation

Table 4. All models used in distance sampling analysis of spotlight surveys with truncation of the upper portion of detection distances to a distance of 134 m, with truncation of lower distances of the distribution by 20 m for white-tailed deer in the Security Area, Arnold Air Force Base, Tullahoma, Tennessee, USA, 8–12 February, 2010.

Model	AIC_c[a]	ΔAIC_c	ω_i[b]	D[c]	CV[d]
Left and right truncation (20–134 m)					
Half-normal no adjustment	189.26	0.00	0.14	23.61	0.13
Uniform cosine adjustment	189.47	0.21	0.14	22.65	0.11
Uniform simple polynomial adjustment	190.00	0.74	0.13	21.49	0.12
Half-normal simple polynomial adjustment	191.22	1.96	0.12	25.27	0.25
Half-normal cosine adjustment	191.23	1.96	0.12	25.09	0.19
Half-normal hermite adjustment	191.38	2.12	0.12	23.62	0.19
Uniform hermite adjustment	191.67	2.40	0.12	22.45	0.18
Uniform no adjustment	213.90	24.64	0.04	11.59	0.07
Model average				21.42	0.15

[a] Akaike's Information Criterion adjusted for small n

[b] Akaike wt.

[c] Density (no. of deer/km^2)

[d] Coefficient of variation

III. EFFECTS OF DEER DENSITY AND SEASON ON FORAGE AVAILABILITY AND NUTRITIONAL QUALITY

ABSTRACT

Overabundant white-tailed deer (*Odocoileus virginianus*; hereafter deer) can alter the structure and composition of the forest understory and limit food and cover resources for other wildlife species. Because managers would benefit from a better understanding of the effects of deer density on plant communities, I evaluated and compared forage availability at a high deer density (20.3 deer/km^2) site and a low deer density (7.7 deer/km^2) site during winter (February–March) and summer (June–July) within 4 forested vegetation types in the Eastern Highland Rim physiographic province of Tennessee, USA 2010. I also compared seasonal effects across the forested types and within early successional vegetation. I evaluated availability (kg/ha) of important deer forages across each vegetation type, deer density level, and season. I calculated availability of crude protein (CP) and total digestible nutrients (TDN) for available forage (CP or TDN x kg/ha) in the summer. Forage availability was consistently greater during summer within middle-aged and young pine stands at the low deer density site than the high deer density site. Both CP and TDN values were similar regardless of deer density. Forage availability was consistently greater across all vegetation types during summer than winter. I recommend that managers consider implementing management practices that would reduce deer density and increase forage availability when forage availability beings to decline and deer density estimates approach levels seen detrimental from other studies.

KEY WORDS early succession, forage availability, mature hardwoods, nutritional quality, *Odocoileus virginianus*, pine plantation, white-tailed deer

INTRODUCTION

White-tailed deer (*Odocoileus virginianus*; hereafter deer) are considered keystone herbivores in the eastern United States (Waller and Alverson 1997, Russell et al. 2001, Miller et al. 2003) and elevated density levels can significantly alter the structure and species composition of the forest understory (Casey and Hein 1983, Tilghman 1989, Russell et al. 2001, Rossell et al. 2005). Chronic overbrowsing limits the availability of food and cover for many wildlife species in the Eastern Deciduous Forest (Casey and Hein 1983, de Calesta 1994) and can have detrimental impacts on both faunal and floral species diversity (Augustine and Frelich 1998). Chronic overbrowsing also affects the overall health of the deer population by reducing available nutrition for body maintenance and productivity (Anderson and Katz 1993, Johnson et al. 1995, Webster et al. 2005, Jackson et al. 2007).

The magnitude of browsing on plant communities is largely dependent on deer density and the quantity and quality of available forage (Russell et al. 2001, Côté et al. 2004, Rossell et al. 2007). Deer density affects presence and magnitude of deer browsing (Russell et al. 2001). However, factors that may modify effects of deer density on forage quality and quantity are poorly understood and are not consistent across the species range (Russell et al. 2001). Study results have been affected by vegetative community, season, site location, deer density level, and year (Russell et al. 2001, Rossell et al. 2007).

Deer density may be a misleading indicator of habitat quality because of delayed population responses (van Horne 1983, Knops et al. 2000). Over time, selective deer browsing changes the composition of plant communities and affects forage quality (Ritchie and Tilman 1995, Ritchie et al. 1998, Knops et al. 2000, Rooney and Waller 2003). Although deer have some capacity to forage selectively based on energy and protein content, they are still forced to choose from what is available (Castleberry et al. 1999). Vegetative communities may be used at select times of the year based on nutritional demands associated with the current biological state of deer (Berteaux et al. 1998, Castleberry et al. 1999; Russell et al. 2001, Parker et al. 2009).

Therefore, availability of food and cover resources must be considered with population density to guide managers when considering deer harvest recommendations.

The objective of my study was to compare seasonal forage availability and nutritional quality for 2 areas with low and high deer densities within 4 vegetative community types in the Eastern Highland Rim physiographic province. Little information exists on the level of browsing that can be sustained before forage availability and nutritional quality wanes in various vegetation types within this region. I hypothesized deer density would affect nutrition and available forage (Russell et al. 2001, Horsley et al. 2003, Rooney and Waller 2003, Rossell et al. 2007). Furthermore, because deer exhibit selective browsing behavior, I expected density effects would differ by vegetation type (Ritchie and Tilman 1995, Ritchie et al. 1998, Knops et al. 2000, Rooney and Waller 2003).

STUDY AREA

Arnold Air Force Base encompasses 15,816 ha in Coffee and Franklin Counties, Tennessee. The base is approximately 113 km southeast of Nashville and positioned between Manchester, Tullahoma, and Winchester. Arnold Air Force Base is within the Duck River and Elk River watersheds. It is located within the Interior Low Plateau geomorphic province. The Interior Low Plateau is composed of 2 physiographic provinces, the Central Basin and the Highland Rim. Arnold Air Force Base is within the Eastern Highland Rim physiographic province (U.S. Department of Defense 2006).

Most of Arnold Air Force Base is composed of either cultivated loblolly pine (*Pinus taeda*) plantations (2,223 ha) or continuous hardwood forest (9,329 ha), which consisted mostly of southern red oak (*Quercus falcata*), scarlet oak (*Quercus coccinea*), post oak (*Quercus stellata*), black oak (*Quercus velutina)*, white oak (*Quercus alba*), willow oak (*Quercus phellos*), water oak (*Quercus nigra*), and blackjack oak (*Quercus marilandica*). The forest understory included dogwoods (*Cornus* spp.), maples (*Acer* spp.), sassafras (*Sassafras albidum*), sourwood (*Oxydendrum arboretum),* blueberries (*Vaccinium* spp.), hickories (*Carya* spp.), and blackgum (*Nyssa sylvatica*). Grasslands and early successional vegetation in utility rights-of-way occupied 898 ha. The remaining 1,895 ha were occupied by buildings and structures, mowed areas, and other open areas (including landfills and roads; U.S. Department of Defense 2006).

Arnold Air Force Base commander and his staff of military personnel and civil service employees are responsible for the overall planning, direction, scheduling, assignment, and funding associated with mission requirements. The US Fish and Wildlife Services and Tennessee Wildlife Resource Agency are cooperating agencies with the base. Arnold Air Force Base is managed jointly by Department of Defense and Tennessee Wildlife Resource Agency, while the Security Area is managed through Arnold Engineering Development Center and is open to hunting only by its employees. The Security Area is surrounded by a wire fence 2-m in height. The area outside the Security Area is open to public hunting and is managed as a Wildlife Management Area (WMA) through Tennessee Wildlife Resource Agency. The WMA is divided into 6 units (U.S. Department of Defense 2006).

METHODS

Vegetation stratification.—I divided Arnold Air Force Base into 2 treatments, based on deer density levels. I determined deer densities for the 2 study areas using the same infrared-triggered camera surveys method performed in early autumn (pre-hunting season) during 2008–2010 and averaged density over the three years.WMA Units 1 and 2 had low densities (7.7 deer/km^2), whereas the Security Area had a high density (20.3 deer/km^2). I stratified plant composition into 5 vegetation types, based on site characteristics and species composition. I defined mature upland closed-canopy hardwoods (MH; ≥30 years), young closed-canopy pines (YP; closed-canopy present and no thinning), middle-aged pines (MDP; row-thinned), mature pines (MAT; row-thinned and retention cut), and early succession for comparison. Row-thinning occurred at 15 years of age for MAT and MDP. MDP had been thinned ≥2 years prior to study. A retention cut was conducted in MAT ≥2 years prior to the study, leaving scattered pines approximately 30 years old. All 5 vegetation types were represented across both treatment areas and composed >65% of the study area (Fig. 8). The remaining area was occupied by buildings and structures, open water, mowed areas, or vegetation types not represented across both areas (<10%).

I did not include the early succession vegetation type in my analysis because it was maintained by different methods in the 2 deer density areas. Inside the Security Area, early succession consisted of barrens restoration, which involved an intensive burning regime. Repeated annual burning reduces woody composition and increases the herbaceous component (Lewis and Harshbarger 1976, Adams et al. 1982). On WMA Units 1 and 2, the majority of early succession represented powerline rights-of-ways, which were cut or mowed every few years and not burned. However, I did analyze the early succession data separately at the low deer density site and the high deer density site for seasonal comparison.

Important deer forages.—I compiled a list of important deer forages (Table 5) from species identified in the literature (Harlow and Hooper 1972, Warren and Hurst 1981, Miller and Miller 1999) and from preliminary browse transects conducted on the study area during summer 2009. I based deer browsing preference on extent of browsing present on each individual plant surveyed. I used a ranking (1–5) based on percentage of plant determined browsed by deer. I based rankings on increments of 20% with a ranking of 1 constituting 0–20% of the plant browsed. I only used those species determined as potential moderate-use (3) and greater for analysis.

Forage sampling.—I used GIS (ArcView GIS, Version 9.3, Redlands, CA) to map 5 100-m transects across each major vegetation type for both treatments areas. I excluded a 50-m buffer zone along each vegetation type boundary to prevent edge effects. I established all transects in an east-west direction to ensure systematic placement. I divided each transect into 5 sampling plots (2 m L × 1 m W) occurring at 10, 30, 50, 70, and 90 m. Within each sample plot, I collected all leaf biomass from woody species and entire herbaceous plants (excluding large stems) to represent consumable plant portions for each deer forage species $\leq$1.5 m aboveground. This process was repeated during winter (4 February–4 March) and summer (7 June–7 July) 2010. I used the original GPS locations for each transect during both seasons. However, I used a handheld GPS (Garmin GPSmap 76Cx, Olathe, Kansas) with a reported accuracy typically <10 m so transects did not start in the exact location for both seasons to ensure leaf biomass removal in winter did not affect data collection in summer.

I recorded wet weight (g) in the field for deer forages by species (Jones et al. 2009, Mixon et al. 2009, Iglay et al., 2010). I collected $\geq$30 g of wet-weight field samples for each forage species within each vegetation type, deer density level, and season for nutritional analysis. Forages were grouped into 3 forage classes (briers-brambles-vines, forbs, and trees-shrubs) for analysis. Forage samples were dried at 55^{o} C to constant mass in a forced-air oven, then re-weighed to determine wet:dry mass ratio for each species. I summed total dry matter available (kg/ha) across all 5 sampling plots per transect for each forage class. I ground forage samples using a 1-mm-mesh Wiley mill, and sent them to SURE-TECH^{TM} Laboratories (Indianapolis, IN) for analysis using traditional chemical methods (wet chemistry) for the summer 2010 collection period and reported determined crude protein (CP) and estimated total digestible nutrients (TDN) calculated primarily from acid detergent fiber. I determined nutritional forage availability by multiplying CP and TDN values by total forage availability (CP × kg/ha) and (TDN × kg/ha).

Analysis.— I evaluated availability of each forage class across each vegetation type, deer density level, and season. I used a mixed-model analysis of variance (SAS 9.2; SAS Institute Inc., Cary, NC) with a completely randomized split-plot study design, with a factorial between vegetation type and deer density level in the whole plot, and season in the subplot. I tested main effects of vegetation type, deer density level, season, and interactions for forage availability by forage class using. I also analyzed early succession using a mixed-model analysis of variance. However, I only evaluated forage availability by season because of the different management strategies in the 2 study areas for early successional habitat. I evaluated nutritional quality (CP and TDN) per forage class across vegetation type and deer density level, using similar analysis techniques. However, because I only performed nutritional analysis for the summer collection period, I have no seasonal effect. Therefore, my nutritional quality model was a completely randomized design with a factorial between vegetation type and deer density. I used log transformations to meet the assumption of normality in both models and used back-transformed least-squares mean estimates for both interaction and main effect means.

RESULTS

Vegetation × density interactions occurred in briers-brambles-vines and trees-shrubs. Forb availability showed no density main effect or density interaction (Table 6). Forage availability varied among vegetation types by season (Table 7). During summer, more briers-brambles-vines were available in MDP and YP, more forbs were available in MDP, and more trees-shrubs were available in MDP and YP at the low deer density site than at high deer density site. During winter, more briers-brambles-vines were available in MDP and more trees-shrubs were available in MDP at the low deer density site than at high deer density site.

A vegetation × density interaction occurred in all 3 forage classes for both CP and TDN availability (Table 6). CP and TDN estimates were similar at the low deer density and high deer density sites (Table 8). A vegetation × season interaction occurred in forbs and trees-shrubs and a season main effect occurred for briers-brambles-vines (Table 6). Forage availability was consistently greater during summer than winter except for forbs in MH because they were largely absent both seasons. Forage availability was relatively low ($\leq$ 50 kg/ha) during winter across all vegetation types and forage classes (Table 7). The number of important deer forage species was similar among vegetation types (Table 9). However, the low deer density on average showed 1.4 more important deer forage species per vegetation type.

Total seasonal forage availability for all important deer forages within early succession was greater in summer than winter for both the high deer density (3,287 vs. 64 kg/ha) and low deer density (6,363 vs. 125 kg/ha, Table 10). All 3 forage classes were more abundant in summer than winter at the low deer density. However, only forbs and briers-brambles-vines were more abundant in summer than winter at the high deer density. At the low deer density site, the largest seasonal difference was in trees-shrubs, whereas briers-brambles-vines and forbs were most important at the high deer density site.

DISCUSSION

Important deer forage species responded differently to deer density by vegetation type. Differences were most often found in MDP and YP. The additional protective cover in these vegetation types may have led to increased deer foraging pressure. Other work has found deer selectively browse across forest types in order to increase their fitness and indicate they can influence forested communities (Augustine and McNaughton 1998, Russell et al. 2001, Liang and Seagle 2002). In deciduous forests deer herbivory has driven highly palatable plants toward extirpation, while less-palatable plants remained in the understory (Anderson 1994, Augustine and Frelich 1998). deCalesta (1994), Horsley et al. (2003), and Banta et al. (2005) have also reported changes in hardwood forest understory species composition with increasing deer densities.

I found no density effects or interactions of density with vegetation type on forbs. Forbs were generally more available in MDP and YP at the low deer density site, but forb coverage was relatively limited at all sites. Lashley et al. (2011) and Shaw et al. (2010) noted limited forb availability in forested habitat because of limited sunlight and competition among woody species. Ritchie et al. (1998) and Ritchie and Tilman (1995) found legumes and woody plants more abundant in enclosures where deer browsing had been eliminated, but grasses and forbs were more abundant in the presence of deer. Banta et al. (2005), deCalesta (1994), Horsley et al. (2003), and Tilghman (1989) found no impacts on herbaceous cover at 5 different deer densities (0–30 deer/km^2) in uncut hardwood forest in northwestern and north-central Pennsylvania.

The biggest density effect occurred with trees-shrubs and briers-brambles-vines. This is similar to previous work that showed deer browsing decreased seedling survival rates of preferred woody plant species (Rossell et al. 2005). Liang and Seagle (2002) reported a deer density (20–30 km^2) similar to that at my high deer density site reduced density of important woody species. When total forage availability was summed across all forage classes and vegetation types, I saw a decrease of >1,300 kg/ha, suggesting deer density was impacting important deer forage availability at Arnold Air Force Base.

Nutritional availability analysis of CP and TDN showed vegetation × density interactions for all forage classes with an inverse relationship between nutritional availability and deer density. Several studies have reported decreases in available soil nutrition in coordination with an increase in unpalatable plants following increased deer browsing (Ritchie and Tilman 1995, Ritchie et al. 1998, Rooney and Waller 2003). Knops et al. (2000) recorded an increase in soil nitrogen levels when deer were excluded. It is believed overbrowsing of palatable deer forage species reduces competitive interactions, which allows increased production of unpalatable species. Banta et al. (2005), deCalesta (1994), and Horsley et al. (2003) all reported decreases in palatable forbs and flowering plants with increasing deer density, while unpalatable ferns and grasses increased.

Almost identical responses were seen between CP and TDN with a vegetation × density interaction occurring in all 3 forage classes for both CP and TDN availability analysis (Table 6). Protein and energy are closely correlated in forage plants (Westoby 1974, Robbins 1993). Jones et al. (2009) also expected correlation between CP and digestible energy to occur, especially in regions of good soil fertility. I used TDN estimates from deer forage analysis because it is commonly used as a proxy for digestible energy (Mangino et al. 2002) and can be obtained using wet chemistry forage analysis, which tends to have lower variability than other approaches (Oba and Allen 2005).

The number of important deer forage species was similar among vegetation types (Table 9). Other studies have shown browsing at deer densities $\geq$30 deer/km^2 can cause dramatic shifts in species composition, and eventually decrease species richness of trees, herbs, and shrubs (Tilghman 1989, Healy 1997, Augustine et al. 1998, Rossell et al. 2005). Chronic overbrowsing has affected dominant species in both the understory (Webb et al. 1956, Bowers and Sacchi

1991) and canopy layers in various vegetative communities (Harlow and Downing 1970, Tilghman 1989). I did not measure total species richness, but only the number of species identified as an important deer forage plant and my finding that browsing had no effect on number of important deer forage species should be considered with caution because of the intermittent distribution of several species (Rossell et al. 2007; Table 11). Although there was no appreciable difference in the number of deer forage species, it is possible true species richness was lower at the high deer density site. Webb et al. (1956) indicated where deer density may not be sufficiently elevated to eliminate important herbs from forest understories, deer may increase species diversity of herbaceous layers by reducing competition and regeneration of important trees and shrubs.

Information evaluating the effects of deer density on legumes and other herbaceous species, especially in early succession, is limited (Russell et al. 2001, Rossell et al. 2005). This is surprising considering the amount of important deer forage plants available in this vegetation type, and especially considering forbs often represent more than half of a deer's diet during spring and summer (Whittington 1984, Rossell et al. 2005). Forbs are important contributors to deer carrying capacity estimates (Iglay et al. 2010, Shaw et al. 2010, Lashley et al. 2011). However, availability of sunlight and moisture may confound the effects of deer density, and interactions among these factors should not be discounted when formulating future research questions (Saunders and Puettmann 1999, Russell et al. 2001).

It is commonly accepted that important deer forage availability is lower during winter than summer (Wallmo et al. 1977). As expected, briers-brambles-vines showed a season main effect with availability consistently lower across all vegetation types during winter (Table 6). Also, within early succession, which was only analyzed for seasonal effects, forage availability for all 3 forage classes was greater in summer than winter at the low deer density site (6,363 vs. 125) and for briers-brambles-vines and forbs at the high deer density site (3,287 vs. 64 kg/ha). However, trees-shrubs were not dominant within early succession at the high deer density site because early succession was maintained by frequent prescribed fire. Early succession at the low deer density site was maintained by frequent mowing. Thus, trees-shrubs were the dominant cover as mowing does not kill trees-shrubs, but only promotes resprouting. Field management studies have found similar results (Lewis and Harshbarger 1976, Adams et al. 1982, Gruchy et al. 2009).

Both forb and trees-shrubs showed a vegetation × season interaction effect, which was a result of canopy closure (Table 6). Lashley et al. (2011) showed less forage available in closed-canopy forest as compared to stands that allowed more sunlight through the canopy following retention cutting and prescribed fire. There was no forb interaction effect in MH because forbs were essentially absent during both winter and summer (Table 7). Lashley et al. (2011) and Shaw et al. (2010) also saw similar results with a lack of forb availability in MH vegetation. The interaction seen in trees-shrubs was a result of MH and YP having similar forage availability estimates from summer to winter than in MAT and MDP, which was a result of MH and YP having less trees-shrubs forage available due to closed-canopy.

MANAGEMENT IMPLICATIONS

When managing deer populations, landowners should evaluate the quantity and quality of available forage across the dominant vegetation types when considering management options. My data suggest deer density effects on forage availability and quality may differ by vegetation type; however, deer density at or above the high density level in my study (>20 km^2) can reduce briers-brambles-vines and trees-shrubs forage availability to levels that may be detrimental to other wildlife species, especially those dependent upon dense understory growth. This density is greater than the estimated carrying capacities of 15.4 deer/km^2 for the Piedmont Plateau (Whittington 1984) and 12 deer/km^2 (Barber 1984, Jenks et al. 2002) for the Eastern Mixed Forest regions. Therefore, I recommend that managers consider implementing management practices that would reduce deer density and increase forage availability when forage availability beings to decline and deer density estimates approach levels seen detrimental from other studies.

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APPENDIX

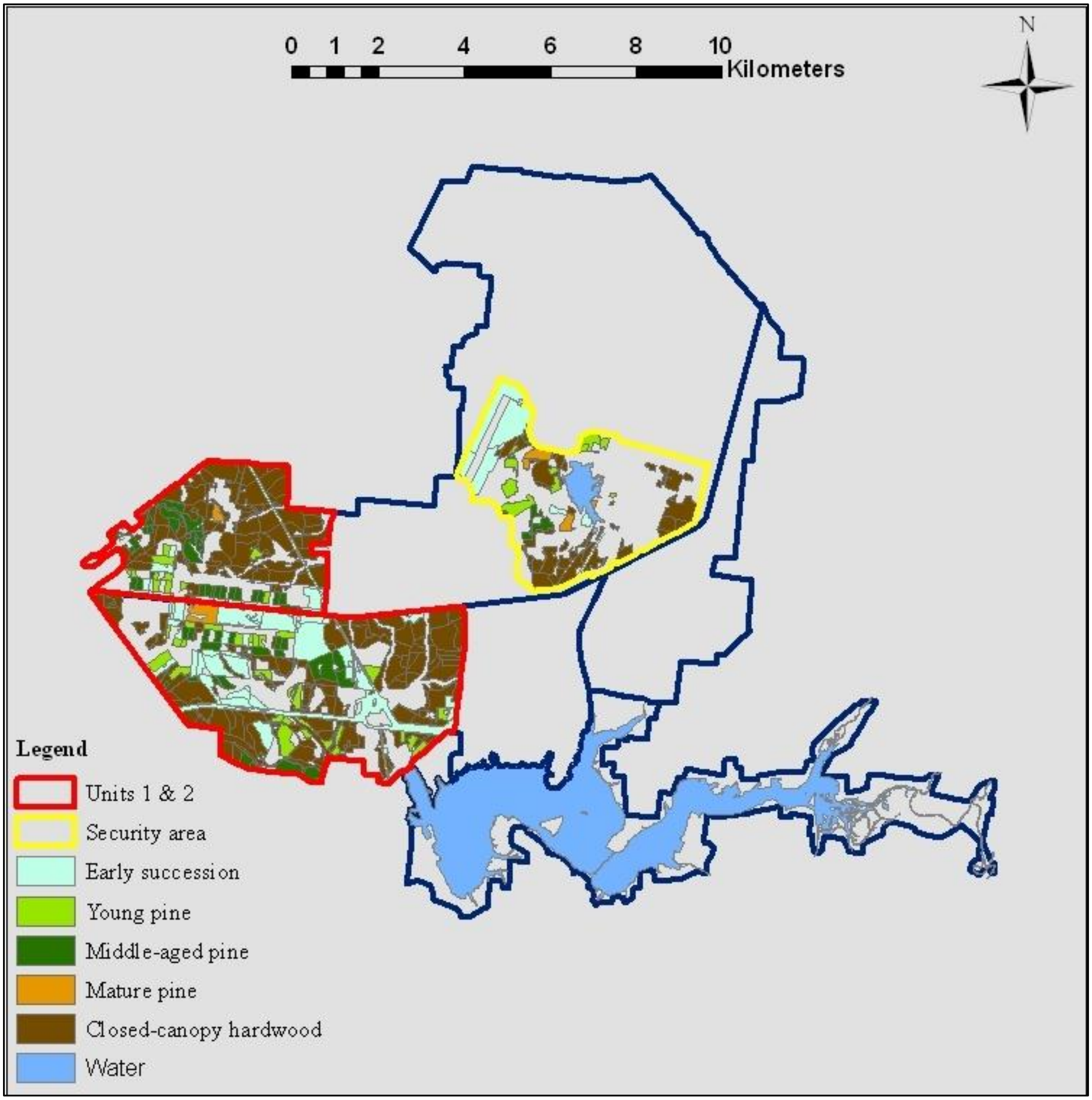

Figure 8. Vegetation types on Wildlife Management Area (WMA) Units 1 and 2 and the Security Area at Arnold Air Force Base, Tullahoma, Tennessee, USA, 2010. WMA Units 1 and 2 had low deer density (7.7 deer/km^2) and the Security Area had high deer density (20.3 deer/km^2). Collection of important deer forages occurred in the winter dormant (February–March) and summer growing (June–July) season.

Table 5. Important white-tailed deer forage species used for seasonal forage availability and nutritional quality estimates across vegetation type and deer density level at Arnold Air Force Base, Tullahoma, Tennessee, USA, during winter (February–March) and summer (June–July) 2010.

Forage class	Species
Trees-shrubs	Blueberry (*Vaccinium* spp.)
	Blackgum (*Nyssa sylvatica*)
	Strawberrybush (*Euonymus americanus*)
	Flowering dogwood (*Cornus florida*)
	Sumac (*Rhus* spp.)
	Maples (*Acer* spp.)
	Oaks (*Quercus* spp.)
	Elm (*Ulmus* spp.)
	Devil's walkingstick (*Aralia spinosa*)
	Privet (*Ligustrum* spp.)
Briers-brambles-vines	Cat greenbrier (*Smilax glauca*)
	Saw greenbrier (*Smilax bona-nox*)
	Roundleaf greenbrier (*Smilax rotundifolia*)
	Blackberry (*Rubus* spp.)
	Grape (*Vitis* spp.)
	Japanese honeysuckle (*Lonicera japonica*)
	Multiflora rose (*Rosa multiflora*)
	Virginia creeper (*Parthenocissus quinquefolia*)
	Poison ivy (*Toxicodendron radicans*)

Table 5. Continued

Forage class	Species
Forbs	Morningglory (*Ipomoea* spp.)
	Tick-trefoil (*Desmodium* spp.)
	Ragweed (*Ambrosia* spp.)
	Cinquefoil (*Potentilla* spp.)
	Bedstraws (*Galium* spp.)
	Violet (*Viola* spp.)
	Asters *(Symphyotrichum* spp.*)*
	Thoroughworts *(Eupatorium* spp.)
	Goldenrods (*Solidago* spp.)
	Tickseeds (*Coreopsis* spp.)

Table 6. Mixed model analysis of variance results of vegetation type, white-tailed deer density, and season with forage availability (kg/ha) and nutritional quality (crude protein and total digestible nutrients) of important deer forages from 4 vegetation types at 2 deer density levels for Wildlife Management Area (WMA) Units 1 and 2 and the Security Area at Arnold Air Force Base, Tullahoma, Tennessee, USA, during winter (February–March) and summer (June–July) 2010.

	Veg[c]	Density[d]	Season	Veg × density	Veg × season	Density × season	Veg × density × season
Variable[a]	*P*-value	*P*-value	*P*-value	*P*-value	*P*-value	*P*-value	*P*-value
Forage availability							
Briers-brambles-vines	0.005	0.015	<0.001	0.015	0.124	0.113	0.451
Forbs	<0.001	0.663	<0.001	0.663	<0.001	0.117	0.177
Trees and shrubs	0.000	0.001	<0.001	0.030	0.005	0.306	0.166
Crude protein[b]							
Briers-brambles-vines	0.011	0.006		0.028			
Forbs	<0.001	0.316		0.001			
Trees and shrubs	0.001	0.000		0.037			
Total digestible nutrients[b]							
Briers-brambles-vines	0.009	0.007		0.040			
Forbs	<0.001	0.507		0.024			
Trees and shrubs	0.001	0.000		0.028			

[a] Briers-brambles-vines, Forbs, Trees-shrubs.

[b] Nutritional quality estimates are a measure of crude protein (CP) availability (CP×(kg/ha)) and total digestible nutrients (TDN) availability (TDN×(kg/ha)). Nutritional quality analysis was only conducted for the summer collection and therefore did not have any seasonal effects.

[c] Vegetation types: mature upland closed-canopy hardwoods (MH; $\geq$ 30 years), young closed-canopy pines (YP; closed-canopy present and no thinning), middle-aged pines (MDP; row thinned), and mature pines (MAT; row-thinned and cut).

[d] Low deer density (7.7 deer/km^2) is represented by WMA Units 1 and 2 and high deer density (20.3 deer/km^2) represented by the Security Area.

Table 7. Seasonal forage availability (kg/ha) estimates by forage class of important white-tailed deer forages across 4 vegetation types and 2 population density levels at Arnold Air Force Base, Tullahoma, Tennessee, USA, winter (February–March) and summer (June–July) 2010.

Forage Class[d]	Vegetation[a]	Winter						Summer					
		Low density[b]			High density			Low density			High density		
		Mean	SE[c]	Letter group[c]	Mean	SE	Letter group	Mean	SE	Letter group	Mean	SE	Letter group
BBV	Hardwoods	6.74	0.09	G	5.80	0.06	G	124.80	1.29	BC	95.94	1.29	CDE
	Mature pines	20.45	0.27	FG	18.92	0.16	DEF	322.07	2.38	AB	326.04	2.20	A
	Middle age pines	47.41	0.49	CD	8.91	0.08	FG	339.33	2.13	A	97.72	0.85	BC
	Young pines	17.75	0.31	EFG	4.51	0.04	G	324.11	2.21	A	49.24	0.26	CD
Forbs	Hardwoods	0.00	0.00	E	0.00	0.00	E	0.00	0.00	E	0.26	0.00	E
	Mature pines	0.74	0.03	DE	18.26	0.61	D	46.52	0.22	AB	225.46	1.71	A
	Middle age pines	0.00	0.00	E	0.36	0.02	E	134.04	0.73	A	23.20	0.17	BC
	Young pines	0.00	0.00	E	0.44	0.02	E	48.22	0.24	BC	21.69	0.14	C
TS	Hardwoods	24.60	0.46	C	38.32	0.54	C	266.41	1.57	AB	294.80	2.47	AB
	Mature pines	33.15	0.54	DE	9.27	0.14	CD	1268.18	9.81	A	1043.54	6.16	A
	Middle age pines	9.59	0.17	F	0.10	0.00	CD	422.04	3.10	A	85.95	0.58	BC
	Young pines	43.49	1.14	E	5.07	0.08	DE	396.27	2.65	A	51.44	0.56	CD

[a] Vegetation types: mature upland closed-canopy hardwoods (MH; $\geq$ 30 years), young closed-canopy pines (YP; closed-canopy present and no thinning), middle-aged pines (MDP; row thinned), mature pines (MAT; row-thinned and cut).

[b] Low deer density (7.7 deer/km^2) is represented by WMA Units 1 and 2 and high deer density (20.3 deer/km^2) by the Security Area.

[c] Reported SE and letter groupings in the same row are from back transformed least-square mean estimates of full interaction model, and means with the same letter do not differ within respective forage class across seasons ($P > 0.05$).

[d] Briers-brambles-vines (BBV), Forbs, trees-shrubs (TS).

Table 8. Total forage availability (kg/ha), crude protein (CP), and total digestible nutrient (TDN) for each important white-tailed deer forage species across all vegetation types and deer density levels at Arnold Air Force Base in Tullahoma, Tennessee, USA, summer (June–July) 2010.

Vegetation[a]	Species[d]	Low deer density[b]			High deer density		
		Forage[c] availability	CP[c]	TDN[c]	Forage availability	CP	TDN
Hardwoods	Cat greenbrier (*Smilax glauca*)	66	11.8	56	26	10.4	59
	Roundleaf greenbrier (*Smilax rotundifolia*)	20	11.8	67	15	11.3	73
	Poison ivy (*Toxicodendron radicans*)	1	11.4	71			
	Grape (*Vitis* spp.)	37	11	66	55	10.6	59
	Maples (*Acer* spp.)	60	9.9	71	5	9.7	72
	Strawberrybush (*Euonymus americanus*)				2		
	Blackgum (*Nyssa sylvatica*)	16	10.2	75	9	10	75
	Oaks (*Quercus* spp.)	37	10.4	60	60	11.9	66
	Blueberry (*Vaccinium* spp.)	154	8.9	45	219	7.9	50
	Japanese honeysuckle (*Lonicera japonica*)	4	8.9	74	4	9.7	77
Mature pines	Virginia creeper (*Parthenocissus quinquefolia*)	6	14.6	60	13	11.9	51
	Blackberry (*Rubus* spp.)	105	11.6	64	222	9.3	71
	Cat greenbrier (*Smilax glauca*)	67	11.4	63	6	9.7	64
	Roundleaf greenbrier (*Smilax rotundifolia*)	55	10.7	79	37	10.1	66
	Poison ivy (*Toxicodendron radicans*)	72	11.3	75	17	10.3	60
	Grape (*Vitis* spp.)	12	11.5	65	26	11.6	53
	Ragweed (*Ambrosia* spp.)				1		
	Asters (*Symphyotrichum* spp.)	10	11.6	57	10	9.2	70
	Tickseeds (*Coreopsis* spp.)	9	9.8	60			
	Tick-trefoil (*Desmodium* spp.)	1	16.9	47	142	16.5	32
	Thoroughworts (*Eupatorium* spp.)	9	11.3	74	46	15.6	82

Table 8. Continued

Vegetation[a]	Species[d]	Low deer density[b]			High deer density		
		Forage[c] availability	CP[c]	TDN[c]	Forage availability	CP	TDN
	Bedstraws (*Galium* spp.)	4					
	Morningglory (*Ipomoea* spp.)				2	13.5	54
	Cinquefoil (*Potentilla* spp.)	12	15.9	63	17	11	59
	Goldenrods (*Solidago* spp.)	2	13.7	63	8	11.9	61
	Maples (*Acer* spp.)	164	8.7	70	265	10.7	63
	Devil's walkingstick (*Aralia spinosa*)	22	11.6	56	74	11.6	56
	Flowering dogwood (*Cornus florida*)				36	9.3	83
	Privet (*Ligustrum* spp.)				2	10.2	67
	Blackgum (*Nyssa sylvatica*)	49	9.6	76	6	9.2	79
	Oaks (*Quercus* spp.)	894	10.2	52	447	11.7	55
	Sumac (*Rhus* spp.)	36	12.1	83	182	13.2	71
	Elm (*Ulmus* spp.)				5	11.5	57
	Blueberry (*Vaccinium* spp.)	104	8.3	72	28	7.4	50
	Japanese honeysuckle (*Lonicera japonica*)	51	12.1	56	8	13	70
Middle-age pines	Virginia creeper (*Parthenocissus quinquefolia*)	9	13.3		8	10	57
	Blackberry (*Rubus* spp.)	134	11.1	68	7	12.5	65
	Cat greenbrier (*Smilax glauca*)	74	11.7	61	12	11.3	66
	Roundleaf greenbrier (*Smilax rotundifolia*)	22	9.7	61	1	15.2	77
	Poison ivy (*Toxicodendron radicans*)	21	12.1	65	2	12.4	70
	Grape (*Vitis* spp.)	28	13.4		59	10.4	69
	Asters (*Symphyotrichum* spp.)	31	16.2	74	1	13.4	72
	Tickseeds (*Coreopsis* spp.)	20	9	67			
	Tick-trefoil (*Desmodium* spp.)	14	16.7	48	2	18.8	60

Table 8. Continued

Vegetation[a]	Species[d]	Low deer density[b]			High deer density		
		Forage[c] availability	CP[c]	TDN[c]	Forage availability	CP	TDN
	Morningglory (*Ipomoea* spp.)	3	17.5	68	1	25.3	70
	Thoroughworts (*Eupatorium* spp.)	42	14.2	67	12	13.5	73
	Bedstraws (*Galium* spp.)				3	11.3	61
	Cinquefoil (*Potentilla* spp.)	22	10.8	69	5	12.2	
	Ragweed (*Ambrosia* spp.)				1	25.4	76
	Goldenrods (*Solidago* spp.)	3	20.4	55			
	Maples (*Acer* spp.)	118	10.3	69	29	9.9	58
	Devil's walkingstick (*Aralia spinosa*)	7	11.5	68			
	Flowering dogwood (*Cornus florida*)				6	11	76
	Privet (*Ligustrum* spp.)	84	8.4	70	5	17.2	79
	Blackgum (*Nyssa sylvatica*)	28	10.8	75	17	14.5	49
	Oaks (*Quercus* spp.)	176	12.5	56	24	12.3	59
	Sumac (*Rhus* spp.)	4	10.6	85	5	11.8	79
	Elm (*Ulmus* spp.)	3	13	52			
	Blueberry (*Vaccinium* spp.)	2	8.3	54			
Young pines	Japanese honeysuckle (*Lonicera japonica*)	24	10.2	65	3	14.2	60
	Virginia creeper (*Parthenocissus quinquefolia*)	11	11	58	5	16.3	56
	Blackberry (*Rubus* spp.)	150	12.3	56	7	20.3	70
	Saw greenbrier (*Smilax bona-nox*)	3					
	Cat greenbrier (*Smilax glauca*)	42	12.6	67	9	14.7	61
	Roundleaf greenbrier (*Smilax rotundifolia*)	25	11.3	44	3	13.7	71
	Poison ivy (*Toxicodendron radicans*)	46	12.5	72	12	15.8	63
	Grape (*Vitis* spp.)	23	11.7	57	9	16.9	

Table 8. Continued

Vegetation[a]	Species[d]	Low deer density[b]			High deer density		
		Forage[c] availability	CP[c]	TDN[c]	Forage availability	CP	TDN
	Ragweed (*Ambrosia* spp.)	1			2	31.6	70
	Asters (*Symphyotrichum* spp.)	13	10.8	75	5	18.4	67
	Tick-trefoil (*Desmodium* spp.)	13	23.8	59	3	25.4	64
	Thoroughworts (*Eupatorium* spp.)	6	21	68	1	15.2	71
	Bedstraws (*Galium* spp.)	1	13.4	35	7		
	Cinquefoil (*Potentilla* spp.)	9	10.4	67	3	12.6	70
	Goldenrods (*Solidago* spp.)	4	14.4	67	1	21.8	70
	Violet (*Viola* spp.)	1					
	Maples (*Acer* spp.)	23	11.7	76	14	14.4	67
	Flowering dogwood (*Cornus florida*)				4	11.9	66
	Privet (*Ligustrum* spp.)	44	15.9	78			
	Blackgum (*Nyssa sylvatica*)	45	11.7	73	3	12.7	63
	Oaks (*Quercus* spp.)	53	11.4	81	28	12.1	64
	Sumac (*Rhus* spp.)	201	12.6	75	3	12.6	75
	Elm (*Ulmus* spp.)	16	19.8	78			
	Blueberry (*Vaccinium* spp.)	14	10.1	45			

[a] Vegetation types: mature upland closed-canopy hardwoods (MH; $\geq$ 30 years), young closed-canopy pines (YP; closed-canopy present and no thinning), middle-aged pines (MDP; row thinned), mature pines (MAT; row-thinned and cut), and early succession.
[b] Low deer density (7.7 deer/km^2) is represented by WMA Units 1 and 2 and high deer density (20.3 deer/km^2) by the Security Area.
[c] No forage availability data present indicates species was absent. Forage availability estimates present but lacking CP and/or TDN indicate certain nutritional data was not obtainable for that species due to negligible amounts.
[d] See Table 5 for forage class breakdown.

Table 9. Number of important white-tailed deer forage species recorded across all vegetation types and deer density levels at Arnold Air Force Base, Tullahoma, Tennessee, USA, winter (February–March) and summer (June–July) 2010.

Vegetation type	No. of important deer forages	
	Low deer density	High deer density
Early succession	21	17
Hardwoods	8	8
Mature pines	20	23
Middle-age pines	22	20
Young pines	23	19
Mean	18.8	17.4

[a] Vegetation types: mature upland closed-canopy hardwoods (MH; $\geq$ 30 years), young closed-canopy pines (YP; closed-canopy present and no thinning), middle-aged pines (MDP; row thinned), mature pines (MAT; row-thinned and cut), and early succession.
[b] Low deer density (7.7 deer/km^2) is represented by WMA Units 1 and 2 and high deer density (20.3 deer/km^2) by the Security Area.

Table 10. Total seasonal forage availability (kg/ha) estimates by forage class of important white-tailed deer forage species across early successional vegetation at 2 deer density levels at Arnold Air Force Base in Tullahoma, Tennessee, USA, winter (February–March) and summer (June–July) 2010.

Forage Class	Low deer density[a]		High deer density	
	Winter[b]	Summer	Winter	Summer
Briers, brambles, and vines	52.60 B	1398.42 A	12.11 B	1612.93 A
Forbs	44.94 B	521.59 A	39.90 B	1024.80 A
Trees and shrubs	27.95 B	4443.35 A	11.73 A	649.42 A
All forages	125.48 B	6363.36 A	63.74 B	3287.14 A

[a] Low deer density (7.7 deer/km^2) is represented by WMA Units 1 and 2 and high deer density (20.3 deer/km^2) by the Security Area.

[b] Reported letter groupings are from back transformed least-square mean estimates of seasonal analysis for early succession. Means with the same letter do not differ within respective forage class across seasons ($P > 0.05$).

Table 11. Total seasonal forage availability (kg/ha) estimates for each important white-tailed deer forage species across all vegetation types for each deer density at Arnold Air Force Base in Tullahoma, Tennessee, USA, winter (February–March) and summer (June–July) 2010.

Vegetation[a]	Species[d]	Winter[e]		Summer[e]	
		Low[c]	High	Low	High
Early succession[b]	Japanese honeysuckle (*Lonicera japonica*)	42.79	0.09	231.46	182.20
	Blackberry (*Rubus* spp.)	3.19	6.03	398.26	1168.40
	Roundleaf greenbrier (*Smilax rotundifolia*)	0.95	1.06	34.23	22.11
	Multiflora rose (*Rosa multiflora*)	0.47		26.79	
	Cat greenbrier (*Smilax glauca*)	3.64	4.13	597.48	
	Grape (*Vitis* spp.)	1.25		94.92	
	Poison ivy (*Toxicodendron radicans*)			15.27	16.62
	Asters (*Symphyotrichum* spp.)	14.64	6.17	154.52	423.28
	Tickseeds (*Coreopsis* spp.)			39.22	9.19
	Tick-trefoil (*Desmodium* spp.)			7.47	12.84
	Thoroughworts (*Eupatorium* spp.)	9.92	2.04	208.69	449.94
	Bedstraws (*Galium* spp.)			1.70	0.70
	Morningglory (*Ipomoea* spp.)			6.19	5.44
	Cinquefoil (*Potentilla* spp.)	0.31	0.81	65.30	78.30
	Goldenrods (*Solidago* spp.)	20.38	31.68	38.51	40.61
	Violet (*Viola* spp.)				2.18
	Maples (*Acer* spp.)	0.57	3.59	78.68	42.13
	Privet (*Ligustrum* spp.)	5.25		57.79	
	Blackgum (*Nyssa sylvatica*)	3.77	3.14	573.45	
	Oaks (*Quercus* spp.)	13.36	2.96	2203.93	313.01
	Sumac (*Rhus* spp.)			1370.18	203.31
	Blueberry (*Vaccinium* spp.)	4.99	2.048	159.31	90.96
Hardwoods	Cat greenbrier (*Smilax glauca*)	3.74	3.92	66.16	25.76
	Roundleaf greenbrier (*Smilax rotundifolia*)	0.31	1.33	20.40	14.74
	Poison ivy (*Toxicodendron radicans*)			1.37	
	Grape (*Vitis* spp.)	2.70	0.55	36.79	54.96
	Maples (*Acer* spp.)	0.79	0.74	60.18	4.70
	Strawberrybush (*Euonymus americanus*)				2.44
	Blackgum (*Nyssa sylvatica*)			15.60	8.68
	Oaks (*Quercus* spp.)	0.31	1.19	37.02	59.99
	Blueberry (*Vaccinium* spp.)	23.49	36.39	153.61	218.98
	Japanese honeysuckle (*Lonicera japonica*)	8.06	1.64	4.43	4.20
Mature pines	Virginia creeper (*Parthenocissus quinquefolia*)			6.22	12.78

Table 11. Continued

Vegetation[a]	Species[d]	Winter[e]		Summer[e]	
		Low[c]	High	Low	High
	Blackberry (*Rubus* spp.)	2.39	4.97	105.36	222.29
	Cat greenbrier (*Smilax glauca*)	10.00	11.39	66.61	6.15
	Roundleaf greenbrier (*Smilax rotundifolia*)			54.54	36.91
	Poison ivy (*Toxicodendron radicans*)			72.45	17.47
	Grape (*Vitis* spp.)		0.52	12.47	26.25
	Ragweed (*Ambrosia* spp.)				1.01
	Asters (*Symphyotrichum* spp.)			9.53	10.03
	Tickseeds (*Coreopsis* spp.)			9.35	
	Tick-trefoil (*Desmodium* spp.)			0.53	141.91
	Thoroughworts (*Eupatorium* spp.)	0.52	15.53	9.12	45.54
	Bedstraws (*Galium* spp.)			4.08	
	Morningglory (*Ipomoea* spp.)				2.20
	Cinquefoil (*Potentilla* spp.)		0.40	11.59	17.01
	Goldenrods (*Solidago* spp.)	0.23	2.63	2.32	7.77
	Maples (*Acer* spp.)	6.55	2.55	163.64	264.67
	Devil's walkingstick (*Aralia spinosa*)			22.20	73.84
	Flowering dogwood (*Cornus florida*)		0.37		35.81
	Privet (*Ligustrum* spp.)				2.18
	Blackgum (*Nyssa sylvatica*)		0.05	49.44	6.44
	Oaks (*Quercus* spp.)	24.89	6.10	893.70	446.80
	Sumac (*Rhus* spp.)			35.53	181.61
	Elm (*Ulmus* spp.)				4.65
	Blueberry (*Vaccinium* spp.)	1.72	0.21	103.68	27.56
	Japanese honeysuckle (*Lonicera japonica*)	25.99	2.18	50.95	8.10
Middle-age pines	Virginia creeper (*Parthenocissus quinquefolia*)			8.78	7.96
	Blackberry (*Rubus* spp.)	5.92	1.70	134.17	6.64
	Cat greenbrier (*Smilax glauca*)	11.03	4.82	74.34	12.38
	Roundleaf greenbrier (*Smilax rotundifolia*)	3.64	0.21	22.34	1.08
	Poison ivy (*Toxicodendron radicans*)			21.02	1.93
	Grape (*Vitis* spp.)	0.73		27.73	59.48
	Asters (*Symphyotrichum* spp.)			31.07	0.68
	Tickseeds (*Coreopsis* spp.)			19.89	
	Tick-trefoil (*Desmodium* spp.)			13.50	2.34
	Thoroughworts (*Eupatorium* spp.)		0.36	42.44	11.53
	Bedstraws (*Galium* spp.)				2.72
	Morningglory (*Ipomoea* spp.)			2.87	1.10

Table 11. Continued

Vegetation[a]	Species[d]	Winter[e]		Summer[e]	
		Low[c]	High	Low	High
	Cinquefoil (*Potentilla* spp.)	0.11		21.63	4.50
	Ragweed (*Ambrosia* spp.)				1.00
	Goldenrods (*Solidago* spp.)			2.64	
	Maples (*Acer* spp.)	1.01	0.10	117.77	28.99
	Devil's walkingstick (*Aralia spinosa*)			7.02	
	Flowering dogwood (*Cornus florida*)				5.64
	Privet (*Ligustrum* spp.)	2.08		83.96	4.56
	Blackgum (*Nyssa sylvatica*)			28.29	16.95
	Oaks (*Quercus* spp.)	5.92		176.29	24.47
	Sumac (*Rhus* spp.)			3.76	5.15
	Elm (*Ulmus* spp.)			3.18	
	Blueberry (*Vaccinium* spp.)	0.58		1.77	
Young pines	Japanese honeysuckle (*Lonicera japonica*)	13.34	0.70	24.39	2.52
	Virginia creeper (*Parthenocissus quinquefolia*)			11.40	5.39
	Blackberry (*Rubus* spp.)	1.27	0.71	150.00	7.33
	Saw greenbrier (*Smilax bona-nox*)			3.50	
	Cat greenbrier (*Smilax glauca*)	2.31	2.63	41.85	9.39
	Roundleaf greenbrier (*Smilax rotundifolia*)	0.84	0.30	24.58	2.96
	Poison ivy (*Toxicodendron radicans*)			45.60	12.47
	Grape (*Vitis* spp.)		0.17	22.81	9.17
	Ragweed (*Ambrosia* spp.)			0.80	2.12
	Asters (*Symphyotrichum* spp.)			13.04	5.12
	Tick-trefoil (*Desmodium* spp.)			12.79	2.88
	Thoroughworts (*Eupatorium* spp.)		0.35	6.26	1.04
	Bedstraws (*Galium* spp.)			0.92	7.39
	Cinquefoil (*Potentilla* spp.)			9.05	2.90
	Goldenrods (*Solidago* spp.)		0.10	4.06	1.00
	Violet (*Viola* spp.)			1.30	
	Maples (*Acer* spp.)	0.65	2.55	23.42	14.10
	Flowering dogwood (*Cornus florida*)	1.22	0.14		3.66
	Privet (*Ligustrum* spp.)	36.98		44.14	
	Blackgum (*Nyssa sylvatica*)			45.35	2.54
	Oaks (*Quercus* spp.)	2.62	2.38	52.72	27.91
	Sumac (*Rhus* spp.)			200.60	3.24
	Elm (*Ulmus* spp.)			16.34	
	Blueberry (*Vaccinium* spp.)	2.01		13.70	

Table 11. Continued

Vegetation[a]	Species[d]	Winter[e]		Summer[e]	
		Low[c]	High	Low	High

[a] Vegetation types: mature upland closed-canopy hardwoods (MH; $\geq$ 30 years), young closed-canopy pines (YP; closed-canopy present and no thinning), middle-aged pines (MDP; row thinned), mature pines (MAT; row-thinned and cut), and early succession.
[b] Early succession was maintained by different methods at the low (mowing) and high (burning) deer densities.
[c] Low deer density (7.7 deer/km^2) is represented by WMA Units 1 and 2 and high deer density (20.3 deer/km^2) by the Security Area.
[d] See Table 5 for forage class breakdown.
[e] No seasonal forage availability data present indicates species was absent.

VITA

Jared Tyler Beaver was born in Salisbury, North Carolina in December 1985. He was raised hunting and fishing in the Piedmont of North Carolina and graduated as valedictorian from West Rowan High School in 2004. He attended Wake Forest University where he earned his Bachelor of Science degree in Biological Sciences in 2008. Prior to accepting a graduate research assistantship at the University of Tennessee in January 2009, he worked with the National Park Service in Great Smoky Mountains National Park. Upon completion of his Master of Science Degree in Wildlife and Fisheries Science, Jared moved to Texas to be with fiancée and work on a white-tailed deer project with Texas A&M—Kingsville.