

EVALUATING HELICOPTER SURVEYS AND HABITAT SELECTION OF WHITE-
TAILED DEER (*ODOCOILEUS VIRGINIANUS*) IN CENTRAL FLORIDA

by

JORDAN RYAN DYAL

(Under the Direction of GINO J. D'ANGELO)

ABSTRACT

The white-tailed deer (*Odocoileus virginianus*) is the most economically important game species in North America, resulting in an incentive to effectively manage deer habitats and populations. Habitat management is guided by availability and selection of resources by animals, whereas, population management relies on surveys to estimate abundance, which are often biased due to imperfect detection. I developed a sightability model for helicopter surveys using surrogates to improve accuracy of population estimates, examined deer movement in response to helicopter surveys, and evaluated resource selection of deer relative to livestock management practices. The top sightability model indicated that distance from the transect and vegetative obstruction negatively affected deer detection. Helicopter surveys had little effect on deer movement and resource selection of bucks varied between seasons with bucks selecting areas closer to pastures that were grazed approximately 140–220 days when the preceding stocking rate was heavy. Information gained from this research will allow managers to prescribe sustainable harvest recommendations and make better informed habitat management decisions.

INDEX WORDS: deer management, Florida, helicopter survey, livestock
management, *Odocoileus virginianus*, population estimation,
resource selection, sightability, space-use

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DEDICATION

Dedicated to my parents, Guy and Marie Dyal. Thank you for teaching me lessons of hard work and responsibility at a young age. I am beyond blessed to have you both as role models and parents. I hope one day to live up to the example you set for me. “Train up a child in the way he should go, and when he is old he will not depart from it.”

Proverbs 22:6

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CHAPTER 1

INTRODUCTION, BACKGROUND, OBJECTIVES, STUDY AREA, AND THESIS FORMAT

INTRODUCTION

White-tailed deer (*Odocoileus virginianus*), North America's most popular game species (Leonard 2004), provide significant recreational opportunities important to private landowners. In 2016, U.S. hunters spent \$26.2 billion on hunting-related expenditures, and 85% of hunters recreated on private land (U.S. Fish and Wildlife Service 2016). Most states in the white-tailed deer's range are comprised of over 90% private land (Grossman 2018). The economic value of wildlife is becoming increasingly important on private lands, and revenue from hunting leases often provides substantial income in addition to traditional revenue sources, such as cattle-ranching operations (Adams et al. 2000). For effective management to occur, game managers must obtain knowledge of interspecies interactions, habitat use, and population parameters, such as density, sex ratio, and age structure (Jacobson et al. 1997, Amos et al. 2014).

BACKGROUND

Ground-based Survey Methods

Obtaining accurate estimates of the abundance and demographics of a wildlife population aids in developing management prescriptions. White-tailed deer managers estimate deer population parameters with multiple survey methods including infrared cameras (Jacobson et al. 1997), spotlights (Collier et al. 2007), and helicopters (DeYoung 1985,

DeYoung 2011). Infrared camera surveys are easy to implement, low cost, time efficient, and can be applied to a wide variety of habitats (Jacobson et al. 1997). However, infrared camera surveys typically violate the assumption of equal detection between sexes and among age classes (McCoy et al. 2011, Weckel et al. 2011). Adult female deer have the highest probability of being photographed (Weckel et al. 2011), and ignoring differences in detection rates could lead to inaccurate estimates. Spotlight surveys are commonly used because they are inexpensive and simple to conduct. However, estimates from spotlight surveys tend to be associated with high variability and questionable accuracy (McCullough 1982, Fafarman and DeYoung 1986, Whipple et al. 1994, Collier et al. 2007). Additionally, sex ratio estimates vary with season, and fawns are typically underrepresented using spotlight surveys (DeYoung 2011). Distance sampling can be incorporated with conventional spotlight surveys to reduce variability of counts (Buckland et al. 2001). However, distance sampling has several key assumptions that are often violated in practice, such as perfect detection directly on the transect (Koenen et al. 2002). Collier et al. (2013) suggested the greatest potential bias of spotlight surveys is due to road-based convenience sampling, where transects are not randomly spaced.

Aerial Surveys

Helicopter surveys are often considered the most accurate (DeYoung 1985, Koerth et al. 1997) and practical (McIntosh et al. 2009, Peters et al. 2014) method to estimate densities of white-tailed deer and other ungulates across large sampling areas with limited canopy cover. Maneuverability, visibility, slow speed, and low-altitude capability have made the helicopter the preferred choice for aerial surveys (DeYoung 2011). However, helicopter

surveys come with many limitations including cost and the health risk they pose for operators (Sasse 2003).

Helicopter surveys can be used with both quadrat sampling (Bartmann et al. 1986, Samuel et al. 1987, Fieberg and Lenarz 2012) and line transects (DeYoung 1985, Zabransky et al. 2016, Bristow et al. 2019). Transects can be randomly or systematically placed to reduce potential bias associated with convenience sampling (Siniff and Skoog 1964). Previous research has demonstrated no sex- or age-bias of deer encountered on aerial surveys in south Texas (Leon et al. 1987). Although many biologists consider aerial line transect surveys to be accurate, reports in the literature conflict (DeYoung 1985, White et al. 1989). For instance, the proportion of marked deer observed varied from 17-75% in repeated surveys in a study area in south Texas comprised of mainly mesquite (*Prosopis glandulosa*) and mixed brush canopy cover of 40–60% (Beasom et al. 1986). With high variability, it is important to address detection probability when examining survey results to minimize biases in abundance estimation. Often, differences in observation rates are due to either sampling variance (i.e., spatial variability of animals; Steinhorst and Samuel 1989) or visibility bias where only a portion of animals will be observed (Samuel et al. 1987). Detectability can decline as distance from the flight path increases (DeYoung et al. 1989, White et al. 1989); however, cover type most likely has the greatest influence on detection probability (Zabransky et al. 2016). Because cover types vary by region, detection probability models should be developed in regions and study areas of interest to investigators to better understand region-specific detection.

Sightability Models

Sightability models are an alternative method for population estimation that account for imperfect detection. These models have been used to survey elk (*Cervus canadensis*; McIntosh et al. 2009, Bristow et al. 2019), moose (*Alces alces*; Anderson and Lindzey 1996, Peters et al. 2014), mule deer (*O. hemionus*; Zabransky et al. 2016), and pronghorn (*Antilocapra americana*; Jacques et al. 2014). Sightability models require an initial experimental survey using observations of animals with known locations, which are usually radio-collared individuals (Anderson and Lindzey 1996, Zabransky et al. 2016, Bristow et al. 2019). When individuals are detected, observers record variables that may influence detection such as group size, terrain, vegetative cover, animal activity, and light conditions. Known individuals which were not detected during the survey are located following the survey to record the same variables. Using these data, the relationship between defined covariates and the probability of detection in a survey can be estimated (Anderson et al. 1998), and abundance estimates can then be corrected by compensating for imperfect detection (Griffin et al. 2013). One important assumption of sightability models is that detection covariates of undetected individuals do not change between the initial and follow-up surveys (Bristow et al. 2019). To eliminate this bias, researchers must know simultaneous, accurate locations of the surveyor and undetected animals at the moment an observation was missed to obtain accurate covariate information. Because this is nearly impossible for free-ranging wildlife, some studies have incorporated surrogates, such as inanimate objects (Koski et al. 2009), decoys (Butler et al. 2007, Pearse et al. 2008), and humans (Kissell and Tappe 2004) to acquire the initial experimental dataset. Once developed, sightability models can be applied without radio-

collared or marked animals under the assumption that relationships among the covariates estimated do not change in future surveys (Williams et al. 2002).

Ungulate Behavior Relative to Aerial Surveys

Certain wildlife species have demonstrated habituation towards aircraft in areas with increased aircraft traffic, while others have only slightly habituated or not habituated at all (Andersen et al. 1989, Conomy et al. 1998, Côté et al. 2013, Goldstein et al. 2005, Krausman et al. 1986). Variable responses in ungulate behavior have been reported. In only 3 of 70 desert mule deer (*O. h. crooki*) observations, animals changed habitat use in response to aerial telemetry triangulation with up to 5 passes for each observation (Krausman et al. 1986). Mountain goats (*Oreamnos americanus*) appeared to be more sensitive to aircraft traffic than other ungulates showing a strong behavioral response, often fleeing toward rocky cliffs, from most flights within 500 m (Côté 1996).

Of the previous studies regarding aircraft disturbance, relatively few have utilized Global Positioning Systems (GPS) technology (Campbell et al. 2010), with many studies using individual human observers to document animal behavior (Côté 1996, Côté et al. 2013, Frid 2003, Krausman and Hervert 1983, Krausman et al. 1986). Additionally, accelerometers in GPS collars can collect information that can be used to draw inferences regarding activity patterns (e.g., foraging, resting) relative to the change of location (Gottardi et al. 2010, Krop-Benesch et al. 2013). Therefore, utilization of modern GPS technology may better evaluate animal activity and movements in response to aircraft disturbance.

Livestock Management

There are 257 million ha of non-Federal (i.e., private, state, and tribally owned) and approximately 101 million ha of Federal grazing lands in the United States (Hardy Vincent 2018, USDA 2018), supporting an estimated 94.4 million cattle (*Bos taurus*) (USDA 2020). These rangelands are often managed for multi-use production, with wildlife management becoming increasingly important. The economic value of wildlife is becoming progressively more important on private lands, and revenue from hunting leases often provides substantial income in addition to traditional revenue sources, such as cattle-ranching operations (Adams et al. 2000). To successfully manage ranching operations for multiple use, it is important to understand wildlife distributions and interactions with livestock. In addition, it is important to understand how management actions designed to benefit cattle, may positively (or negatively) impact wildlife populations

Management of cattle grazing is used to achieve a variety of goals, including livestock production, wildlife habitat enhancement, and environmental sustainability for continued long-term use (Krausman et al. 2009). In general, properly applied grazing can increase habitat diversity, nutritional value of forage, and forage productivity (Vavra 2005). For example, previous research has shown that moderate- to light-stocking rates can increase forb production through reduction of competition from grass, stimulating growth and increasing range conditions (Anderson and McCuiston 2008). This is just one such example where range management can reduce costs and yield greater financial returns for livestock production while simultaneously improving wildlife habitat (Anderson and McCuiston 2008).

Deer Response to Livestock Management

The presence of livestock can lead to reduced white-tailed deer space-use and shifts in habitat selection (Merrill et al. 1957, McMahan 1966, Ellisor 1969, Sparrowe and Springer 1970, Hood and Inglis 1974). In other cases, extensive spatial overlap between cattle and white-tailed deer has occurred but was mediated by strong temporal separation (Cooper et al. 2008). Temporal separation may be due to social interactions rather than direct competition (Compton et al. 1988). In all cases, it is likely that stocking rate of cattle mitigates these relationships. For example, white-tailed deer in Texas coexist with cattle during a continuous grazing system but avoided high concentrations of cattle in short-duration, high-intensity grazing systems (Cohen et al. 1989). Thus, it appears that the presence of cattle is correlated with reduced space use by deer, however, it is unknown whether the response by deer is caused by direct dietary competition.

Dietary overlap between deer and cattle increased from 12% in summer to 46% in winter in forested pine-hardwood systems of central Louisiana (Thill 1984). Dietary overlap also can increase from natural events such as drought, forcing competition due to reduced forage availability (Ortega et al. 1997). However, in non-drought years, growing season (i.e., late-spring to early fall) cattle grazing has little negative impact on deer forage availability (Thill and Martin 1989). Therefore, if any avoidance behavior of deer toward cattle is documented between late-spring and early fall, it is unlikely due to direct competition and is likely be attributed to social intolerance.

If social intolerance is a driving force in negative cattle-deer interactions, it is critical to understand whether specific management actions for cattle may mediate or increase those interactions. Such management actions commonly applied include

fertilizers, herbicides, and biosolids (treated sewage sludge). Cattle managers often apply fertilizers to stimulate herbaceous plant growth, improve forage quality, and improve soil fertility. Biosolids are a low-cost and potentially inexhaustible resource (McFarland et al. 2010), often used in agricultural systems to increase plant biomass and cover, decrease soil erosion, and improve soil fertility (Washburn and Begier 2011). Long-term application of biosolids have demonstrated no effect on deer habitat preference (Washburn and Begier 2011). However, Milorganite®, a trade name fertilizer product derived from sewage sludge, can be used to temporarily repel deer from food plots to reduce browsing pressure (Stephens et al. 2005). Additionally, cattle managers readily apply herbicides in pastures to reduce competition from undesired plant species. While multiple management treatments are implemented to increase forage quantity and quality for cattle, little is known about their effect on white-tailed deer space use and habitat selection.

OBJECTIVES

This research was conducted to address three primary objectives:

1. Develop a sightability model for aerial surveys of white-tailed deer that would be practical to reproduce and implement in this region.
2. Evaluate the effect of helicopter surveys on male deer fine-scale movements and resource selection.
3. Model temporal variation in habitat selection and space-use of male white-tailed deer relative to the presence of cattle and management actions designed to benefit cattle (e.g., fertilizer, herbicide, biosolid application).

THESIS FORMAT

This thesis is presented in a manuscript format. Chapter 1 is an introduction with background and rationale of relevant studies related to my research. Chapter 2 contains the results of developing a sightability model for helicopter surveys using surrogates of white-tailed deer. Chapter 3 evaluates male deer movements and resource selection relative to helicopter surveys. Chapter 4 investigates temporal variation in male deer resource selection relative to livestock management practices. And lastly, Chapter 5 consists of conclusion and management implications of this research.

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CHAPTER 2

ESTIMATING SIGHTABILITY FOR HELICOPTER SURVEYS USING SURROGATES OF WHITE-TAILED DEER (*ODOCOILEUS VIRGINIANUS*)

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ABSTRACT

On large management units where terrain allows observation of white-tailed deer (*Odocoileus virginianus*) from the air, helicopter surveys may provide managers with cost-effective and accurate estimates of population abundance. However, imperfect detection of deer introduces negative bias, which could result in potentially inappropriate management recommendations (e.g., harvest prescriptions). Sightability estimators are designed to model detection heterogeneity based on factors, such as vegetation type and distance from transect, that affect observer detection of target animals. Sightability models are widely used to estimate ungulate abundance. However, no previous studies have applied sightability models to correct for detectability of white-tailed deer during helicopter surveys in the southeastern U.S. The study objectives were to: 1) model detection probability of white-tailed deer as a function of covariates including distance from transect, vegetative obstruction, and light conditions to improve population estimates derived from helicopter surveys, and 2) apply this model in operational helicopter surveys. The study was conducted on a 399.4-km² study area within a 1209.7-km² cattle ranch in central Florida. We placed 3-D archery targets as surrogates for white-tailed deer at assigned locations unknown to observers across a combination of stratified bins of vegetative obstruction (i.e., categories) and distances from the transect. The top model indicated that distance from the transect and vegetative obstruction negatively affected detection of deer. Detection probability on the flight transect ranged from 0.95 (95% CI = 0.89–0.98) for 0–25% vegetative obstruction and 0–25 m distance from transect to 0.05 (95% CI = 0.01–0.18) for 76–100% vegetative obstruction and 100–125 m distance from transect. We applied the sightability model to operational surveys on

3 units (i.e., management zones), which produced population estimates averaging 26% higher than those derived from uncorrected counts. Observers simultaneously recorded live deer during operational flights, of which 60% of deer groups were observed while stationary. We recommend wildlife managers adopt using “stationary” surrogates to develop region-specific sightability models in other study areas to account for imperfect detection during helicopter surveys of white-tailed deer.

KEY WORDS: density estimation, detection, Florida, helicopter survey, *Odocoileus virginianus*, population estimation, sightability, surrogate

INTRODUCTION

Obtaining accurate estimates of the abundance and demographics of a wildlife population aid in monitoring and the development of management prescriptions. Helicopter surveys are often considered the most accurate (DeYoung 1985, Koerth et al. 1997) and practical (McIntosh et al. 2009, Peters et al. 2014) method to estimate densities of white-tailed deer (*Odocoileus virginianus*) and other ungulates across large sampling areas with limited canopy cover. Maneuverability, visibility, slow speed, and low-altitude capability have made the helicopter the preferred choice for aerial surveys (DeYoung 2011).

However, helicopter surveys come with many limitations including high cost for small survey areas and the health risk they pose for operators (Sasse 2003).

Helicopter surveys can be used with both quadrat sampling (Samuel et al. 1987, Fieberg and Lenarz 2012) and line transects (DeYoung 1985, Zabransky et al. 2016, Bristow et al. 2019). Transects can be randomly or systematically placed to reduce potential bias associated with convenience sampling (Siniff and Skoog 1964). Previous research has demonstrated no sex- or age-bias of deer encountered on aerial surveys in

south Texas (Leon et al. 1987). Although many biologists consider aerial line transect surveys to be accurate, reports in the literature conflict (DeYoung 1985, White et al. 1989). For instance, the proportion of marked deer observed varied from 17-75% in repeated surveys in a study area in south Texas comprised of mainly mesquite (*Prosopis glandulosa*) and mixed brush canopy cover of 40–60% (Beasom et al. 1986). With high variability among counts, it is important to address detection probability when examining survey results to minimize biases in abundance estimation. Often, differences in observation rates are due to spatial variability of animals (Steinhorst and Samuel 1989) and visibility bias where only a portion of animals will be observed (Samuel et al. 1987). Detectability can decline as distance from the flight path increases (DeYoung et al. 1989, White et al. 1989); however, cover type most likely has the greatest influence on detection probability (Zabransky et al. 2016). Because cover types vary by region, detection probability models should be developed in cover types represented in a study area.

Mark-recapture approaches provide robust abundance estimates when used with aerial surveys (Barker 2008). In this approach, observers usually “recapture” marked or uniquely identifiable individuals by re-sighting them. Historically, it has been expensive and logistically challenging to physically mark and re-sight individuals over large areas (Bartmann et al. 1987), often making the technique impractical.

Sightability models are an alternative method for population estimation that do not always involve marking animals after model development. These models have been used to survey elk (*Cervus canadensis*; McIntosh et al. 2009, Bristow et al. 2019), moose (*Alces alces*; Anderson and Lindzey 1996, Peters et al. 2014), mule deer (*O. hemionus*;

Zabransky et al. 2016), and pronghorn (*Antilocapra americana*; Jacques et al. 2014). Sightability models require an initial experimental survey using observations of animals with known locations, which are usually radio-collared individuals (Anderson and Lindzey 1996, Zabransky et al. 2016, Bristow et al. 2019). When individuals are detected, observers record variables that may influence detection such as group size, terrain, vegetative cover, animal activity, and light conditions. Known individuals which were not detected during the survey are located following the survey to record the same variables. Using these data, the relationship between defined covariates and the probability of detection in a survey can be estimated (Anderson et al. 1998) and abundance estimates corrected by compensating for imperfect detection (Griffin et al. 2013). One important assumption of sightability models is that detection covariates of undetected individuals do not change between the initial and follow-up surveys (Bristow et al. 2019). To eliminate this bias, researchers must know simultaneous, accurate locations of the surveyor and undetected animals at the moment an observation was missed to obtain accurate covariate information. Because this is nearly impossible for free-ranging wildlife, some studies have incorporated surrogates, such as inanimate objects (Koski et al. 2009), decoys (Butler et al. 2007, Pearse et al. 2008), and humans (Kissell and Tappe 2004) to acquire the initial experimental dataset. Once developed, sightability models can be applied without radio-collared or marked animals under the assumption that relationships among the covariates estimated do not change in future surveys (Williams et al. 2002).

Investigators should carefully consider which predictor variables to include before model development (Giudice et al. 2012). Including too many covariates in the model-

building process increases the chance of fitting noise in the data rather than the underlying relationship between response and predictors (Giudice et al. 2012). In the southeastern coastal plain of the United States, deer seldom form large groups (Hardin et al. 1976, Lagory 1986), and there is limited topographic relief to negatively influence detection rates. While predictor variables such as group size and topographic relief may be important to other study systems, they are less informative in the southeastern United States. Therefore, we chose to examine only 3 predictor variables (e.g., vegetative obstruction, distance from transect, and light conditions) that we felt most significantly influenced detection probability of deer on the study site.

Most sightability models for ungulates have been developed for populations in western North America (Samuel et al. 1987, Anderson et al. 1998, Bristow et al. 2019). Managers in many areas of the southeastern United States conduct annual aerial surveys before hunting seasons to obtain population estimates used to develop harvest prescriptions for deer populations. However, there are no existing sightability models that represent open vegetation types of southeastern rangelands. The study objectives were to: 1) develop a sightability model for aerial surveys of white-tailed deer, using surrogates, that would be practical to reproduce and implement in rangelands of the southeastern United States and 2) apply our sightability model to operational helicopter surveys of live deer to demonstrate its use. We expected detection rates to decrease as vegetative obstruction and distance from the transect increased. However, we did not expect differences in detection rates with changing light conditions, since extensive areas of improved pasture in southeastern rangelands reduce the opportunity for high-contrast observations.

STUDY AREA

The study was conducted on a 1209.7-km² ranch in Brevard, Orange, and Osceola Counties of Florida between the cities of Melbourne and St. Cloud (Fig. 2.1). The ranch is privately owned and managed primarily for cattle. However, during the study multiple-use management was conducted to support revenues from timber harvest, row crops, citrus, sod farming, and hunting leases. The study area comprised 399.4-km and is bordered entirely by the St. Johns River marsh to the east. There was little forest canopy cover, although forest canopy cover increased gradually from approximately 2% at the eastern edge to approximately 20% towards the western edge of the study area. The landscape is representative of most relatively flat, open southeastern rangelands with interspersed forest. This study area was selected because of the extensive road network, relatively high deer densities, and limited canopy cover, making it suitable for aerial surveys.

The habitat across the study area is generally characterized as improved pasture (65%) and agriculture (6%) with scattered hardwood hammocks (11%), cypress domes (6%), flatwoods (5%), freshwater marshes and prairies (3%), and open water (4%; Kawula and Redner 2018). Soil types were sandy including Smyrna fine sand, Riviera fine sand, and Mayakka fine sand (U.S. Department of Agriculture, Natural Resources Conservation Service 2018). Improved pastures were planted in perennials, including bahiagrass (*Paspalum notatum*) and limpograss (*Hemarthria altissima*), and seasonally planted with annuals like ryegrass (*Lolium multiflorum*) for winter forage. Improved pastures were historically over-seeded with various legumes such as American jointvetch (*Aeschynomene americana*), perennial peanut (*Arachis glabrata*), and partridge pea

(*Chamaecrista fasciculata*). The majority of these plants were still abundant during the study. Below 10 m elevation, common trees and shrubs included cabbage palm (*Sabal palmetto*), Brazilian peppertree (*Schinus terebinthifolius*), bald cypress (*Taxodium distichum*), Carolina willow (*Salix caroliniana*), wax myrtle (*Morella cerifera*), swamp rosemallow (*Hibiscus grandifloras*), and common buttonbush (*Cephalanthus occidentalis*). The most common trees and shrubs at elevations above 10 m included pond cypress (*T. ascendens*), live oak (*Quercus virginiana*), longleaf pine (*Pinus palustris*), laurel oak (*Q. laurifolia*), loblolly bay (*Gordonia lasianthus*), red maple (*Acer rubrum*), sweetgum (*Liquidambar styraciflua*), gallberry (*Ilex glabra*), saw palmetto (*Serona repens*), and saltbush (*Baccharis halimifolia*). Canopy cover was sparse due to the establishment of improved pasture creating a relatively open environment with pockets of dense vegetation interspersed throughout. Average summer temperatures were hot (27°C) and average winter temperatures were mild (18°C), and annual precipitation averaged 136.1 cm (Shin et al. 2020).

METHODS

Experimental Helicopter Surveys

We used high-density foam 3-D archery targets (Field Logic, Inc., Superior, WI, USA; Delta McKenzie Targets, Dike, IA, USA) as surrogates for white-tailed deer during experimental helicopter surveys to develop the sightability model. The targets were designed to be similar in size and color to deer (Fig. 2.1). Individual surrogates were assigned locations unknown to observers that represented the designated covariates (e.g., vegetative obstruction, distance from transect, and light conditions) prior to experimental flights (Fig. 2.2). All surrogates were placed facing north to maintain consistency among

observations. We assigned locations of surrogates into stratified bins of vegetative obstruction (i.e., categories) and distances from transect at equal ratios by using the “buffer” tool in ArcMap 10.5.1 (Environmental Systems Research Institute, Inc., Redlands, CA, USA) to ensure adequate distribution across covariates.

We classified vegetation using 2018 Florida Natural Areas Inventory imagery (Kawula and Redner 2018) with the classification tool in ArcMap 10.5.1 to determine land cover classes. Land cover classes were reclassified into percent vegetative obstruction in the following categories: < 25% obstruction (e.g., improved pasture, bare ground, and agricultural fields), 26–50% obstruction (e.g., freshwater marshes and prairies, fallow pastures with scattered saw palmetto, Brazilian peppertree, brambles, wax myrtle, and scrub), 51–75% obstruction (e.g., flatwoods), and 76–100% obstruction (e.g., hardwood hammocks and cypress domes) based on a 9 m radius around each location (Anderson and Lindzey 1996).

We conducted experimental flights in July 2019 using a Robinson-R44 helicopter (Robinson Helicopter Company, Torrance, CA, USA). Experimental flights took place on an 18.2-km² area within the study area from sunrise to sunset (Fig. 2.2). During experimental flights, we surveyed a pre-established 200-m wide strip transect systematically spaced 400-m apart facing north to south which was navigated using Motion X-GPS (Fullpower Technologies Inc., Santa Cruz, CA, USA). We tracked each flight path using a handheld GPS unit (Garmin, Olathe, KS, USA). We used the same transect for all 12 flights, however, with each replication the survey began on the opposite end (i.e., forwards, backwards). The overall transect length was 72 km. The helicopter flew 20–25 m above ground level at 30–40 knots, and we removed all doors

from the aircraft to increase visibility. The pilot maintained altitude and speed by keeping altitude high enough to avoid potential hazards while also maximizing observability. All flights consisted of 3 observers and a pilot working together to sight surrogates, during which the left-rear observer recorded observations and covariates (e.g., percent vegetative obstruction, perpendicular distance from transect, and light conditions) using Collector for ArcGIS on iOS (Environmental Systems Research Institute, Inc., Redlands, CA, USA). The same observers participated in all flights, and their seating positions remained the same for each flight. Qualifications for observers included prior experience flying aerial surveys for deer in central Florida and training on survey protocols before their first flight, which included a safety meeting and instructions regarding assignment of covariate values. Observers were not informed of the location of surrogates before each flight and surrogate locations changed each flight.

For each surrogate detected during helicopter surveys, the time of observation, vegetative obstruction, distance from transect, and light conditions were recorded. Observers visually estimated vegetative obstruction into 25% bins (0–25%, 26–50%, 51–75%, and 76–100%) for observed surrogates in a 9-m radius centered on the location where the surrogate was detected (Anderson and Lindzey 1996). Observers used laser rangefinders (Leupold, Beaverton, OR, USA) to calibrate their visual distance to ≤ 100 m throughout surveys, then estimated perpendicular distances from the transect where the surrogate was first detected. Due to the difficulty of estimating distance during flights, observers recorded distances into 25-m bins (0–25 m, 26–50 m, 51–75 m, and 76–100 m). We compared observer estimated distance bins to actual measured distances obtained using the GPS flight log and surrogate locations derived from handheld GPS units to

obtain observer bias. Observers recorded light conditions of each observation as flat (e.g., low contrast between sunny and shady areas) or high contrast (e.g., high contrast between sunny and shady areas) (Griffin et al. 2013). For example, while flying in early morning, the observers facing east were looking toward the sun where sightings might be backlit. This would be considered high contrast lighting conditions. Conversely, at the same location and time, observers facing west were looking away from the sun where sightings have good illumination, producing flat lighting conditions.

We assigned undetected surrogates vegetative obstruction measured during pre-processing using ArcMap 10.5.1. Perpendicular distance from transect was measured using the georeferenced helicopter flight path and the ArcGIS 10.5.1 measure tool for both detected and undetected surrogates. We assigned light conditions for undetected surrogates using time-stamped observations recorded throughout each flight as flat or high contrast (Griffin et al. 2013) based on light conditions recorded by observers and which cardinal direction surrogates were relative to the helicopter.

Operational Helicopter Surveys

We conducted 3 operational flights to apply the sightability model using data collected during experimental flights to live deer observations. Operational flights were assigned to 3 units within the study area with approximate areas of 34.9, 15.2, and 38.3 km² (Figs. 2.3–2.5). Each unit represented a different management unit separated by natural and anthropogenic features (i.e., roads and creeks) and were assumed to contain naïve deer in each unit which were not previously surveyed. While operational units differed in size and vegetation type, they collectively represented similar vegetative obstruction proportions (Table 2.1). We conducted operational flights using a Bell Model 206 Jet

Ranger (Bell Helicopter Textron, Inc., Fort Worth, TX) due to local availability in August 2019. While we were not able to use the same helicopter type between experimental and operational flights, the helicopters were structurally similar except for engine type and both afforded similar good visibility (Anderson and Lindzey 1996, Anderson et al. 1998). Flights occurred from 0700-1000 hours and from 1700-2000 hours to coincide with crepuscular activity patterns of deer (DeYoung and Miller 2011). Altitude and speed were the same as experimental flights, while transects were reduced to 285 m apart to increase survey coverage to approximately 70%, since surveying >70% of a unit provides similar precision to 100% coverage (Conroy et al. 2018). During operational flights, observers counted live deer within the 200-m strip and recorded the same covariates as in experimental flights using the same protocol. As each group of live deer was encountered, we recorded whether the first individual observed was “moving” or “stationary” to evaluate the efficacy of using stationary surrogates for experimental flights. We assumed the population was closed across the 1-week operational survey period, and animals were equally distributed across the study area.

Sightability Model Analysis

Data were analyzed using the glm function in program R 3.5.1 (R Core Team 2019). This approach uses binary logistic regression to estimate the probability of detection where the response variable was a binomial response (i.e., detected or not) and predictor variables were categorical (i.e., vegetative obstruction, distance from transect, and light conditions) because variables were grouped into bins. The logistic regression function was:

$$g(\mu_i) = \beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \beta_3 x_{i3}$$

$$y_i \sim f(u_i)$$

where, g was the logit link function, β 's were coefficients estimated using binary logistic regression, x_i 's were predictor variables (i.e., vegetative obstruction, distance from transect, and light conditions), and f was a binomial probability distribution. All covariates were treated as factors since we binned vegetative obstruction and distance from transect, and light was considered a categorical variable (i.e., flat or high contrast) (Bristow et al. 2019). We used multi-model inference (Burnham and Anderson 2002) to compare sightability models using Akaike's Information Criterion adjusted for small sample size (AIC_c), AIC_c differences (Δ_c), and AIC_c weights (ω_i). AIC_c weight can be interpreted as the probability that a candidate model is the best model, given the data and the set of models (Burnham and Anderson 2002). Additionally, goodness of fit was evaluated by calculating the coefficient of determination (R^2) for each candidate model using the `rsq` package (Zhang 2020) in program R version 3.5.1 (R Core Team 2019). While model averaging based on ω_i is often recommended to assess relative importance of individual predictor variables (Burnham and Anderson 2002), it is really a measure of relative importance of each model with little information about the importance of contributions of predictor variables compared to other measures such as effect size or variance reduction (Cade 2015). Therefore, we chose not to average competing models; instead, we considered the model with the fewest parameters from the competitive set of models (i.e., $\Delta_c \leq 2$) to best explain the data. Once our top model was selected, we used the R `SightabilityModel` package (Fieberg 2012) to estimate population size on operational flight units. The R `SightabilityModel` package estimates population size of a sampling unit using a modified Horvitz-Thompson estimator, in which animal counts are

divided by plot-level sampling probabilities and detection probabilities determined from our top model (Fieberg 2012).

Sightability Model Validation

We used the known population of surrogates to test the accuracy and precision of population estimates derived from our sightability model. We used the R `SightabilityModel` package to derive an estimated surrogate population using our top model and surrogate observations unique to each experimental flight. Then, the estimated surrogate density was compared to the known surrogate density to measure the accuracy of the sightability model estimated population. Last, we measured the precision of population estimates by calculating the coefficient of variation (CV) ($SD/mean$) among estimates from repeated experimental flights.

RESULTS

Experimental Helicopter Surveys

We conducted 12 experimental flights between 22–25 July 2019 covering a total of 864-km of transect (72 km per flight) for a total of 336 potential surrogate observations (Table 2.2). Environmental conditions were variable, with winds ranging from calm to 10.8 km/h and sunny to cloudy conditions. Since the aircraft was not able to stay directly on transects 100% of the time, some surrogates were located >100 m from the transect. We recorded 17 potential observations between 101 and 125 meters; therefore, we allowed the model to predict for observations from 0 to 125 m. Observers identified 212 of the 336 possible surrogate observations (Table 2.2). The proportion of available surrogates detected decreased as percent vegetative obstruction and distance from the transect increased. We ran 8 candidate models to obtain the top model that explained the most

variation in the data while maximizing parsimony (Burnham and Anderson 2002) (Table 2.3). The top model resulted in vegetative obstruction and distance from transect being considered as the most influential covariates affecting detection probability ($\Delta AICc = 0$, $\omega_i = 0.61$) and had a coefficient of determination (R^2) of 0.41 (Table 2.3). Beta coefficients associated with vegetative obstruction levels $<50\%$ and distances <50 m were uninformative parameters because their 95% confidence intervals overlapped 0 and p-values were >0.05 (Table 2.4); while observations occurring at vegetative obstruction levels $>50\%$ and distances >50 m significantly reduced detection probability (Fig. 2.6).

Probability of detecting a surrogate was negatively related to vegetative obstruction and distance from transect (Table 2.4). Detection probability on the flight transect ranged from 0.95 (95% CI = 0.89–0.98) for 0–25% vegetative obstruction and 0–25 m distance from transect to 0.05 (95% CI = 0.01–0.18) for 76–100% vegetative obstruction and 100–125 m distance from transect (Fig. 2.6). Observer accuracy was evaluated by comparing estimated distances from observers to actual distances acquired from handheld GPS units of observed surrogates ≤ 100 m from the helicopter. Observers assigned 64% (130/203) of all distances correctly to bins, while 98% (199/203) were recorded within one bin of the correct value (Table 2.5).

To validate the model, we used population estimates derived from experimental flights with a known density of surrogates. Each of the 12 experimental flights contained 28 surrogates available to observers, establishing a known surrogate density of 1.94 surrogates/km². The sightability model produced estimates similar to the known surrogate population. Surrogate population density estimates derived from replicate experimental flights averaged 1.79 surrogates/km² (CV = 0.21, SD = 0.37). Across all flights, the

sightability model predicted a surrogate population of 309 (95% CI = 274–374) individuals, resulting in an estimate well within the 95% confidence interval and containing 92% of the known surrogate population of 336 individuals.

Operational Helicopter Surveys

We conducted 3 operational flights (1 for each unit) between 7–9 August 2019 covering a total of 125, 48, and 136 km of transect within Units 1, 2, and 3, respectively.

Environmental and vegetation conditions were similar to experimental flights. During operational flights, we documented only 40% (95% CI = 32%–48%) of groups of deer as “moving” when the group was first observed. We observed 102, 31, and 118 live deer during operational flights in Units 1, 2, and 3, respectively, with an average group size of 2.1 (95% CI = 1.81–2.32). Observers did not record deer >100 m from transects; therefore, the sightability model we used to estimate population size was not provided any observations >100 m from the transect. We estimated the deer density for Unit 1 to be 4.6 deer/km² (95% CI = 3.3–27.4), for Unit 2 to be 5.7 deer/km² (95% CI = 3.0–27.6), and for Unit 3 to be 5.4 deer/km² (95% CI = 3.6–28.2) using the top model (Table 2.6). However, deer density estimates derived from uncorrected counts were only 4.1, 3.2, and 4.3 deer/km² for Units 1, 2, and 3, respectively. Specifically, population estimates were 12%, 77%, and 26% higher using the sightability model than those derived from uncorrected counts without accounting for imperfect detection.

DISCUSSION

Sightability models account for imperfect detection during aerial surveys (Zabransky et al. 2016, Bristow et al. 2019). Different covariates seem to be important in influencing detection for different species, seasons, and study areas (e.g., light conditions, group size,

etc.) (Samuel et al. 1987, Anderson and Lindzey 1996, McIntosh et al. 2009, Zabransky et al. 2016), thus, reinforcing the need to develop sightability models in geographical regions in which they will be applied. Distance from transect and vegetative obstruction negatively affected detection of deer, especially at vegetative obstruction levels >50% and distances >50 m. These results are most likely due to the ability of observers to see through tree canopies when flying directly above. Conversely, farther distances would result in angles that could negatively influence an observer's ability to see through tree canopies. Similar to McIntosh et al. (2009), light conditions as measured did not significantly influence detection probability. In contrast, Bristow et al. (2019) found detection of elk to be better in high-contrast light versus flat light. One of the major advantages to using surrogates is the ability to compare population estimates with a known population of surrogates to evaluate model accuracy. When the sightability model was applied to observations from repeated experimental flights, population estimates were well within our 95% confidence intervals and represented 92% of the known population of surrogates. The sightability model was then applied to operational surveys on 3 units, which produced population estimates averaging 26% higher than those derived from uncorrected counts leading to more accurate population estimates.

For sightability models to produce reliable population estimates, covariates must be accurately recorded (Griffin et al. 2013). This study used location data from surrogates for white-tailed deer, unlike most studies that used live animals marked with VHF or GPS collars to provide locations for estimation of sightability (Anderson and Lindzey 1996, Zabransky et al. 2016, Bristow et al. 2019). In study designs using marked animals, detection covariates are often recorded during a subsequent flight for undetected

individuals, which allows for potential animal movement leading to erroneous estimation of covariates between where the individual was recorded and where it was actually missed during a survey (Bristow et al. 2019). Our method ensured accurate recording of covariates and eliminated biases associated with potential animal movements between initial and follow-up flights.

During experimental flights, the difficulty of accurately assigning distances to observations by measuring observer bias was demonstrated. When observers misclassified distance bins they showed a tendency to overestimate distances. These misclassified overestimates could lead to recorded observations with lower detection probabilities than reality and thus producing higher population estimates. Since most deer observations occur within a matter of seconds, observers may inaccurately estimate detailed covariates such as distance, especially when recording distance as a continuous number. In practice, observer bias can be reduced by assigning distance from transect in bins (i.e., 0–25 m) and treating distance bins as factors in analyses.

Group size was not a covariate included in the study, unlike previous studies for sightability models of other ungulate species (Anderson and Lindzey 1996, Anderson et al. 1998, Conroy et al. 2014, Jacques et al. 2014, Bristow et al. 2019). Logistical and financial constraints allowed access to only 28 archery targets. In order to evaluate the effect of group size, we would have had to cluster archery targets in pairs or groups of 3, greatly reducing independent observations and statistical power. Additionally, deer in the southeastern United States are seldom found in large groups (Hardin et al. 1976, Lagory 1986), therefore, evaluating the relationship between group size and detection rate was not applicable to the study area. The average group size was 2.1 deer during operational

flights, which was much less than those reported for other ungulate species such as elk ($\bar{x} = 14.6$, $SD = 33.5$) (Bristow et al. 2019) and pronghorn ($\bar{x} = 7.3$, $SD = 5.9$) (Jacques et al. 2014). Investigators should carefully consider the predictor variables they include in model development. If group size is considered an important predictor of detection in another study system, its inclusion in model development is recommended by clustering surrogates.

We were unable to assess biases associated with animal movements during experimental surveys, because 3-D archery targets cannot move. However, some movement was noted in the operational surveys. Movements of animals in response to helicopters can influence the ability of observers to detect a live animal (McIntosh et al. 2009, Zabransky et al. 2016, Bristow et al. 2019). However, during operational flights 60% of deer groups were observed while no movement occurred, providing support for the use of “stationary” surrogates. Biases may be minimized by measuring covariates associated with surrogates (e.g., distance measured via Geographic Information Systems) in the development of site-specific sightability models instead of estimation of covariates by observers during experimental surveys. While surrogates may not allow for the estimation of the effect of movement on detection, we suggest use of surrogates offers several advantages over the use of live deer for development of sightability models. Location of surrogates at the exact moment of observations can be measured with a handheld GPS unit and is known with absolute certainty, which may not be the case even for high resolution GPS collar data on live deer. This results in greater accuracy of covariates measurements (i.e., distance, cover type) used in the sightability model relative to approaches using live deer. Additionally, using 3-D archery targets as surrogates also

provides knowledge of a known population to assess model accuracy and reduced costs. Flight time, often the highest cost incurred, can be greatly reduced during model development, because surrogates can be placed in smaller areas representative of the study area, rather than attempting to encounter marked animals distributed across the landscape. Further research could assess deer activity and movements during helicopter surveys, the reactions of deer to different types of helicopters, and their effects on detection probability.

The same aircraft was not used in both experimental and operational flights. Therefore, differences in aircraft could have potentially influenced detection probability. While the R-44 and Bell Model 206 have similar seating configurations, they have different engine types, which produce differing noise levels (Novak 2008). Differing noise levels could induce different responses from wildlife, however, it had no effect on our experimental flight results, because surrogates cannot elicit a response. Additionally, forward visibility is also slightly different between the two helicopter models, therefore, the influence of helicopter type on detection probability may warrant further investigation. However, it is quite common for wildlife surveys to be flown in multiple helicopter types (DeYoung et al. 1989, Anderson and Lindzey 1996, Anderson et al. 1998, Griffin et al. 2013, Zabransky et al. 2016). In our case, availability dictated the helicopter type used in surveys, which is likely the case in many areas. While it would be optimal to conduct surveys in one helicopter type, this is difficult in practice. Therefore, bias can be reduced by conducting surveys in aircraft structurally similar to one another, as has been done in previous studies (Anderson and Lindzey 1996, Anderson et al. 1998).

For models to account for deer with lower detection probabilities (i.e., 76–100% vegetative obstruction), at least some individuals need to be counted within covariate categories with lower detection probabilities. Some deer might not be available for correction by the sightability model because of this constraint (Zabransky et al. 2016). We demonstrated this discrepancy between Units 1 and 2 in operational surveys. Unit 1 was generally comprised of improved pasture, while Unit 2 was generally comprised of densely vegetated flatwoods. Therefore, we expected to observe a greater frequency of observations in open areas for Unit 1 and a greater frequency of observations in areas of increased vegetative obstruction in Unit 2. Compared to uncorrected counts, density estimates derived from our sightability model on operational units increased by 12.3% and 77.1% for Units 1 and 2, respectively. Differences in density estimates observed between Units 1 and 2 demonstrate how population estimates can drastically change across sampling units as a function of vegetative cover. Since no 2 management units are the same, it is important to account for detection heterogeneity (i.e., by sampling across covariate combinations) to increase the accuracy of population estimates.

While previous literature has shown sightability models to be relatively accurate, their large confidence intervals suggest they are less precise than alternative methods, such as hybrid and double observer models (Bristow et al. 2019). Similarly, the 95% confidence intervals obtained from the sightability model were large for density estimates of operational flights using the R `SightabilityModel` package. In this model, most of the variance was attributed to sampling uncertainty associated with incomplete coverage. Sampling uncertainty can be reduced by surveying a greater proportion of a management unit or implementing a more efficient sampling design (Fieberg and Lenarz 2012). In this

case, approximately 70% of individual operational units was surveyed. However, during experimental flights all surrogates were available for detection allowing for complete coverage. During these repeated experimental flights, our model was relatively accurate and precise when estimating a known population of surrogates (i.e., 92% accurate and 0.21 CV). While increasing coverage to 100% would reduce variance of model outputs and reduce confidence intervals, it is important for managers to balance precision of population estimates, effort, and flight costs when developing survey protocols.

MANAGEMENT IMPLICATIONS

When using helicopter surveys to derive population estimates, it is imperative to account for detection heterogeneity. Without accounting for detection heterogeneity, it is difficult to determine if changes in annual estimates of population abundance are caused by actual population variability or variation in detection probability among surveys. While sightability models require substantial effort and cost to develop, they can be applied to future surveys without acquiring additional experimental data under the assumption that estimated covariate relationships remain unchanged in future surveys. Our approach seems ideally suited for populations of wildlife where life-sized surrogates (e.g., archery targets, decoys) are available and where the effects of movement are minimal. Using surrogates to construct region-specific sightability models allows managers to have a known population to evaluate model accuracy and reduce costs, labor, and biases associated with model development. This sightability model was developed for practical implementation in central Florida by measuring vegetative obstruction and distance from transect in bins to reduce recorder bias. We recommend using surrogates and binning covariates to calibrate detection probability models in other landscapes to account for

imperfect detection. Relative to uncorrected counts, our model accounted for detection heterogeneity to improve population estimates derived from helicopter surveys of white-tailed deer in central Florida. While additional predictor variables like group size, animal movement, and topographic relief were not evaluated, further investigation of these variables in regions outside of central Florida could be warranted.

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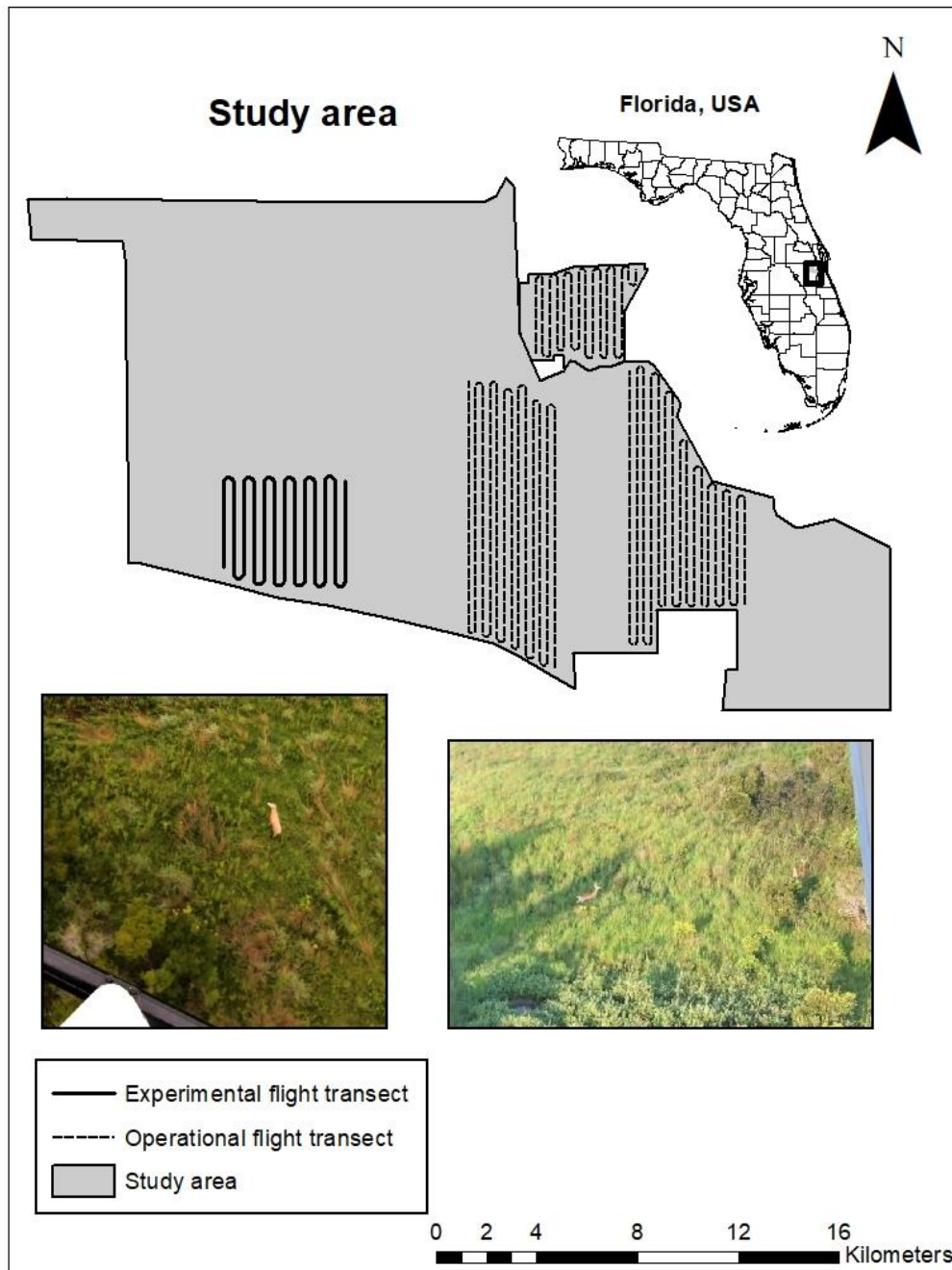


Figure 2.1. Study area with experimental and operational flight transects used to develop and apply a sightability model for helicopter survey of white-tailed deer in central Florida, USA, during July-August 2019. Pictured is an aerial view of a white-tailed deer surrogate and a live white-tailed deer side by side.

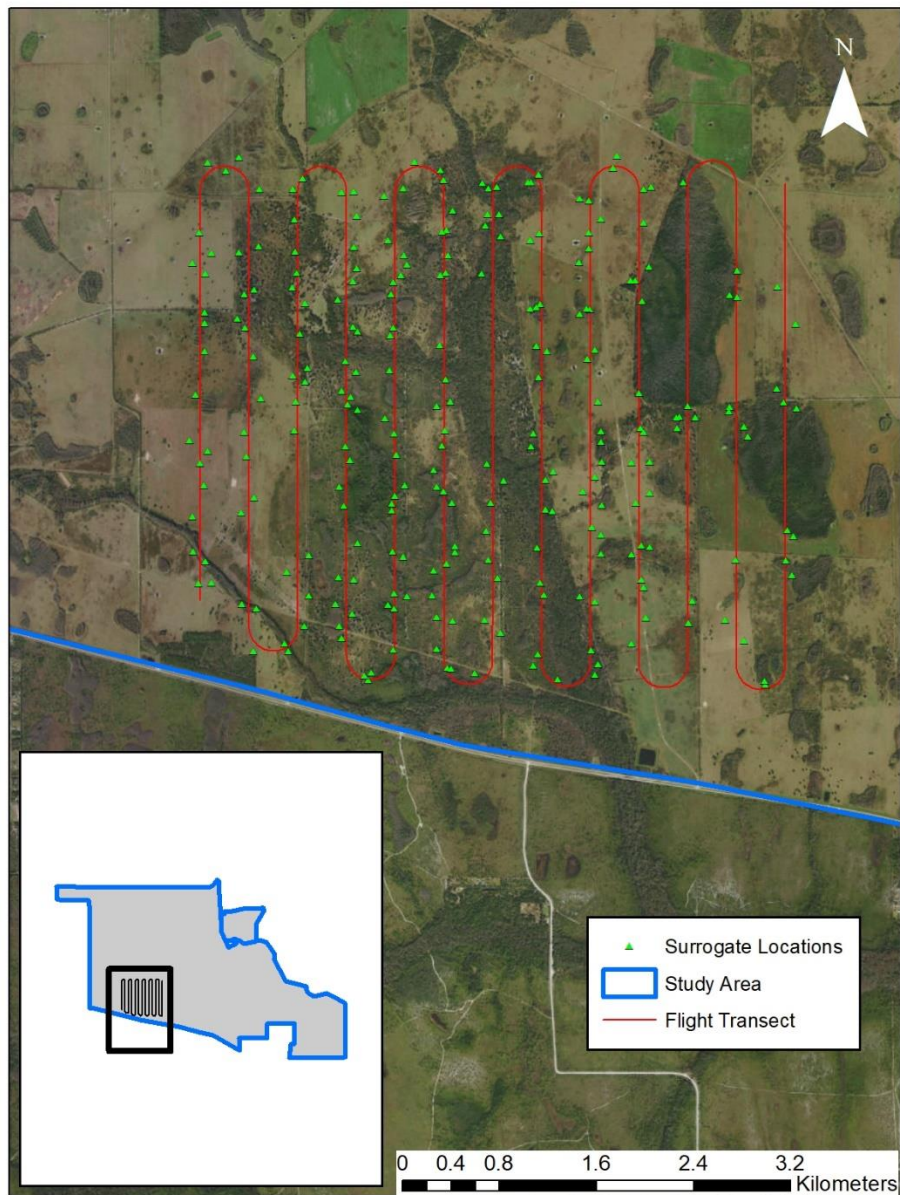


Figure 2.2. Experimental flight transects and surrogate locations used to develop sightability models for helicopter surveys of white-tailed deer in central Florida, USA during July 2019.

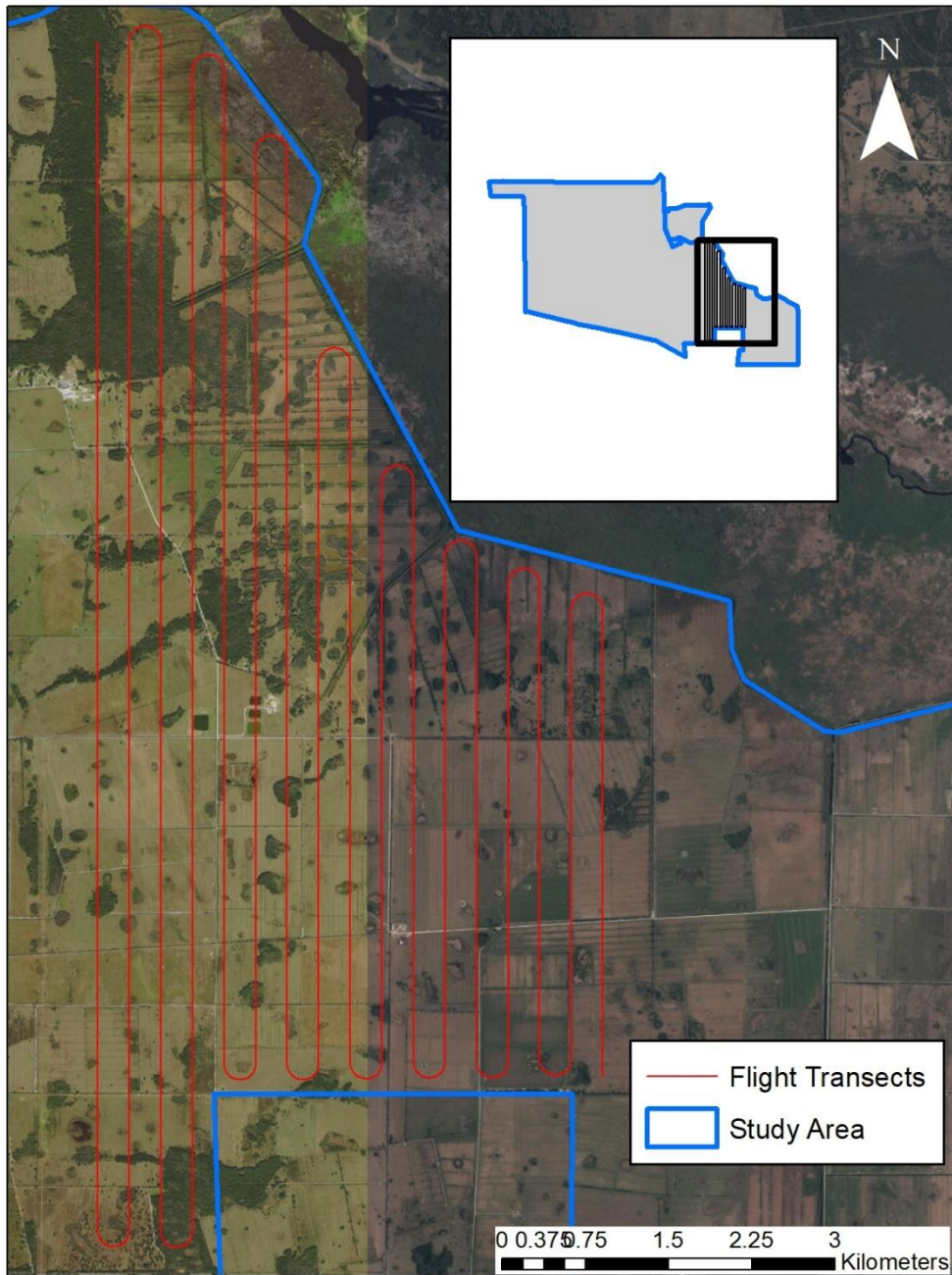


Figure 2.3. Operational flight transects for Unit 1 where live white-tailed deer were counted and sightability model was applied in central Florida, USA, during August 2019.

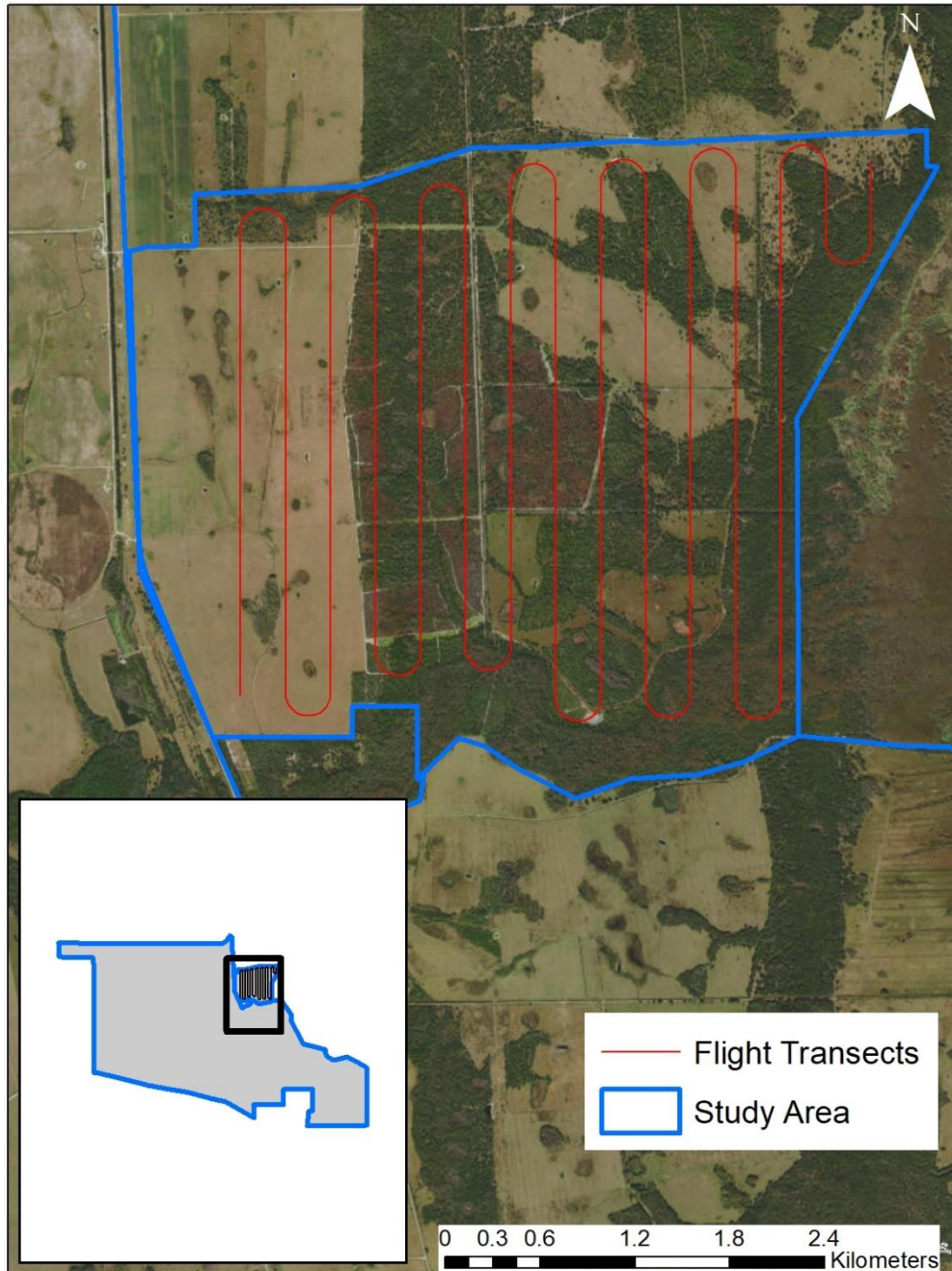


Figure 2.4. Operational flight transects for Unit 2 where live white-tailed deer were counted and sightability model was applied in central Florida, USA, during August 2019.

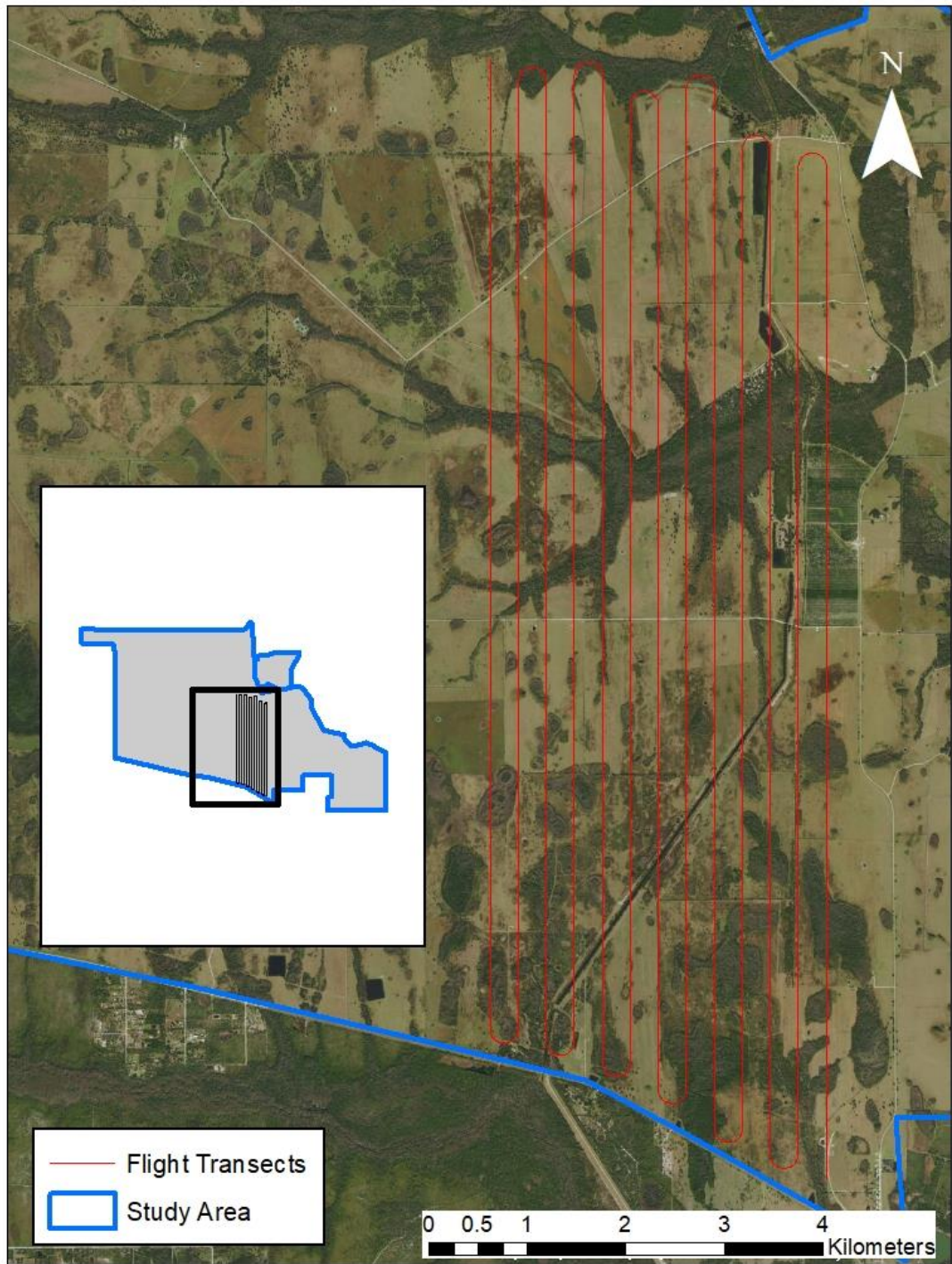


Figure 2.5. Operational flight transects for Unit 3 where live white-tailed deer were counted and sightability model was applied in central Florida, USA, during August 2019.

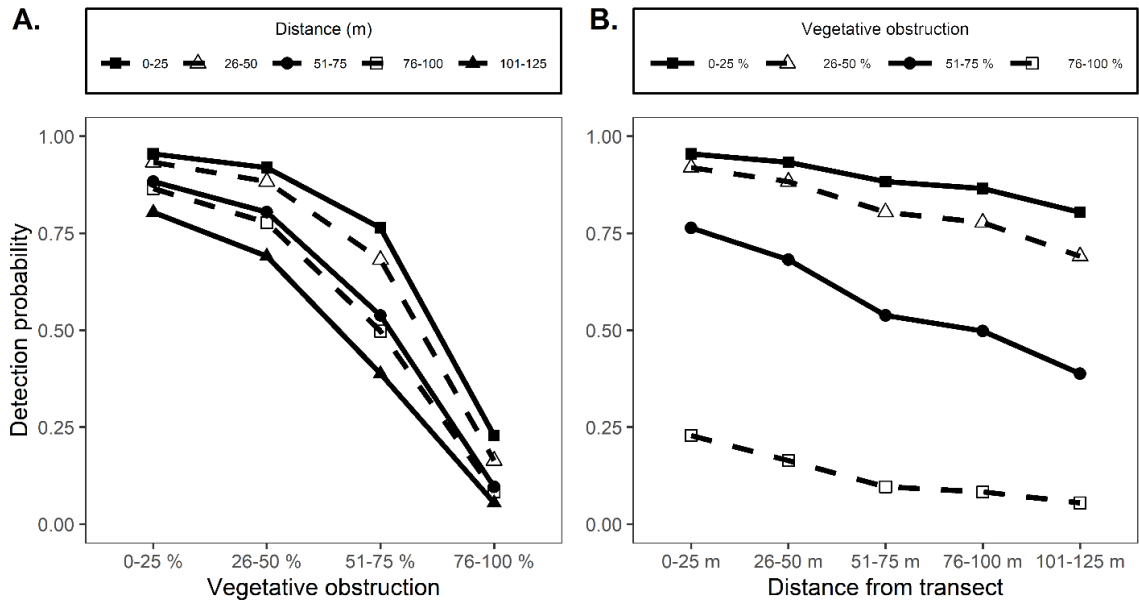


Figure 2.6. Predicted detection probability of white-tailed deer as influenced by: (A) vegetative obstruction bins (0–25%, 26–50%, 51–75%, and 76–100%) and (B) perpendicular distance from transect bins (0–25 m, 26–50 m, 51–75 m, 76–100 m, and 101–125 m) during experimental surveys from a helicopter to develop a sightability model for central Florida, USA, during July 2019.

Table 2.1. Proportion vegetative obstruction class by experimental unit (Exp. Unit) and operational units with operational unit average (Avg op. unit) of flights used to develop and apply sightability models of white-tailed deer detection for helicopter surveys conducted in central Florida, USA, during July-August 2019.

Vegetative obstruction	Proportion vegetative obstruction class				
	Exp. unit	Avg op. unit	Unit 1	Unit 2	Unit 3
0–25%	0.48	0.62	0.75	0.39	0.70
26–50%	0.12	0.09	0.11	0.04	0.11
51–75%	0.24	0.14	0.01	0.41	0.03
76–100%	0.16	0.15	0.13	0.16	0.16

Table 2.2. Number of observed and available surrogates by individual covariate and the proportion of which were observed with 95% confidence intervals during repeated experimental helicopter flights conducted in central Florida, USA, during July 2019. Vegetative obstruction bins include (0–25%, 26–50%, 51–75%, and 76–100%) and perpendicular distance from transect bins include (0–25 m, 26–50 m, 51–75 m, 76–100 m, and 101–125 m).

Covariate	Bin	Observed	Available	Proportion observed	95% CI
Vegetative obstruction	0–25%	76	84	0.90	0.84 - 0.97
	26–50%	72	85	0.85	0.77 - 0.92
	51–75%	52	85	0.61	0.51 - 0.72
	76–100%	12	82	0.15	0.08 - 0.21
Distance from transect	0–25m	63	89	0.71	0.61 - 0.80
	26–50m	57	84	0.68	0.58 - 0.78
	51–75m	46	80	0.58	0.47 - 0.68
	76–100m	37	66	0.56	0.44 - 0.68
	101–125 m	9	17	0.53	0.28 - 0.77
Light	Flat	177	274	0.65	0.59 - 0.70
	High contrast	35	62	0.56	0.44 - 0.69

Table 2.3. Akaike's Information Criterion adjusted for small sample size (AIC_c), number of parameters (K), delta AIC_c (ΔAIC_c), AIC_c weights (ω_i), cumulative AIC_c weights (Cum ω_i), log likelihood (LL), and coefficient of determination (R^2) for sightability models based on surrogates of white-tailed deer detection from helicopter surveys conducted in central Florida, USA, during July 2019. Covariates included percent vegetative obstruction (Vegetation), perpendicular distance from transect (Distance), and light conditions (Light). The model with the lowest AIC_c value and highest ω_i was considered our top sightability model.

Model	K	AIC_c	ΔAIC_c	ω_i	Cum.Wt	LL	R^2
Vegetation + Distance	8	311.8	0	0.61	0.61	-147.68	0.41
Vegetation + Distance + Light	9	313.61	1.82	0.25	0.86	-147.53	0.41
Vegetation	4	315.5	3.71	0.1	0.96	-153.69	0.38
Vegetation + Light	5	317.42	5.62	0.04	0.99	-153.62	0.38
Vegetation * Light	8	321.8	10	0	1	-152.68	0.38
Vegetation * Distance	20	321.9	10.11	0	1	-139.62	0.43
Vegetation * Distance * Light	39	346.67	34.88	0	1	-129.07	0.46
Null	1	444.49	132.69	0	1	-221.24	0.00
Light	2	445.09	133.3	0	1	-220.53	0.00
Distance	5	446.33	134.53	0	1	-218.07	0.02
Distance + Light	6	446.98	135.18	0	1	-217.36	0.02
Distance * Light	10	453.01	141.21	0	1	-216.17	0.03

Table 2.4. Logit-scale beta coefficients (β) and 95% confidence intervals and p-values (P) for the top model of white-tailed deer detection of surrogates from helicopter surveys conducted in central Florida, USA, during July 2019.

Covariate	β	Lower 95% CI	Upper 95% CI	P
Intercept	3.04	2.14	4.07	<0.001
Vegetative obstruction 26–50% ^a	-0.61	-1.60	0.33	0.215
Vegetative obstruction 51–75% ^a	-1.87	-2.80	-1.04	<0.001
Vegetative obstruction 76–100% ^a	-4.26	-5.33	-3.32	<0.001
Distance 26–50 m ^b	-0.41	-1.29	0.45	0.349
Distance 51–75 m ^b	-1.02	-1.87	-0.20	0.016
Distance 76–100 m ^b	-1.18	-2.09	-0.31	0.009
Distance 100–125 m ^b	-1.63	-2.96	-0.29	0.016

^a Interpreted relative to vegetative obstruction 0–25%

^b Interpreted relative to distance 0–25 m

Table 2.5. Observer accuracy of assigning surrogate observations to perpendicular distance from transect bins comparing recorded and measured (actual) distance, with sample size (n), during experimental flights for development of sightability models of white-tailed deer detection for helicopter surveys conducted in central Florida, USA, during July 2019.

Recorded distance interval (m)	Actual distance interval (m)			
	0–25 (n=63)	26–50 (n=57)	51–75 (n=46)	76–100 (n=37)
0–25 (n=64)	83.9%	19.7%	0.0%	0.0%
26–50 (n=52)	14.5%	50.8%	21.4%	7.9%
51–75 (n=45)	1.6%	29.5%	45.2%	18.4%
76–100 (n=42)	0.0%	0.0%	33.3%	73.7%

Table 2.6. Population density estimates of white-tailed deer with 95% confidence intervals derived from top sightability model and uncorrected counts for operational flight units during helicopter surveys conducted in central Florida, USA, during August 2019.

Study area	Number of deer observed	Area surveyed (km ²)	Total area (km ²)	Sightability density estimate (deer/km ²)	Uncorrected density estimate (deer/km ²)
Unit 1	102	24.9	34.9	4.6 (3.3–27.4)	4.1 (3.2–30.3)
Unit 2	31	9.6	15.2	5.7 (3.0–27.6)	3.2 (2.3–23.6)
Unit 3	165	27.4	38.3	5.4 (3.6–28.2)	4.3 (3.3–31.9)

APPENDIX: Predicted detection probabilities with 95% confidence intervals of white-tailed deer as influenced by vegetative obstruction groups (Vegetation) (0–25%, 26–50%, 51–75%, and 76–100%) and perpendicular distance from transect groups (Distance) (0–25 m, 26–50 m, 51–75 m, 76–100 m, and 101–125 m) during helicopter surveys conducted in central Florida, USA, during July 2019.

Vegetation	Distance	Detection probability	Lower 95% CI	Upper 95% CI
0–25%	0–25 m	95.44%	88.93%	98.20%
0–25%	26–50 m	93.27%	84.35%	97.27%
0–25%	51–75 m	88.30%	75.86%	94.77%
0–25%	76–100 m	86.51%	72.13%	94.09%
0–25%	100–125 m	80.40%	53.48%	93.60%
26–50%	0–25 m	91.94%	82.89%	96.42%
26–50%	26–50 m	88.32%	77.48%	94.32%
26–50%	51–75 m	80.46%	65.08%	90.09%
26–50%	76–100 m	77.77%	61.65%	88.39%
26–50%	100–125 m	69.10%	38.41%	88.91%
51–75%	0–25 m	76.38%	61.47%	86.76%
51–75%	26–50 m	68.17%	50.67%	81.71%
51–75%	51–75 m	53.84%	38.60%	68.39%
51–75%	76–100 m	49.78%	32.21%	67.40%
51–75%	100–125 m	38.78%	15.90%	67.97%
76–100%	0–25 m	22.82%	12.24%	38.53%
76–100%	26–50 m	16.38%	8.04%	30.51%
76–100%	51–75 m	9.64%	4.39%	19.87%
76–100%	76–100 m	8.31%	3.59%	18.08%
76–100%	100–125 m	5.48%	1.49%	18.16%

CHAPTER 3

WHITE-TAILED DEER (*ODOCOILEUS VIRGINIANUS*) MOVEMENTS AND
ACTIVITY IN RESPONSE TO HELICOPTER SURVEYS

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ABSTRACT

Wildlife managers often employ aerial survey techniques to estimate population abundance. However, disturbance from aircraft could affect foraging behavior or displace animals into suboptimal areas. We monitored 14 GPS-instrumented male white-tailed deer (*Odocoileus virginianus*) before, during, and after helicopter surveys to determine if the surveys influenced deer behavior. We collected GPS locations at 10-min fix intervals during designated monitoring periods (i.e., 0700–1000 hours), before, during, and after helicopter surveys. To determine if deer alter activity, step-lengths, or habitat selection at different temporal scales, we subset locations into 3 temporal windows: 72 hr before and after flights, 48 hr before and after flights, and 24 hr before and after flights occurred. For example, the 72-hr temporal window represented the 3-hr monitoring period on the 3 days before, the 3-hr monitoring period on the day of the flight, and the 3 days after the flights occurred. We evaluated activity rates and step-lengths of deer using generalized linear mixed effect models (GLMMs) and habitat selection using step-selection functions (SSFs). Activity rates and step-lengths of deer did not differ before, during, or after the helicopter surveys. We detected a difference in habitat selection for vegetative cover within the 72-hr temporal window. Deer selected for areas closer to vegetative cover before flights compared to after flights. While these results indicate a shift in habitat selection, deer did not disperse to new areas or seek vegetative cover after helicopter disturbance. Therefore, helicopter wildlife surveys had minimal impact on deer movement and our results suggest that evasion is short-term with bucks settling back into normal movement behaviors soon thereafter.

KEY WORDS: aircraft, behavior, disturbance, Florida, habitat selection, helicopter survey, movement *Odocoileus virginianus*.

INTRODUCTION

Aerial surveys have been used to monitor abundance of wild animals for decades (Wang et al. 2019). However, disturbance from aircraft could influence animals by affecting foraging behavior (Frid 2003) or displacing animals into riskier areas with higher predation rates (Lima and Dill 1990) leading to decreased fitness. Additionally, changes in animal behavior could introduce bias across repeated surveys (Beasom et al. 1986, Diquelou and Griffin 2020).

Aerial surveys may be the only practical method of obtaining population estimates of large ungulates across broad areas (Walter and Hone 2003). Helicopter surveys are used commonly to develop harvest prescriptions for white-tailed deer (*Odocoileus virginianus*; DeYoung 1985). Previous studies have evaluated sex and age composition (Leon et al. 1987, Conner and McKeever 2020), visibility bias (Stoll et al. 1991), and sampling intensity (Beasom et al. 1986) on the accuracy and precision of white-tailed deer helicopter surveys. Based on re-sighting of marked individuals, low altitude aircraft did not change white-tailed deer behavior over repeated flights (Leon et al. 1987). However, this study did not focus on observation of individual deer responses.

Variable responses in ungulate behavior to aircraft overflight have been reported (Krausman et al. 1986, Andersen et al. 1989, Conomy et al. 1998, Goldstein et al. 2005, Côté et al. 2013). In southern Arizona, in only 3 of 70 desert mule deer (*O. hemionus crooki*) observations, animals changed habitat use in response to aerial telemetry triangulation with up to 5 passes for each observation (Krausman et al. 1986). Mountain

goats (*Oreamnos americanus*) appeared to be more sensitive to aircraft traffic than other ungulates showing a strong behavioral response to most flights within 500 m, often fleeing toward rocky cliffs (Côté 1996). Of the previous studies of ungulate response to aircraft disturbance, to our knowledge only one has utilized Global Positioning Systems (GPS) technology (Campbell et al. 2010), and most studies relied on human observers to document animal behavior (Krausman and Hervert 1983, Krausman et al. 1986, Côté 1996, Frid 2003, Côté et al. 2013). Additionally, accelerometers in GPS collars can collect information for drawing inferences regarding activity patterns (e.g., foraging, resting) relative to the change in location (Gottardi et al. 2010, Krop-Benesch et al. 2013). Therefore, use of GPS and accelerometer technology may better evaluate animal activity and movements in response to aircraft disturbance.

To our knowledge, no research has evaluated changes in white-tailed deer (herein, deer) movements, behavior, or habitat selection in response to helicopter wildlife surveys. The goal of this research was to assess the effect of helicopter disturbance using GPS location data. Therefore, we collared deer with GPS units equipped with accelerometers to observe fine-scale movements before, during, and after helicopter surveys to evaluate the effects of helicopter surveys on deer movements, activity, and habitat selection. We tested the hypothesis that helicopter surveys influence deer behavior. We predicted deer would increase movement and select areas closer to cover during helicopter surveys as a response to perceived risk from the aircraft.

STUDY AREA

The study was conducted on a 39,944-ha portion of a ranch in Brevard, Orange, and Osceola Counties of Florida (Fig. 3.1). The ranch was privately owned and managed

primarily for cattle production; however, multiple-use management supported white-tailed deer populations for hunting leases. The habitat was mostly comprised of relatively flat, open Southeastern rangelands and characterized as improved pasture (65%) and agriculture (6%) with hardwood hammocks (11%), cypress domes (6%), flatwoods (5%), freshwater marshes and prairies (3%), and open water (4%) interspersed (Kawula and Redner 2018). Overall, there was little canopy cover, making it suitable for helicopter survey techniques. Helicopter surveys were conducted on the study area annually since 1998 to obtain population abundance estimates of deer, which were used to develop management recommendations (e.g., harvest prescriptions). Additionally, the study area received seasonal patterns of increased helicopter use for various purposes (e.g., aerial herbicide application and alligator (*Alligator mississippiensis*) egg collection). Improved pastures were established with perennials including bahiagrass (*Paspalum notatum*), limpgrass (*Hemarthria altissima*), and seasonally planted with annuals like ryegrass (*Lolium multiflorum*) for winter forage. Trees and shrubs most common at elevations <10 m include cabbage palm (*Sabal palmetto*), Brazilian peppertree (*Schinus terebinthifolius*), bald cypress (*Taxodium distichum*), Carolina willow (*Salix caroliniana*), wax myrtle (*Morella cerifera*), swamp rosemallow (*Hibiscus grandifloras*), and common buttonbush (*Cephalanthus occidentalis*). The most common trees and shrubs at elevations >10 m include pond cypress (*T. ascendens*), live oak (*Quercus virginiana*), longleaf pine (*Pinus palustris*), laurel oak (*Q. laurifolia*), loblolly bay (*Gordonia lasianthus*), red maple (*Acer rubrum*), sweetgum (*Liquidambar styraciflua*), gallberry (*Ilex glabra*), saw palmetto (*Serona repens*), and saltbush (*Baccharis halimifolia*).

METHODS

Field Methods

We captured 14 adult (≥ 1.5 years old) male deer using a Robinson-44 helicopter (Robinson Helicopter Company, Torrance, CA, USA) and a net gun (Webb et al. 2008) between 3–8 September 2018 (i.e., before hunting season and after bucks shed antler velvet). Animals were pursued ≤ 5 min to minimize capture stress. Once captured, deer were transported to work-up stations located ≤ 2 km from their capture location (Jacques et al. 2009). Capture and release locations were georeferenced using a handheld GPS (Garmin eTrex 20x, Garmin, Olathe, KS, USA). The helicopter crew restrained animals with tie-ropes and used blindfolds to decrease stress. Then, they placed deer in a sling bag for transport to work-up stations. Each buck was affixed with a GPS collar (Advanced Telemetry Systems, ATS, Isanti, MN, USA) and individually numbered livestock ear tags (Allflex USA Inc., Dallas, TX, USA) in each ear. We estimated the age of all bucks via tooth replacement and wear (Severinghaus 1949). Handling time was ≤ 10 minutes, and we released all deer at the work-up station. Capture and handling protocols were in accordance with applicable guidelines from the American Society of Mammalogists (Sikes 2016) and were approved by the Institutional Animal Care and Use Committee at the University of Georgia (AUP #: A2018 06-025-R1) and the Florida Fish and Wildlife Conservation Commission (Permit #: SPGS-18-40-A1).

We conducted 3 aerial surveys using a Bell Model 206 Jet Ranger (Bell Helicopter Textron, Inc., Fort Worth, TX, USA) during 7–9 August 2019, approximately

12 months after GPS collars were deployed. All flights occurred during approximately 0700–1000 hours. The helicopter flew 20–25 m above ground level at 30–40 knots, and we removed all doors from the aircraft to increase visibility. The pilot maintained altitude and speed by keeping altitude high enough to avoid potential hazards while also maximizing observability. We surveyed pre-established 200-m wide strip transects spaced either 285, 400, or 800 m apart, depending upon the management unit, which was navigated using Motion X-GPS (Fullpower Technologies Inc., Santa Cruz, CA, USA). We tracked each flight path using a handheld GPS unit (Garmin eTrex 20x, Garmin, Olathe, KS, USA).

Identification of Monitoring Periods and Temporal Windows

We evaluated activity, step-length, and habitat selection of male white-tailed deer in response to helicopter surveys using GPS locations and activity values from collared individuals acquired at 10-minute intervals. We derived GPS locations from deer 72-hr before and after flights occurred. To determine the temporal extent of the effect of helicopter surveys on deer behavior, we subset GPS locations into 3 datasets representing various temporal windows: 1) 72-hr before and after flights occurred, 2) 48-hr before and after flights occurred, and 3) 24-hr before and after flights occurred. Monitoring periods were set based on aircraft flight logs to ensure weather patterns, time of day, and other factors that may influence deer activity were similar. For example, since all flights took place from 0700–1000 hours, we sampled the same 0700–1000 hours period from the previous and following day(s) for analysis. Therefore, we defined monitoring periods as: 1) 0700–1000 hours the day(s) before flights occurred (i.e., before), 2) 0700–1000 hours the day flights occurred (i.e., during), and 3) 0700–1000 hours the day(s) after flights

occurred (i.e., after). For example, the 72-hr temporal window represented the 3-hr monitoring period on the 3 days before and the 3 days after the flights occurred. Therefore, the 48- and 24-hr temporal windows represented the 3-hr monitoring period on the 2 days and 1 day before and after the flights occurred, respectively. The treatment of the flight (i.e., during) is represented in all temporal windows as the 3-hr monitoring period on the day the flights occurred. During each monitoring period, we recorded activity values of individual deer. The activity value indicates the percentage of seconds the collar detected significant movements within GPS fix intervals (10 min) using an accelerometer (T. Garin, Advanced Telemetry Systems, personal communication). For example, if 60 sec of activity were registered in a 10-min fix interval, the activity value would be 10%. We used the move package (Kranstauber 2019) using program R (version 3.6.1) to calculate step-lengths before, during, and after each flight.

Activity and Movement Analysis

To determine whether activity rates or step-lengths varied by monitoring period (i.e., before, during, or after flight period), we used generalized linear mixed-effect models (GLMMs) with a Gamma distribution and a log-link because activity rate and step-length were non-negative and right skewed. We accounted for repeated observations of the same individual by including a random intercept for individual deer (Gilles et al. 2006). We fit 2 GLMMs, one for activity rate and one for step-length in each temporal window (i.e., 72 hr before and after flight occurred, 48 hr before and after flight occurred, and 24 hr before and after flight occurred) to evaluate if deer activity or movement (i.e., step-length) varied temporally in response to helicopter surveys. We assigned the before monitoring period to be the reference level in both GLMMs because it represented a baseline to

compare to the during and after monitoring periods. We calculated and plotted summary statistics on movement rate (m/hr) of deer to visually assess potential patterns across monitoring periods associated with helicopter flights. Additionally, we visually assessed activity rates of unobserved and one observed individual during flights to determine if any obvious trends were apparent among individuals. All analyses were completed using program R version 3.6.1 (R Core Team 2020) and the lme4 package (Bates et al. 2015).

Habitat Selection Analysis

We classified landcover types using the 2018 Florida Natural Areas Inventory (FNAI) imagery (Kawula and Redner 2018). FNAI imagery classifies 36 landcover types within our study area, therefore, we selected landcover types that represented vegetative cover for deer in our study system and reclassified them into one layer. To directly examine the relationship between deer habitat selection and vegetative cover, we developed a distance to vegetative cover layer (30 x 30 m) using the Euclidean distance tool in ArcMap 10.7.1 (Environmental Systems Research Institute, Inc., Redlands, CA, USA) to create a continuous distance surface (Abernathy et al. 2019).

To assess the effects of helicopter surveys on deer habitat selection, we fit a step-selection function (SSF) using conditional logistic regression to estimate the relative probability of selection (Fortin et al. 2005). SSFs are models where each step is paired with a predetermined number of steps drawn at random from a distribution of step-lengths and turning angles (Thurfjell et al. 2014). This process results in a stratified dataset with a predetermined number of random steps (i.e., available points) associated with each observed location (i.e., used point) (Muff et al. 2020). We created 10 random steps (i.e., available points) for each deer location using a von Mises distribution to

model turning angles and a Gamma distribution to model step-lengths unique to each individual rather than the population (Street et al. 2015). We fit a single SSF for each temporal window (i.e., 72 hr before and after flight occurred, 48 hr before and after flight occurred, and 24 hr before and after flight occurred) to evaluate if deer altered their utilization of vegetative cover temporally in response to helicopter surveys. We exponentiated the coefficients to obtain predictive odds ratios used for interpretation of coefficients after model development. All analyses were completed using program R (version 3.6.1) and the amt (Signer et al. 2019) and survival (Therneau 2020) packages.

RESULTS

We collected 2,022, 1,454, and 933 locations at 10-min fix intervals during designated monitoring periods for each 72-, 48-, and 24-hr temporal window, respectively. We recorded an average GPS collar error (\pm SE) of 4.4 ± 1.1 m in open areas (e.g., improved pasture) and 8.7 ± 0.5 m in closed canopy areas (e.g., hardwood hammocks) resulting in a cumulative average error of 7.6 ± 0.9 m. The mean observed step-length for bucks was 15.9 m, 15.4 m, and 16.9 m, for the before, during, and after monitoring periods, respectively. We observed no differences in activity (Table 3.1) or step-lengths (Table 3.2) between before and during helicopter surveys or before and after helicopter surveys in all 3 temporal windows. Bucks exhibited similar movement rates during our designated monitoring periods regardless of helicopter flight disturbance (Fig. 3.2).

The detection of differences in habitat selection by bucks across temporal windows, suggests that vegetative cover use varied temporally (Table 3.3). In all temporal windows, deer selected areas closer to vegetative cover before flights occurred and exhibited no relationship with vegetative cover during flights (Fig. 3.3). Additionally,

bucks exhibited no relationship with vegetative cover 24 or 48 hr after flights occurred. However, during the 72-hr after flight window, deer selected areas farther from vegetative cover than before the helicopter surveys.

Observers confirmed the sighting of only one deer equipped with a GPS collar during aerial surveys. As the helicopter approached, the deer began to run directly away from the helicopter until it was out of sight from observers. The 10-min GPS fix interval associated with the encounter of this individual had an activity value of 92 and a step-length of 14.8 m (Fig. 3.4). This observation indicated the deer was active during the 10-min fix interval the helicopter passed over; however, short step-lengths indicated the deer returned near its starting point from the prior location. Approximately 40 min after the encounter, activity values decreased to values between 0 and 8 and step-lengths decreased to values between 6 and 11 m for a period of 2 hr. These observations are likely attributed to the animal being bedded because of the reduced activity value and short steps-lengths similar to the average reported GPS collar error of 7.6 m. Similarly, we visualized activity rates for other individuals that were not observed from the helicopter, which demonstrated variability and exhibited no consistent pattern. Similar activity peaks to the observed individual occurred sporadically throughout all monitoring periods (i.e., before, during, after); therefore, without knowing the exact time the helicopter passed over these individuals it is difficult to conclude that any of these peaks in activity were caused by the effect of helicopter flights.

DISCUSSION

We used temporally fine-scale GPS location data to evaluate the response of male white-tailed deer to helicopter surveys in central Florida. Modeling efforts demonstrated no

differences in activity rates or step-lengths of male white-tailed deer between before and during or before and after monitoring periods. However, deer selected areas closer to vegetative cover before flights occurred in all monitoring periods and selected areas farther from cover during the 72-hr temporal window after flights occurred. Based on observer records, a typical encounter with deer during surveys resulted in an initial frozen behavior followed by an attempt at evasion. However, the data suggest that evasion is short-term with bucks settling back into normal movements soon thereafter. While the study design was unable to detect differences in activity or step-lengths in a 3-hr period using 10-min fix intervals, we believe that this observed short-term evasion from helicopter disturbance could introduce detection bias during surveys, but the overall effect on movement patterns is minimal.

While there is conflicting evidence in the literature regarding wildlife habituation to aircraft disturbance, habituation is most likely species and region specific. For example, previous literature has indicated a potential for habituation in mule deer (Krausman et al. 1986), however, mountain goats have shown little habituation to aircraft overflight (Côté et al. 2013). Additionally, aircraft disturbance rates of mountain goats in Alaska were much less (Goldstein et al. 2005) than in Alberta (Côté 1996) or British Columbia (Foster and Rahe 1983). Our study area is located approximately 12 km from Melbourne International Airport, which frequents traffic from both helicopters and fixed wing aircraft, therefore, deer in the study area regularly experience ascending and descending aircraft. Additionally, seasonal helicopter flyovers (e.g., aerial surveys, aerial herbicide application, alligator egg collection) are a regular part of ranch operations on

the study area. Therefore, there is potential for habituation of deer to aircraft disturbance within the study area.

During the 24-, 48-, and 72-hr temporal windows before flights occurred, deer selected areas closer to vegetative cover; however, during flights deer showed no selection patterns for vegetative cover. This could be a result of individual variation in reactions to the treatment of helicopter flights. However, after flights occurred, deer showed no relationship with vegetative cover during the 24- and 48-hr temporal windows but selected areas farther from vegetative cover during the 72-hr window. Therefore, there was no consistent pattern in the relationship of selection for distance to cover before, during, and after helicopter flights. When exposed to disturbances, ungulates demonstrate predictable patterns of seeking reliable cover (Mysterud and Østbye 1999, Pépin et al 1996). However, the animals in our study did not select areas closer to cover during or after flights, suggesting there was extraneous variation for which we could not account, including other drivers of deer movement such as climatic factors (i.e., temperature, precipitation, barometric pressure) (Tomberlin 2007, Stewart et al. 2011, Geothlich 2019).

The bucks in this study were captured by helicopters approximately 11 months before the aerial surveys in this study. Previous research has demonstrated that deer captured with helicopters return to their pre-capture movement patterns within a few days (Northrup et al. 2014). To our knowledge, no literature has compared movements of deer previously captured by helicopters to naïve deer during aerial surveys. However, deer that were previously captured by helicopters may be more likely to change their movement patterns during low altitude helicopter flights than naïve deer. Thus, the observation that

previously captured deer did not alter movements during helicopter surveys indicates that such surveys likely have minimal behavioral impacts on naïve deer. Additionally, our study was limited to adult males, thus evaluation of demographic differences in behavior relative to helicopter surveys would require additional monitoring of females with and without fawns to compare their movements to males.

Alternative forms of human disturbance (e.g., hunting, vehicles) can alter ungulate behavior (St. Clair and Forrest 2009, Little et al. 2014, Marantz et al. 2016); however, responses are typically temporary, with most animals returning to regular activities soon thereafter (Sweeney et al. 1971, D'Angelo et al. 2003, Campbell et al. 2010, Karns et al. 2012). For example, when exposed to controlled hunting with dogs, female white-tailed deer increased their rate of travel and the size of their home range during hunts; however, all returned to regular patterns within 13 hours (D'Angelo et al. 2003). Additionally, hunter induced flight responses of deer in Maryland were temporary, and no changes in daily habits were observed (Karns et al. 2012). In a study using aerial gunning, wild pigs (*Sus scrofa*) exhibited increased activity levels during flights which could last ≤ 9.4 hours throughout the day. However, the majority of wild pigs returned to their initial home ranges within the same diel period (Campbell et al. 2010). In this study there were no differences in step-length or activity rate of deer across monitoring periods (i.e., before, during, and after flights). Since helicopter flyovers occur in a matter of seconds, the 3-hr monitoring window with 10-min fix intervals may be too coarse of a resolution to detect fine-scale differences in movement patterns. The movement patterns immediately after flights were not included in these analyses. Instead, we wanted to compare the same time of day across all temporal windows to minimize variation that

could be related to different movement patterns associated with the diel period. Additionally, we attempted to detect longer-term effects, including displacement of individuals, that may influence foraging strategies and ultimately decrease overall fitness. Therefore, any short-term effects that may exist potentially were not detectable because there was approximately 21 hr between monitoring periods.

MANAGEMENT IMPLICATIONS

While the potential impacts of low altitude flights on ungulate behavior has generated concern (Frid 2003, Goldstein et al. 2005), these results indicate that disturbance associated with helicopter surveys has minimal impacts on white-tailed deer activity, movements, and habitat selection. While we did not observe changes in male white-tailed deer activity in response to helicopter surveys, one collared individual attempted to evade the helicopter. However, based on these results, evasion is short-lived and was not detectable at a 10-min scale or within the monitoring windows evaluated. Therefore, helicopter surveys do not appear to displace individual white-tailed deer. Managers should continue using aerial survey techniques to estimate population abundance in areas where conditions allow visibility of white-tailed deer.

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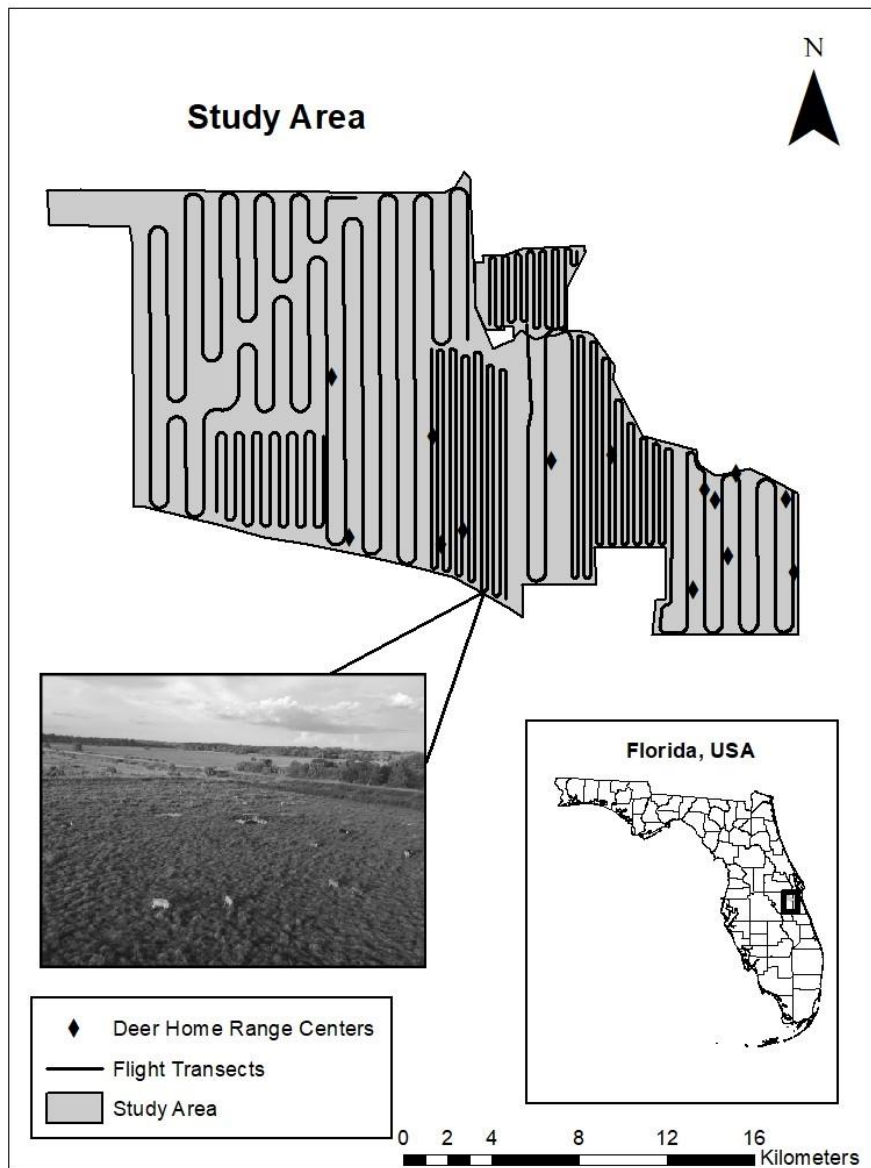


Figure 3.1. Study area with flight transects and white-tailed deer home range centers used to evaluate the effect of helicopter surveys on adult male white-tailed deer activity, step-length, and habitat selection in central Florida, USA, during August 2019. Pictured is an aerial view of the study area including cattle.

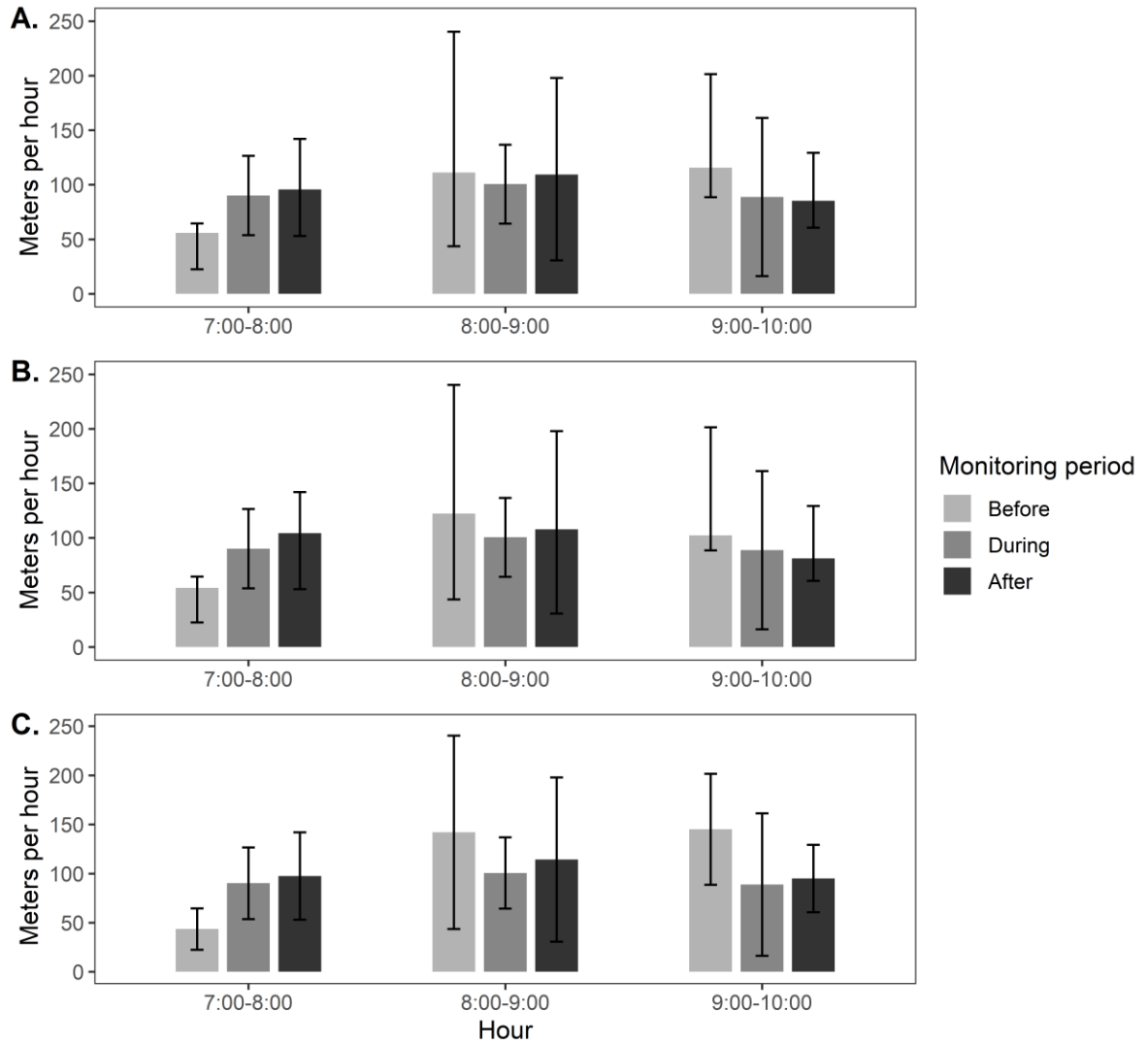


Figure 3.2. Average movement rate (meters per hour) \pm SE of male white-tailed deer relative to helicopter surveys for 3 temporal windows: (A) 72 hr before and after flights occurred, (B) 48 hr before and after flights occurred, (C) 24 hr before and after flights occurred, in central Florida, USA, during August 2019. Monitoring periods were defined as: 1) before (i.e., the day before flights occurred), 2) during (i.e., the day flights occurred), and 3) after (i.e., the day after flights occurred).

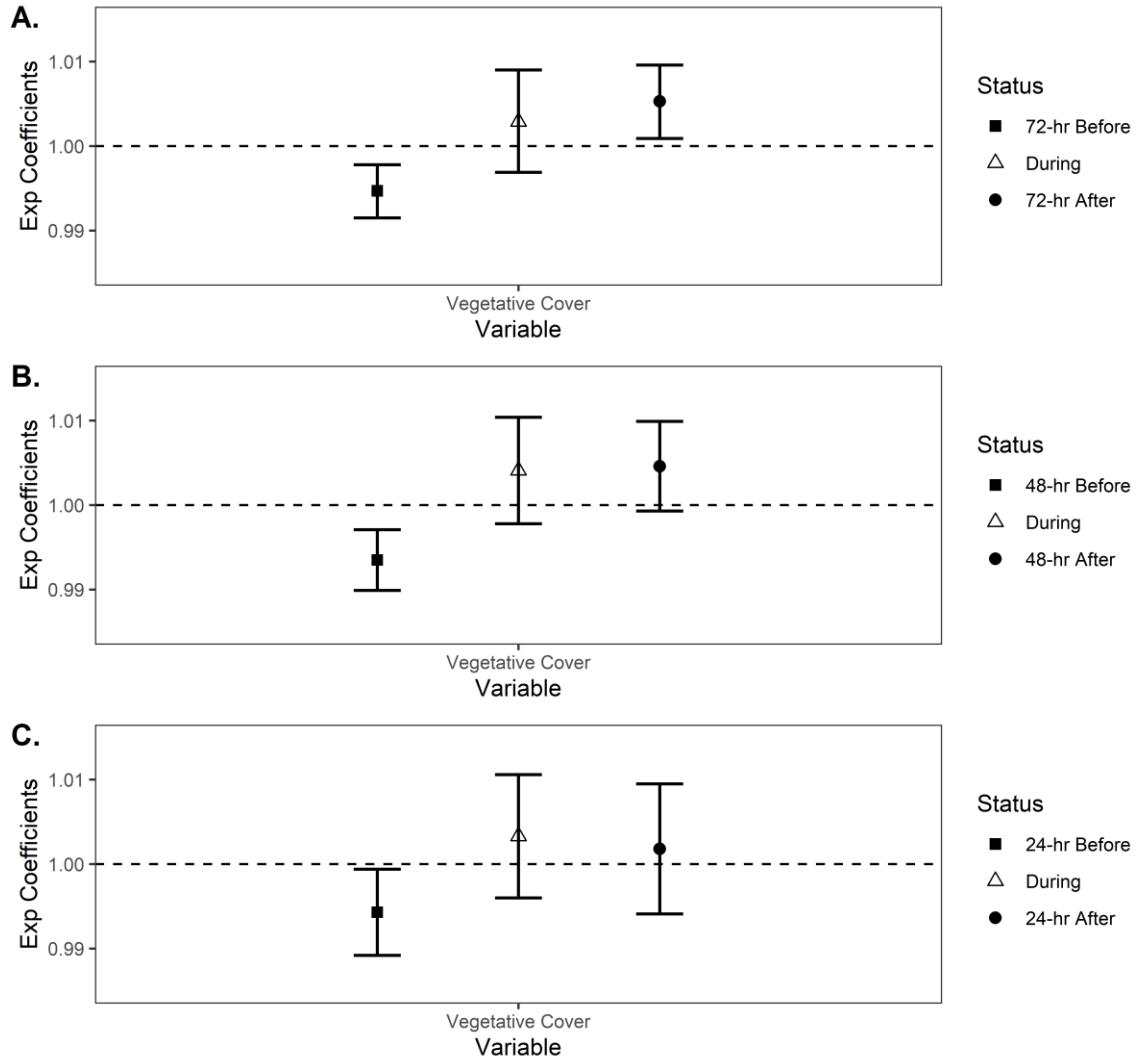


Figure 3.3. Predictive odds ratios of habitat selection of male white-tailed deer relative to distance to vegetative cover with 95% confidence intervals obtained from a step-selection function in central Florida, USA, during August 2019 for 3 temporal windows: (A) 72 hr before and after flights occurred, (B) 48 hr before and after flights occurred, (C) 24 hr before and after flights occurred. Covariates included distance to vegetative cover (Vegetative cover) (m) and y-axis represents the exponentiated beta coefficients.

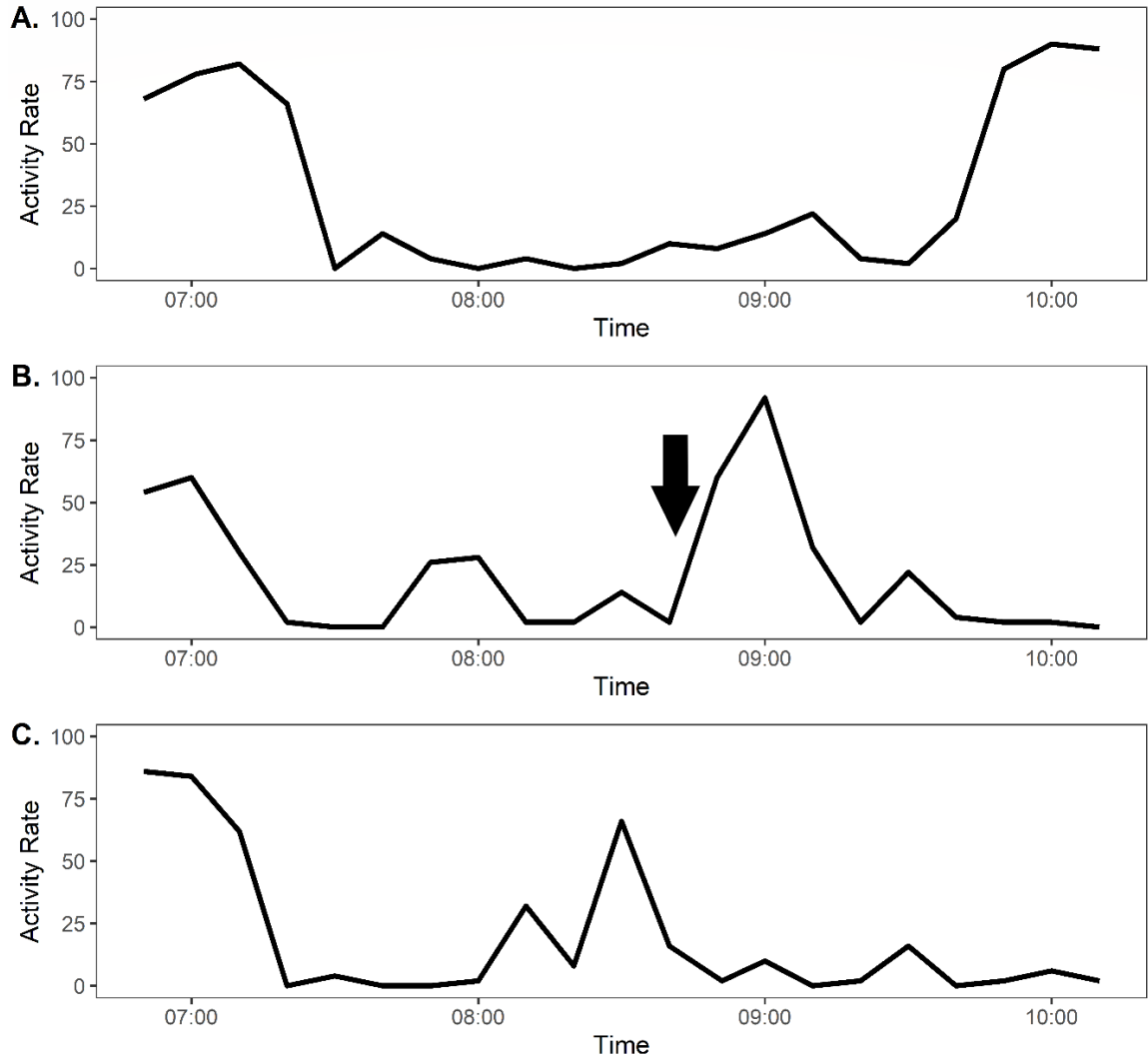


Figure 3.4. Observed GPS tracked activity rates for a single encountered buck 24 hr before (A), during (B), and 24 hr after (C) helicopter flights occurred in central Florida, USA, during August 2019. Activity rates are measured by an accelerometer with values representing the percentage of seconds within a 10-min fix interval that an animal was considered active. The monitoring window was considered 0700 – 1000 hours. The arrow on Figure 4B represents the time at which the helicopter encountered this buck.

Table 3.1. Parameter estimates of generalized linear mixed effects models evaluating activity rates of male white-tailed deer before, during, and after helicopter surveys within 3 temporal windows (72 hr before and after flight occurred, 48 hr before and after flight occurred, and 24 hr before and after flight occurred) in central Florida, USA during August 2019. Comparisons were made between the before and during monitoring periods and the before and after monitoring periods. Shown are regression coefficients (β), standard error (SE), 95% confidence intervals (CI), and P -values (P).

Temporal window	Variable	β	P	SE	Lower 95% CI	Upper 95% CI
72 hr	Intercept	3.319	0.000	0.129	3.065	3.572
	During ^a	0.097	0.422	0.121	-0.140	0.335
	After ^a	0.067	0.430	0.085	-0.099	0.233
48 hr	Intercept	3.297	0.000	0.120	3.063	3.531
	During ^a	0.113	0.375	0.128	-0.137	0.363
	After ^a	0.124	0.231	0.103	-0.079	0.326
24 hr	Intercept	3.462	0.000	0.129	3.210	3.714
	During ^a	-0.068	0.632	0.142	-0.347	0.211
	After ^a	-0.045	0.743	0.138	-0.316	0.225

^a Interpreted relative to before monitoring period

Table 3.2. Parameter estimates of generalized linear mixed effects models evaluating step-lengths of male white-tailed deer before, during, and after helicopter surveys at 3 temporal windows (72 hr before and after flight occurred, 48 hr before and after flight occurred, and 24 hr before and after flight occurred) in central Florida, USA during August 2019. Comparisons were made between the before and during monitoring periods and the before and after monitoring periods. Shown are regression coefficients (β), standard error (SE), 95% confidence intervals (CI), and P -values (P).

Temporal window	Variable	β	P	SE	Lower 95% CI	Upper 95% CI
72 hr	Intercept	2.630	0.000	0.138	2.360	2.899
	During ^a	0.004	0.965	0.044	-0.178	0.186
	After ^a	0.002	0.970	0.037	-0.127	0.131
48 hr	Intercept	2.598	0.000	0.132	2.339	2.857
	During ^a	0.020	0.839	0.100	-0.175	0.215
	After ^a	0.076	0.359	0.083	-0.086	0.238
24 hr	Intercept	2.710	0.000	0.150	2.415	3.004
	During ^a	-0.082	0.479	0.116	-0.310	0.145
	After ^a	-0.125	0.282	0.116	-0.353	0.103

^a Interpreted relative to before monitoring period

Table 3.3. Parameter estimates of step-selection models evaluating distance to vegetative cover of male white-tailed deer locations before, during, and after helicopter surveys at 3 temporal windows (72 hr before and after flight occurred, 48 hr before and after flight occurred, and 24 hr before and after flight occurred) in central Florida, USA during August 2019. Shown are regression coefficients (β), standard error (SE), 95% confidence intervals (CI), and *P*-values.

Temporal window	Variable ^a	β	<i>P</i>	SE	Lower 95% CI	Upper 95% CI
72 hr	Dist_cover	-0.005	0.001	0.002	-0.009	-0.002
	Dist_cover*during ^b	0.003	0.344	0.003	-0.003	0.010
	Dist_cover*after ^b	0.005	0.017	0.002	0.001	0.009
48 hr	Dist_cover	-0.007	0.000	0.002	-0.010	-0.003
	Dist_cover*during ^b	0.004	0.204	0.003	-0.002	0.010
	Dist_cover*after ^b	0.005	0.088	0.003	-0.001	0.010
24 hr	Dist_cover	-0.006	0.028	0.003	-0.011	-0.001
	Dist_cover*during ^b	0.003	0.373	0.004	-0.004	0.011
	Dist_cover*after ^b	0.002	0.649	0.004	-0.006	0.009

^a Variables included distance to cover (Dist_cover) (m), and flight status (before, during, after)

^b Interpreted relative to before monitoring period

CHAPTER 4
RESOURCE SELECTION OF WHITE-TAILED DEER (*ODOCOILEUS*
VIRGINIANUS) RELATIVE TO CATTLE MANAGEMENT

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ABSTRACT

White-tailed deer (*Odocoileus virginianus*) are found throughout 47 states that collectively produce approximately 93% of the cattle in the United States. Understanding resource use of deer relative to livestock management practices is essential to successfully managing ranching operations for multiple revenue sources. In 2018–2020 we used global positioning system data from 42 male white-tailed deer and a mixed conditional logistic regression analysis (i.e., step-selection function) to evaluate resource selection relative to livestock management practices (e.g., grazing, herbicide, fertilizer, biosolids), supplemental feeders, and vegetative communities (e.g., improved pasture, non-forested wetlands, forested wetlands) during the growing (Apr–Sept) and dormant (Oct–Mar) seasons in central Florida. Resource selection of bucks varied between seasons with bucks selecting areas closer to pastures that were grazed approximately 140–220 days prior during the dormant season. During the growing season, deer selected for pastures that were recently grazed with lighter stocking rates. In both seasons, bucks selected areas closer to supplemental feeders and non-forested wetlands. During the growing season, deer selected pastures that were applied with herbicide less recently. We documented no significant relationship between fertilizer or biosolids and relative probability of deer use. Rotational grazing of cattle can provide deer with a multitude of pastures at different stages of herbaceous regeneration, allowing them to balance the tradeoff between forage quality and quantity. When managing pastures, livestock and wildlife managers should strive to create a mosaic of habitats across properties to maximize resources available to deer within active cattle management systems.

KEY WORDS: cattle, Florida, grazing, livestock management, *Odocoileus virginianus*, resource selection, space-use.

INTRODUCTION

There are 257 million ha of non-Federal (i.e., private, state, Tribally owned) and approximately 101 million ha of Federal grazing lands in the United States (Hardy Vincent 2018, USDA 2018), supporting an estimated 94.4 million cattle (*Bos taurus*) (USDA 2020). These rangelands are often managed for multi-use production, including wildlife. The economic value of wildlife is becoming more important on private lands, and revenue from hunting leases often provides substantial income in addition to traditional revenue sources (Adams et al. 2000). In addition, management actions designed to benefit cattle may positively or negatively impact wildlife populations. Therefore, it is important to understand wildlife distributions and interactions with livestock to successfully manage ranching operations for multiple uses.

Cattle grazing management is used to achieve a variety of goals, including livestock production, wildlife habitat enhancement, and environmental sustainability for continued long-term use (Krausman et al. 2009). In general, properly applied grazing can increase habitat diversity, nutritional value of forage, and forage productivity (Vavra 2005). For example, previous research has shown that moderate- to light-stocking rates can increase forb production through reduction of competition from grass, stimulating growth and increasing range conditions (Anderson and McCuistion 2008). This can reduce costs and yield greater financial returns for livestock production while simultaneously improving wildlife habitat (Anderson and McCuistion 2008).

Although cattle management actions may benefit a suite of wildlife species, there is particular interest in how they influence white-tailed deer (*Odocoileus virginianus*). White-tailed deer are found throughout 47 states that cumulatively produce approximately 93% of the cattle in the U.S. (U.S. Department of Agriculture 2020). Furthermore, white-tailed deer management is important due to their recreational and economic potential (e.g., hunting leases; Leonard 2004). As a result, research has been conducted on survey techniques (DeYoung et al. 1989, Moore et al. 2013), nutritional supplementation (Masters et al. 1993, Mixon et al. 2009), and movement patterns (Webb et al. 2007, Peterson et al. 2017) to improve deer management on private lands. However, few studies have examined livestock management in relation to space use and habitat selection of white-tailed deer.

Where deer-cattle interactions have been evaluated, the presence of livestock reduces white-tailed deer use of habitats (Merrill et al. 1957, McMahan 1966, Ellisor 1969, Sparrowe and Springer 1970, Hood and Inglis 1974). In other cases, extensive spatial overlap between cattle and white-tailed deer has occurred but was mediated by strong temporal separation (Cooper et al. 2008). Temporal separation may be due to social interactions between deer and cattle rather than direct competition for resources (Compton et al. 1988). Stocking rate of cattle apparently mitigates these relationships as deer in Texas may coexist with cattle during a continuous grazing system but avoid high concentrations of cattle in short duration, high intensity grazing systems (Cohen et al. 1989). Thus, it appears that the presence of cattle is likely correlated with reduced space use by deer, however, it is unknown whether responses by deer are caused by direct dietary competition.

Dietary overlap between deer and cattle increased from 12% in summer to 46% in winter in forested pine-hardwood systems of central Louisiana (Thill 1984). Dietary overlap also can increase from natural events such as drought, forcing competition due to reduced forage availability (Ortega et al. 1997). However, in non-drought years, cattle grazing during the growing season (i.e., late-spring to early fall) has little negative impact on deer forage availability (Thill and Martin 1989). Therefore, any avoidance of deer toward cattle between late-spring and early fall is likely due to social intolerance.

If social intolerance is a driving force in deer-cattle interactions, it is important to understand whether specific management actions for cattle impact those interactions. Cattle managers often apply fertilizers to stimulate forage production and quality. Biosolids are a low-cost resource (McFarland et al. 2010) used to increase plant biomass, decrease soil erosion, and improve soil conditions (Washburn and Begier 2011). Long-term application of biosolids have demonstrated no effect on deer habitat preference (Washburn and Begier 2011). However, Milorganite®, a trade name fertilizer product derived from sewage sludge, can be used to temporarily repel deer from food plots to reduce browsing pressure (Stephens et al. 2005). Additionally, herbicide applications may be used to alter species composition in pastures as well as control invasive native and exotic plants.

We investigated temporal variation in habitat selection and space-use of male white-tailed deer relative to the presence of cattle and management actions designed to benefit cattle (e.g., fertilizer, herbicide, biosolid application, and supplemental feeders). We utilized data from GPS collars of male deer on a large cattle ranch in central Florida. We tested the hypothesis that white-tailed deer will use areas with increased forage

quality and quantity associated with cattle and ranch management. We expected deer to avoid pastures that were more recently grazed at higher stocking rates and avoid pastures applied with herbicides because of a decrease in forage availability. However, we expected deer to select for pastures where fertilizers and biosolids had been applied because of increased forage biomass, palatability and nutrient content of plants (Sumner et al. 1991).

STUDY AREA

This study was conducted within a 37,024-ha portion of a ranch in Brevard and Osceola Counties of Florida between the cities of Melbourne and St. Cloud (Fig. 4.1). The ranch was privately owned and managed primarily for cattle; however, multiple-use management was conducted to support revenues from timber harvest, row crops, citrus, sod farming, and hunting leases. The study area was bordered entirely by the St. Johns River marsh to the east and US highway 192 to the south.

The habitat across the study area was characterized generally as improved pasture (62%) with hardwood hammocks (8%), cypress domes (4%), flatwoods (5%), freshwater marshes and prairies (17%), and open water (4%) interspersed (Kawula and Redner 2018). Canopy cover was sparse due to the establishment of improved pastures creating a heterogeneous environment with abundant early successional habitats. Soil types were sandy including Smyrna fine sand, Riviera fine sand, and Mayakka fine sand (USDA-NRCS 2018). Improved pastures were mainly planted in perennials including bahiagrass (*Paspalum notatum*) and limpograss (*Hemarthria altissima*) with approximately 85% and 70% of their production occurring during the growing season (i.e., Apr–Sept), respectively (Vendramini et al. 2009, Wallau et al. 2010). Improved pastures were

seasonally planted with annuals like ryegrass (*Lolium multiflorum*) for winter forage. During the growing season, pastures were historically over-seeded with various legumes such as American jointvetch (*Aeschynomene americana*), perennial peanut (*Arachis glabrata*), and partridge pea (*Chamaecrista fasciculata*). The majority of these plants were still abundant during the study. Below 10 m elevation, common trees and shrubs included cabbage palm (*Sabal palmetto*), Brazilian peppertree (*Schinus terebinthifolius*), bald cypress (*Taxodium distichum*), Carolina willow (*Salix caroliniana*), wax myrtle (*Morella cerifera*), swamp rosemallow (*Hibiscus grandifloras*), and common buttonbush (*Cephalanthus occidentalis*). The most common trees and shrubs at elevations above 10 m included pond cypress (*T. ascendens*), live oak (*Quercus virginiana*), longleaf pine (*Pinus palustris*), laurel oak (*Q. laurifolia*), loblolly bay (*Gordonia lasianthus*), red maple (*Acer rubrum*), sweetgum (*Liquidambar styraciflua*), gallberry (*Ilex glabra*), saw palmetto (*Serona repens*), and saltbush (*Baccharis halimifolia*). Average summer temperatures were hot (26–29°C ± SD), average winter temperatures were mild (15–21°C ± SD), and annual precipitation averaged 136.1 cm (Shin et al. 2020).

Management practices to support forage for cattle and wildlife were intensive and diverse, including rotational grazing, fertilizer application, herbicide application, and supplemental feeding. Rotational grazing was intensive with cattle being rotated among pastures roughly every 2 weeks depending on forage availability. Herd sizes ranged from approximately 50 to 450 cattle. During the study, fertilizer was applied to stimulate herbaceous plant growth and improve soil fertility on approximately 12,470 ha annually. Herbicide (e.g., triclopyr and 2,4-D) was sprayed on approximately 5,430 ha annually to reduce competition from undesirable plant species (i.e., dogfennel [*Eupatorium*

capillifolium], goldenrod [*Solidago* spp.], purple thistle [*Cirsium horridulum*], tropical soda apple [*Solanum viarum*], and wax myrtle [*Morella cerifera*]) and to promote herbaceous growth. Biosolids were spread on approximately 990 ha annually to improve soil fertility and increase plant biomass and cover. Shelled corn and pelleted feed were provided to wildlife by hunters at various established sites across the property at approximately 1 feeder/128 ha. Together these management practices effect a conglomeration of resources used by white-tailed deer.

METHODS

Deer Capture and Handling

We captured 19 and 23 adult (≥ 1.5 years old) bucks using a Robinson-44 helicopter (R-44) (Robinson Helicopter Company, Torrance, CA, USA) and net gun (Webb et al. 2008) in September 2018 and August 2019, respectively. We pursued deer ≤ 5 min to minimize capture stress. The helicopter crew restrained bucks with tie-ropes, blindfolded them, and placed them in a sling bag for transport to work-up stations ≤ 2 km from their capture location (Jacques et al. 2009). Capture and release locations were georeferenced using a handheld GPS unit (Garmin eTrex 20x, Garmin, Olathe, KS, USA). We attached a GPS collar (Advanced Telemetry Systems, ATS, Isanti, MN, USA) and numbered livestock ear tags in each ear (Allflex USA Inc., Dallas, TX, USA). Ground crews estimated the age of all bucks via tooth wear and replacement (Severinghaus 1949). Handling time was ≤ 10 min and all deer were released at the work-up station. Capture and handling protocols were in accordance with applicable guidelines from the American Society of Mammalogists (Sikes 2016) and were approved by the Institutional Animal Care and Use

Committee at the University of Georgia (AUP #: A2018 06-025-R1) and the Florida Fish and Wildlife Conservation Commission (Permit #: SPGS-18-40-A1).

We programmed GPS collars to acquire a fix every 6 hours (i.e., hour 0, 6, 12, and 18), and we censored the first 14 days of buck locations to allow for a post-capture acclimation period (Dechen Quinn et al. 2012). We included 2D locations with a horizontal dilution of precision (HDOP) of ≤ 10 and 3D locations with an HDOP of ≤ 15 for “used” points (i.e., GPS locations of bucks, Dussault et al. 2001). Locations of animals that experienced mortality during the study were censored following the last fix known to be alive.

Data Management

We procured information about pasture management from monthly reports completed by cattle foremen. Monthly reports included pasture location, cattle herd size, rotation date, and fertilizer or herbicide treatment information. We used the information in monthly reports to create predictor variables to evaluate the effect of cattle grazing, herbicide, fertilizer, and biosolids on resource selection of bucks. To quantify day(s) since grazing (DSG) we assigned animal locations to a pasture and subtracted the date of the last grazing event from the date of the location. If cattle were present on the date the location was recorded, we assigned a value of 0. Pastures were also assigned the stocking rate (cattle/ha) from the preceding or current grazing. These data enable evaluation of the relationship between cattle stocking rate and deer resource use. To evaluate if habitat selection varied across different values of DSG, we explored if incorporating a quadratic variable improved model fit. Based on preliminary analysis, model fit was improved by including a quadratic variable for DSG, therefore, a quadratic variable for DSG was

included in the global model. We evaluated day(s) since fertilizer (DSF) and day(s) since herbicide (DSH) using the same process as DSG. For biosolids, our data only included the year of application, therefore, we assigned a value for year(s) since biosolid application (YSB). GPS locations within pastures that occurred in the same year of biosolid application were assigned a value of 0 years since application. Some areas within the study area were never grazed, or applied with herbicide, fertilizer, or biosolids (e.g., hardwood hammocks, roads). Because the forage benefits of herbicide and fertilizer applications are short-term in our system, (Hochmuth and Hanlon 2019, Sellers and Devkota 2020) these pastures were assigned 365 days since treatment (1 year). Biosolids exhibit a slow release of nitrogen compared to conventional fertilizers (Kidder 2002); therefore, we assigned a value of 3 YSB for locations within pastures that never received biosolids.

We classified landcover types using the 2018 Florida Natural Areas Inventory imagery (Kawula and Redner 2018). We selected landcovers that most likely influenced deer in our study system and reclassified them into 3 major categories: improved pasture, forested wetlands, and non-forested wetlands. Additionally, hunters reported all supplemental feeder (herein, feeder) locations for deer within the study area. To facilitate direct comparisons between landcover variables and other covariates, we developed distance-to metrics (30 x 30 m) for each landcover type and feeder layer using the Euclidean distance tool in ArcMap 10.7.1 to create a continuous distance surface for each variable (Abernathy et al. 2019).

Step-selection Analysis

We divided deer locations into a growing (Apr–Sept) and dormant season (Oct–Mar), then used step-selection functions (SSFs) to evaluate 3rd order habitat selection (Johnson 1980) and accommodate spatial covariates that varied in time (e.g., DSG) (Thurfjell et al. 2014). SSFs were fit using mixed conditional logistic regression to estimate the relative probability of selection (Fortin et al. 2005, Muff et al. 2020). SSFs are models where each observed step is paired with a predetermined number of steps drawn at random from a distribution of step lengths and turning angles (Thurfjell et al. 2014). This process results in a stratified dataset with a predetermined number of random steps (i.e., available points) associated with each observed location (i.e., used point, Muff et al. 2020). Since continuously monitoring individual animals leads to non-independent data points and pseudoreplication (Duchesne et al. 2010), it is recommended to use random intercepts and coefficients to account for unbalanced sample sizes and individual-specific responses to a particular covariate (Gilles et al. 2006). While standard logistic mixed models can be fit easily, random effects modeling is difficult in conditional logistic regression especially when the number of strata (i.e., paired used and available locations) is >1 and unbalanced (Craiu et al. 2011). However, recent literature has demonstrated that conditional logistic regression is a special case of a multinomial model and a conditional Poisson model produces equivalent β parameter estimates and the same standard errors as conditional logistic regression, thus allowing inclusion of random intercepts and coefficients (Muff et al. 2020). With this approach, it is best to interpret stratum-specific fixed effects as a random effect, however, estimates of random effects will on average be too small (Muff et al. 2020). Therefore, it is recommended to fix the variance at a large value instead of

allowing it to be freely estimated, to ensure stratum-specific intercepts are not pulled toward 0 (Muff et al. 2020). The glmmTMB package (Brooks et al. 2017) allows the option to constrain variance to a large-fixed value, therefore we used glmmTMB to fit SSFs using mixed conditional regression.

We created 10 random steps (i.e., available points) for each buck location using a von Mises distribution to model turn angles and a gamma distribution to model step lengths unique to individuals rather than the population using the ‘amt’ package (Signer et al. 2019) in program R 3.6.1 (R Core Team 2020). To avoid issues with temporal autocorrelation, we resampled buck locations to obtain 1 fix per collar per day, at a random timestamp each day (i.e., hour 0, 6, 12, or 18). We standardized and centered all continuous variables $[(x_i - \bar{x})/SD]$, then back transformed and exponentiated the coefficients for interpretation using predictive odds plots after model development. Then, we used Spearman’s rank correlation coefficient (Boyce 2002) to assess variable correlation and excluded any variables that exhibited high correlation ($|r| > 0.6$). Because we were interested in directly comparing coefficient estimates across seasons, we did not use model selection (Kohl et al. 2013). Instead, one global model was created for both the growing and dormant seasons that included DSG with a quadratic variable, stocking rate, the interaction between DSG and stocking rate, DSF, DSG, YSB, and distance to feeder, pasture, non-forested wetlands, and forested wetlands. We also included step-length in our global models (Forester et al. 2009). Since leave-one-out (LOO) cross-validation is generally more robust in the GLMM framework due to accounting for bias associated with random effects, model fit was assessed using LOO cross-validation (Vehtari et al. 2017). The LOO method builds models excluding one individual at a time and is used to

generate predictions for the withheld individual (Matthiopoulos et al. 2011).

Additionally, we subset strata by hour (i.e., hour 0, 6, 12, and 18) before using LOO cross-validation to avoid bias associated with differing time of day. We calculated the mean correlation for models built with $n-1$ individuals in both the growing and dormant seasons by hour (i.e., 0, 6, 12, and 18) to assess the fit of the models.

RESULTS

We obtained data from GPS collars on 41 and 42 adult (≥ 1.5 years old) male deer during the growing and dormant seasons, respectively. After resampling, we included a total of 10,848 observed locations in the step-selection analysis resulting in 3,178 strata during the growing season and 7,670 strata during the dormant season. We recorded an average GPS collar error (\pm SE) of 4.4 ± 1.1 m in open areas (e.g., improved pasture) and 8.7 ± 0.5 m in closed-canopy areas (e.g., hardwood hammocks) resulting in a cumulative average error of 7.6 ± 0.9 m.

We detected differences between resource selection of bucks during the dormant and growing seasons (Fig. 4.2; Tables 4.1 and 4.2). During the dormant season, deer exhibited a strong selection for pastures with intermediate values of DSG (i.e., 140–220 days) (Fig 4.3A). DSG was also dependent on the preceding stocking rate of grazed pastures. For example, in areas with low and high values of DSG (i.e., 1 and 365 day(s)), deer demonstrated an increase in use of pastures with light preceding stocking rates compared to pastures with medium and heavy preceding stocking rates. However, pastures with intermediate values of DSG (i.e., 140–220 days) had a higher relative probability of use when the preceding stocking rate was heavy (Fig. 4.3A). Distance to feeder location, pasture, and non-forested wetland were also predictors of resource

selection during the dormant season (Fig. 4.2) as the relative probability of use decreased by 5.2%, 31.6%, and 18.0% for every 100 m away from feeders, pasture, and non-forested wetlands, respectively (Fig. 4.4). While deer readily selected areas closer to improved pasture, their relative probability of use decreased when days since grazing values were low. LOO cross-validation revealed a mean correlation of 0.42, 0.27, 0.21, and 0.23 during the dormant season for stratum associated with the 0, 6, 12, and 18 hr, respectively.

During the growing season, our global model indicated distance to feeder, distance to non-forested wetlands, and the interaction between DSG and preceding stocking rate were important predictors of resource selection (Fig. 4.2, Table 4.2). Deer selected for pastures with intermediate values of DSG (i.e., 140–220 days) that were previously grazed at heavier stocking rates and pastures with low values of DSG (i.e., 1 day) that were previously grazed at lighter stocking rates (Fig. 4.3B). Deer also selected for areas associated with higher values of DSH and closer to feeder locations during the growing season (Fig. 4.5). The relative probability of use increased by 18.6% for every 100 days since the application of herbicide and decreased by 9.6% for every 100 m away from feeders. Additionally, DSF, YSB, distance to pasture, and distance to forested wetlands were uninformative predictor variables (Table 4.2). LOO cross-validation revealed a mean correlation of 0.27, 0.29, 0.23 and 0.22 during the growing season for stratum associated with the 0, 6, 12, and 18 hr, respectively.

DISCUSSION

In central Florida rangeland, we documented that male white-tailed deer resource selection varied seasonally relative to cattle management. DSG and the preceding

stocking rate of a grazing event significantly influenced resource selection of bucks in both seasons. In all cases, bucks were less likely to select for pastures occupied or recently vacated by cattle when the preceding stocking rate was heavy. Instead, bucks increased their use in pastures approximately 140–220 days after a heavy grazing event. Alternatively, during the growing season bucks demonstrated an increase in their relative probability of use after light grazing events. When pastures were applied with herbicide, habitat use by bucks increased as DSH increased. Additionally, bucks selected for areas closer to improved pasture during the dormant season, while we documented no significant relationship in the growing season. In both seasons, bucks selected for areas closer to feeder locations and non-forested wetlands and the application of fertilizer and biosolids did not influence deer selection.

While previous literature has documented temporal separation between deer and cattle (Stewart et al. 2002, Cooper et al. 2008), individual deer may not show avoidance toward cattle until they are within 50 m of each other (Cooper et al. 2008). Although, fine-scale separation may have occurred during the growing season in our study, interactions may not cause deer to avoid a pasture. Therefore, differences in space-use of bucks within a rotational grazing system were likely attributable to interspecific competition with cattle and not social intolerance. During the growing season, we documented the highest predicted relative probability of use in lightly grazed pastures that coincide with cattle presence (i.e., 0 DSG) and declined thereafter. While deer and cattle have different foraging strategies (Ortega et al. 1997), limited forage availability forces an increase in dietary overlap during the dormant season. However, during the growing season, forage availability increases due to higher rates of regeneration and the

occurrence of seasonal plants (Hewitt 2011). Dietary overlap between deer and cattle can shift from 12% in the summer months to 46% in the winter months on pine-hardwood sites (Thill 1984). Therefore, cattle grazing should have little impact on deer forage availability during the growing season in non-drought years (Thill and Martin 1989). Since the growing seasons of 2018 and 2019 did not experience any unusual natural events (i.e., drought, hurricanes), the lack of significance of the DSG covariate during the growing season was likely related with an increase in forage availability leading to reduced interspecific competition.

During much of this study, bucks demonstrated selection for pastures that had intermediate DSG values (i.e., 140–220 days). This pattern aligns with the forage maturation hypothesis (Fryxell 1991). When the disturbance of a grazing event occurs within a pasture, forage abundance is decreased. When cattle are rotated out of a pasture, vegetative recovery occurs. While new growth is often the highest quality forage (Hewitt 2011), vegetative quantity may limit animal use until sufficient forage or cover is available (Fryxell 1991). Later, when forages mature, digestibility and digestive passage rates decline (Spalinger and Hobbs 1992, Gross et al. 1993). Increased use of pastures 5-6 months following heavy grazing during the growing season was similar to selection following grazing during the dormant season and reflects time required for vegetative recovery. However, light to moderate grazing during the growing season did not seem to impact deer selection. This pattern could be attributed to bucks balancing forage quality and quantity across pastures because limited forage was left behind after heavily stocked grazing events, while plentiful forage remained following light to moderately stocked

grazing events. Further research incorporating vegetation sampling within pastures should be conducted to assess differences in forage availability.

Deer in this study avoided areas recently applied with herbicides during the growing season. Of pastures that received herbicide, most were treated during the spring months with triclopyr, a broadleaf herbicide (Strid et al. 2018). However, pastures in our study area lacked a woody overstory component, creating a primarily herbaceous plant community. Pastures that receive herbicide often contain the poorest quality forage. These pastures are often dominated by undesirable plants like dogfennel and wax myrtle resulting in decreased broadleaf plants beneficial to deer like greenbriar (*Smilax* spp.) or blackberry (*Rubus* spp.) (Ferrell et al. 2009, Czarnota 2014).

While the application of fertilizer often increases forage yield and total digestible nutrients (TDN) of pasture grasses (Sumner et al. 1991), there was no relationship between buck habitat selection and DSF. The majority of fertilizer was applied in the dormant season during the study (71%). Therefore, the tendency of bucks to select areas closer to pastures and the insignificance of our DSF covariate leads us to believe that fertilizer application has little effect on deer habitat selection. We only acquired the year of application of biosolids for pastures because application dates were not recorded. Therefore, the application of biosolids deserves further evaluation with finer temporal resolution to better evaluate this relationship.

Bucks selected areas closer to non-forested wetlands during both seasons. Scattered wet prairies and marshes throughout pastures within the study area provide taller and denser vegetation than the surrounding improved pasture. Interspersed patches of dense vegetation likely provide deer with cover throughout the open landscape

allowing deer to utilize pastures more effectively. Additionally, in central Florida, the rut peaks during the first week of October (Richter and Labisky 1985) and slowly declines throughout the hunting season causing bucks to change their daily habits to reflect reproductive behavior (DeYoung and Miller 2011). Therefore, we acknowledge the patterns documented in this study were potentially influenced by differing patterns in female deer resource selection (Stewart et al. 2011). Future research should simultaneously monitor male and female deer movements relative to livestock management practices to determine if habitat selection changes temporally in association with reproductive behavior.

MANAGEMENT IMPLICATIONS

Livestock and wildlife managers should consider the effect that livestock management practices have on white-tailed deer habitat selection. When pastures were grazed during the dormant season, deer increased their use of pastures approximately 140–220 days after grazing occurred. Alternatively, deer demonstrated increased use of pastures that were recently grazed at light stocking rates during the growing season. This information can be used to actively manage livestock in a way that maximizes resources available to deer. We recommend the continuation of rotational grazing of cattle to provide deer with a multitude of pastures at different stages of herbaceous regeneration allowing deer to balance the tradeoff between forage quality and quantity. When establishing pastures, we recommend maintaining an interspersed of plant communities that can provide cover (i.e., non-forested wetlands) to increase pasture utilization by deer.

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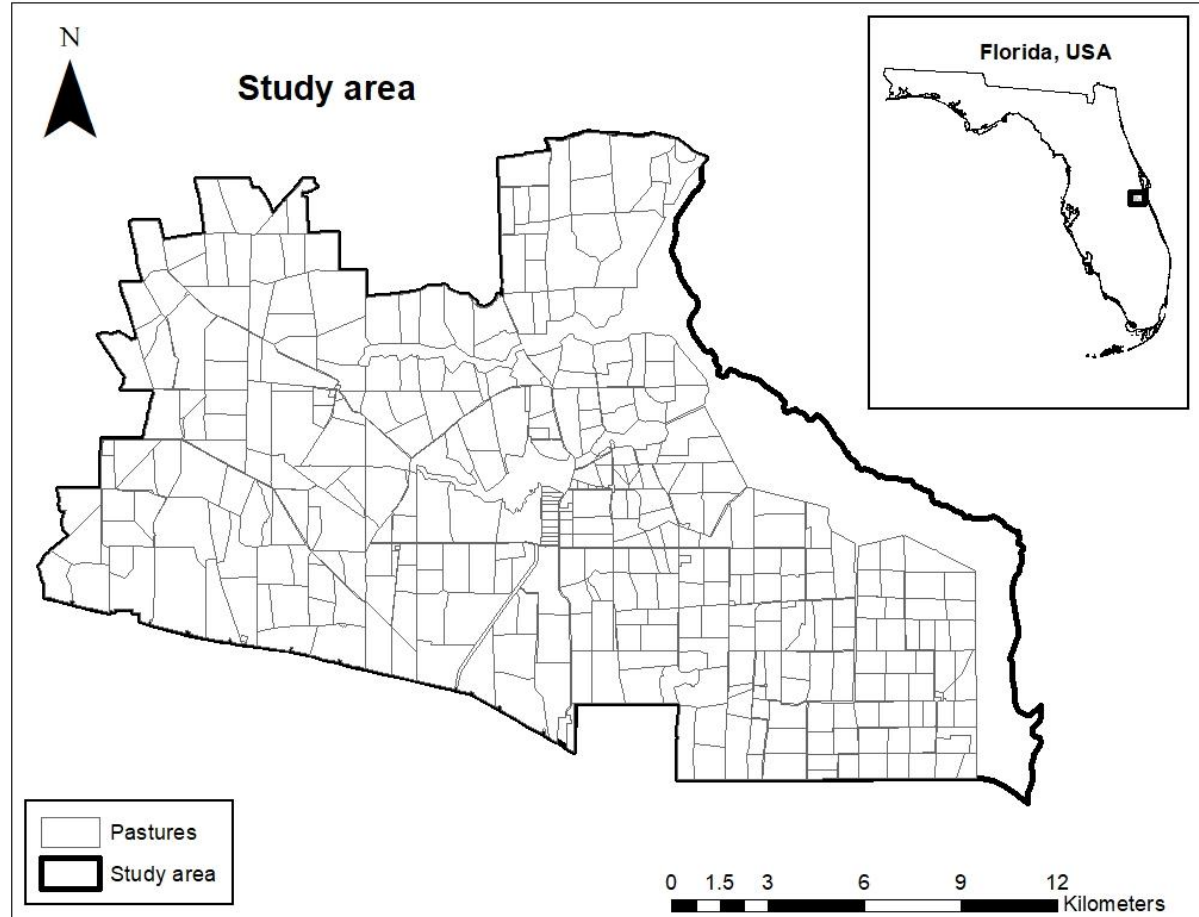


Figure 4.1. Study area with pasture boundaries used to develop mixed conditional logistic regression model for male white-tailed deer resource selection relative to livestock management practices between 2018–2020 in central Florida, USA.

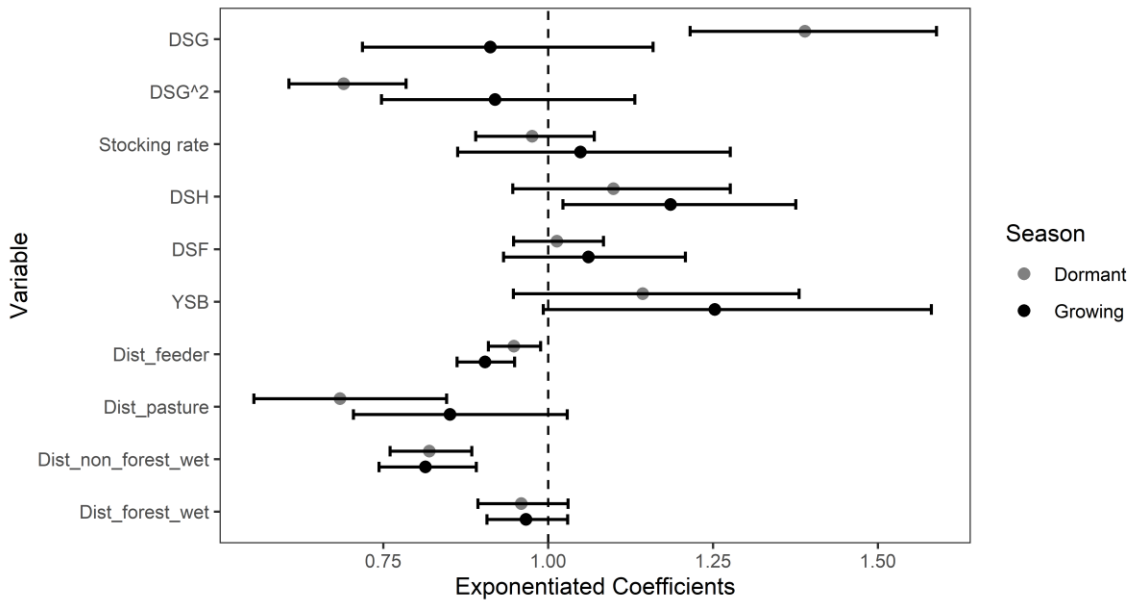


Figure 4.2. Predictive odds ratios of 3rd order resource selection of male white-tailed deer with 95% confidence intervals for 10 continuous variables obtained from two step-selection functions for the dormant (1 Oct–31 Mar) and growing (1 Apr–30 Sept) seasons between 2018–2020 in central Florida, USA. Odds ratios demonstrate selection or avoidance of pastures subject to grazing, herbicide, or fertilizer application for every 100 days since treatment, cattle stocking rate for every 1 cattle/ha increase, pastures subject to biosolid application for every 1 year since treatment, and distance to vegetation types and feeders for every 100 m increase. Covariates included days since grazing with a quadratic variable (DSG, DSG²), cattle stocking rate (Stocking rate[cattle/ha]), days since herbicide (DSH), days since fertilizer (DSF), years since biosolid (YSB), and distance to feeder (Dist_feeder), pasture (Dist_pasture), non-forested wetlands (Dist_non_forest_wet), and forested wetlands (Dist_forest_wet[m]).

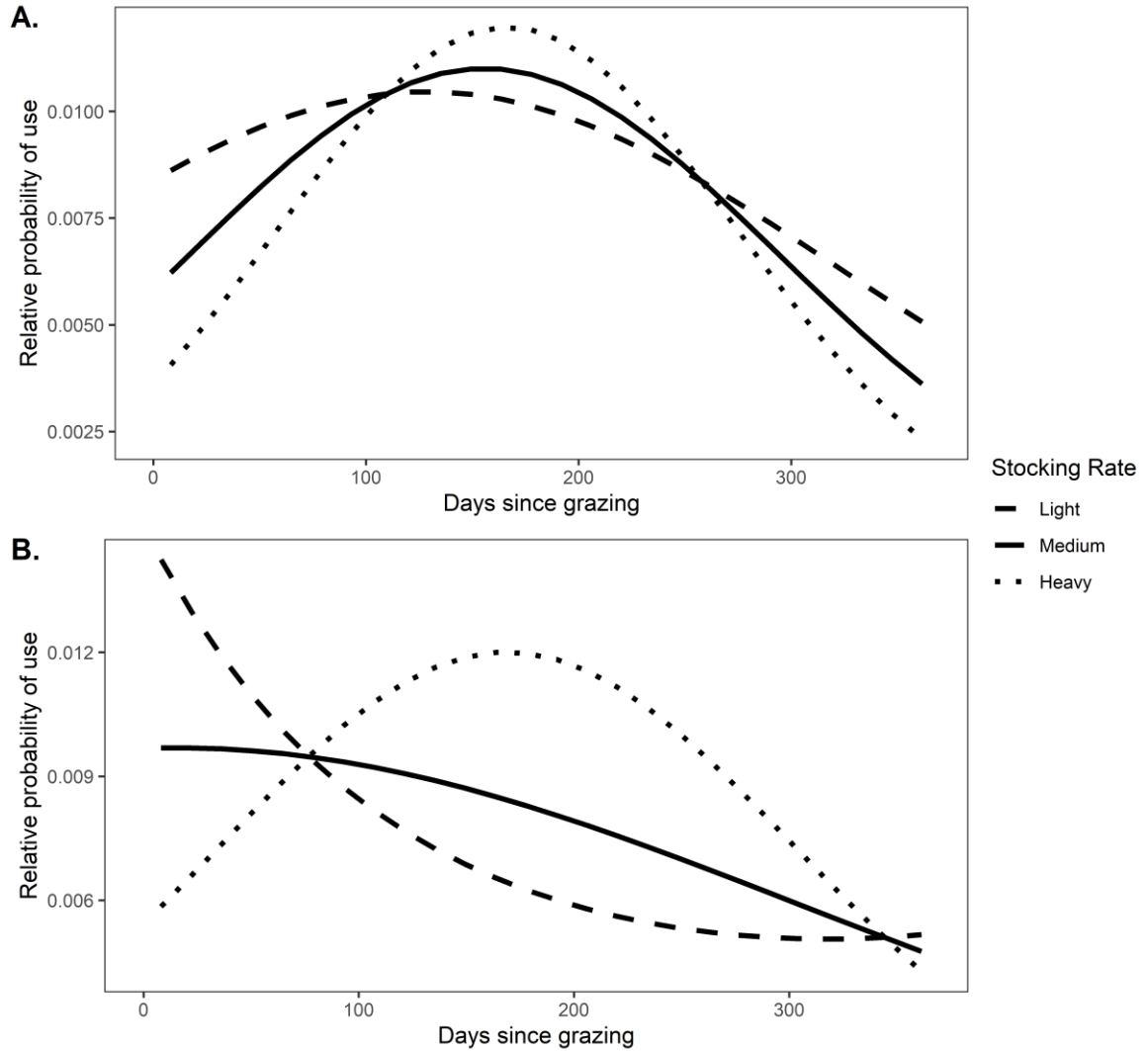


Figure 4.3. Predicted relative probability of use of male white-tailed deer relative to days since cattle grazing during the (A) dormant (1 Oct–31 Mar) and (B) growing seasons (1 Apr–30 Sept) derived from a mixed conditional logistic regression model in central Florida, USA, from 2018–2020. Each line represents different stocking rates of the preceding grazing event. Light (0.99 cattle/ha), medium (1.8 cattle/ha), and heavy (3.7 cattle/ha) stocking rates are represented.

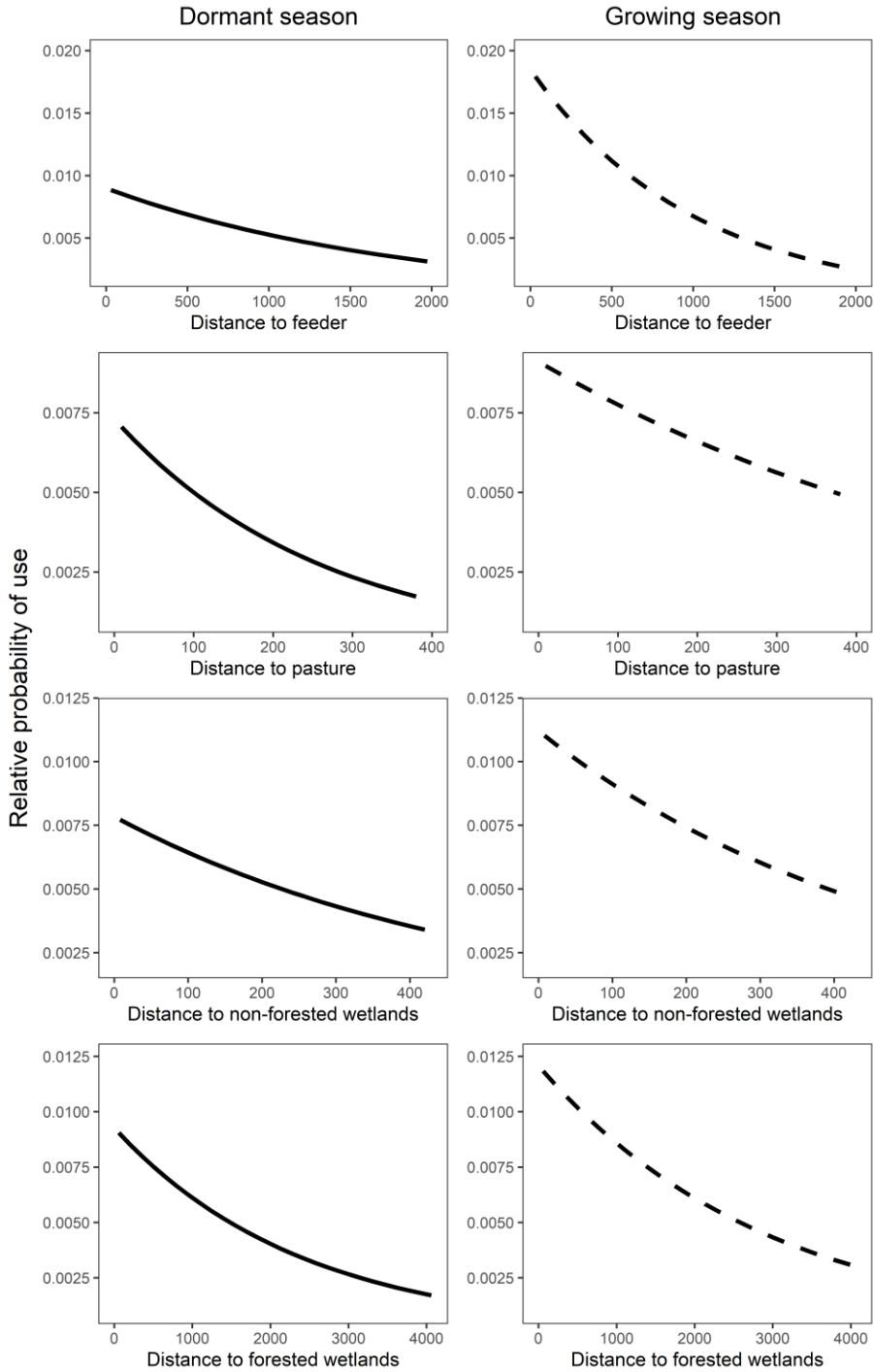


Figure 4.4. Predicted relative probability of use of male white-tailed deer relative to habitat covariates during the dormant (1 Oct–31 Mar) and growing seasons (1 Apr–30 Sept) derived from a mixed conditional logistic regression model in central Florida, USA, from 2018–2020. Covariates included distance to feeder location (feeder), pasture, non-forested wetlands, and forested wetlands (m).

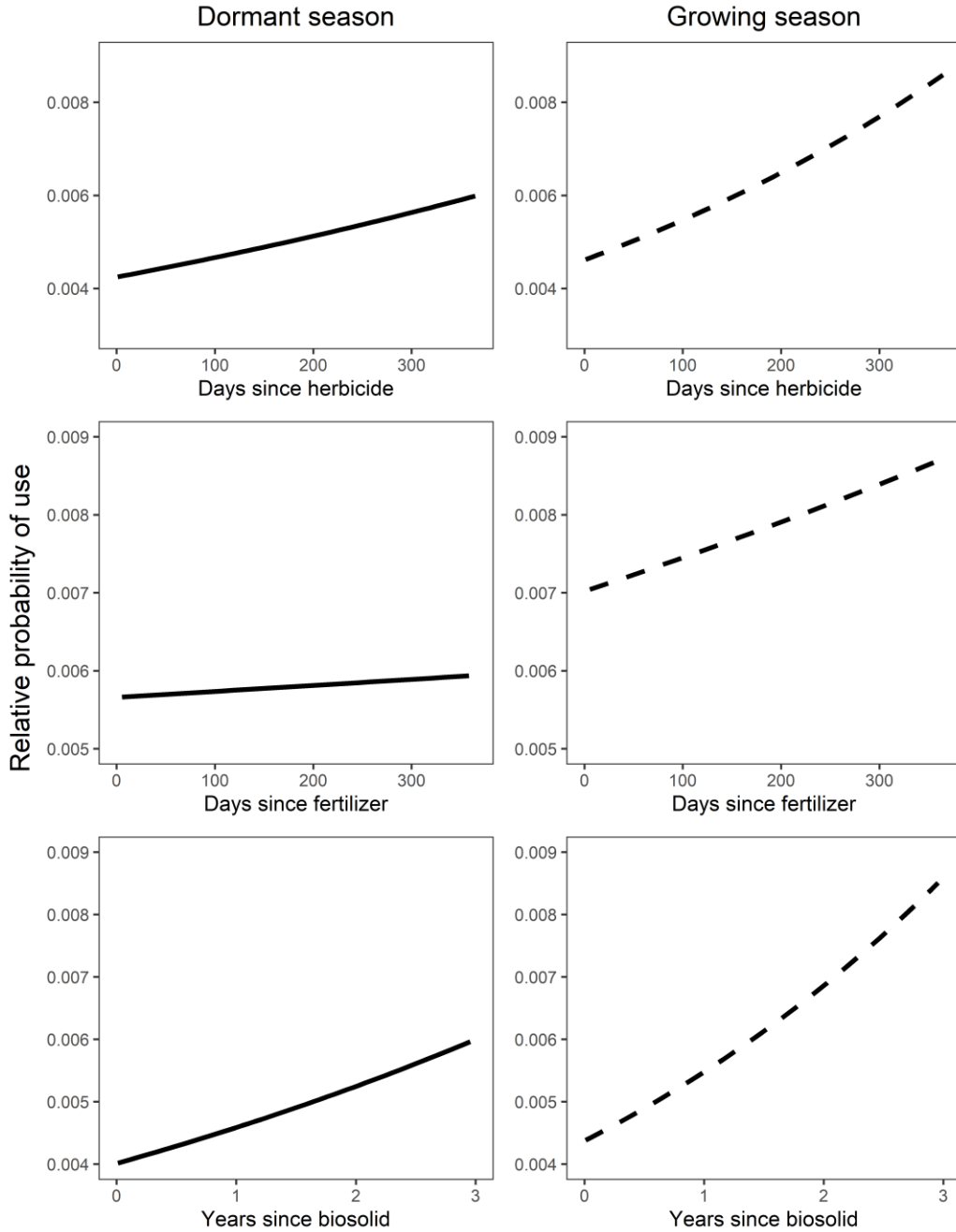


Figure 4.5. Predicted relative probability of use of male white-tailed deer relative to livestock management practices during the dormant (1 Oct–31 Mar) and growing seasons (1 Apr–30 Sept) derived from a mixed conditional logistic regression model in central Florida, USA, from 2018–2020. Covariates included days since herbicide, days since fertilizer, and years since biosolids.

Table 4.1. Parameter estimates of 3rd order step-selection models for male white-tailed deer in central Florida, USA from 2018–2020, during the dormant (1 Oct–31 Mar) season. Shown are regression coefficients (β), standard error (SE), 95% confidence intervals (CI), and *P*-values.

Model variables ^a	β	SE	95% CI	<i>P</i>
Intercept	-5.317	11.420	-27.699, 17.066	0.642
Step length	0.000	0.000	0.000, 0.000	<0.001
log(step length)	0.094	0.020	0.054, 0.133	<0.001
DSG	0.465	0.097	0.275, 0.654	<0.001
DSG ²	-0.525	0.093	-0.706, -0.343	<0.001
Stocking rate	-0.090	0.171	-0.425, 0.245	0.600
DSG:Stocking rate	0.847	0.255	0.348, 1.346	<0.001
DSG ² :Stocking rate	-0.661	0.181	-1.015, -0.307	<0.001
DSH	0.062	0.050	-0.036, 0.161	0.216
DSF	0.017	0.043	-0.068, 0.102	0.700
YSB	0.073	0.052	-0.030, 0.176	0.163
Feeder	-0.314	0.126	-0.561, -0.068	0.012
Pasture	-0.612	0.174	-0.953, -0.270	<0.001
Non-forest	-0.273	0.053	-0.377, -0.169	<0.001
Forest	-0.616	0.538	-1,670, 0.437	0.252

^a Covariates include step length, days since grazing with a quadratic variable (DSG, DSG²), cattle stocking rate (Stocking rate), the interaction between grazing and cattle stocking rate (DSG:Stocking rate, DSG²:Stocking rate) days since herbicide (DSH), days since fertilizer (DSF); years since biosolid (Biosolid); stocking rate (stock rate) (cattle/ha); and distance to feeder (Feeder), pasture (Pasture), non-forested wetlands (Non-forest), and forested wetlands (Forest) (m).

Table 4.2. Parameter estimates of 3rd order step-selection models for male white-tailed deer in central Florida, USA from 2018–2020, during the growing (1 Apr–30 Sept) season. Shown are regression coefficients (β), standard error (SE), 95% confidence intervals (CI), and *P*-values.

Model variables ^a	β	SE	95% CI	<i>P</i>
Intercept	-0.5502	17.740	-40.275, 29.270	0.756
Step length	0.000	0.000	-0.000, 0.000	0.164
log(step length)	0.145	0.031	0.084, 0.206	<0.001
DSG	-0.130	0.173	-0.468, 0.209	0.453
DSG ²	-0.119	0.150	-0.412, 0.174	0.427
Stocking rate	0.175	0.364	-0.539, 0.888	0.631
DSG:Stocking rate	1.426	0.352	0.736, 2.112	<0.001
DSG ² :Stocking rate	-0.857	0.309	-1.463, -0.252	0.006
DSH	0.113	0.050	0.015, 0.211	0.025
DSF	0.075	0.083	-0.089, 0.238	0.370
YSB	0.123	0.065	-0.004, 0.250	0.058
Feeder	-0.592	0.145	-0.877, -0.308	<0.001
Pasture	-0.260	0.156	-0.565, 0.046	0.096
Non-forest	-0.283	0.063	-0.407, -0.159	<0.001
Forest	-0.507	0.478	-1.443, 0.431	0.290

^a Covariates include step length, days since grazing with a quadratic variable (DSG, DSG²), cattle stocking rate (Stocking rate), the interaction between grazing and cattle stocking rate (DSG:Stocking rate, DSG²:Stocking rate) days since herbicide (DSH), days since fertilizer (DSF); years since biosolid (Biosolid); stocking rate (stock rate) (cattle/ha); and distance to feeder (Feeder), pasture (Pasture), non-forested wetlands (Non-forest), and forested wetlands (Forest) (m).

CHAPTER 5

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

CONCLUSIONS

The results from this research suggest the following conclusions:

*Chapter 2 – Estimating Sightability for Helicopter Surveys Using Surrogates of White-tailed Deer (*Odocoileus virginianus*)*

1. Vegetative obstruction and distance from the transect negatively influenced detection probability of white-tailed deer, however, light was considered an insignificant predictor variable.
2. The use of surrogates of white-tailed deer provided many advantages when developing the sightability model including known locations, accurate covariate records, a known population to assess accuracy and precision of population estimates, and reduced cost and labor.
3. When used to predict population estimates of the known surrogate population, the top sightability model produced an estimate that consisted of 92% of the known population.
4. Accuracy of population estimates of operational management units is improved by accounting for imperfect detection using sightability models.

Chapter 3 – White-tailed Deer (Odocoileus virginianus) Movement and Activity in Response to Helicopter Surveys

1. Modeling efforts demonstrated no differences in activity rates or step-lengths of male white-tailed deer between before and during or before and after monitoring periods.
2. Deer selected for areas closer to vegetative cover before flights occurred in all monitoring periods and selected areas farther from cover during the 72-hr temporal window after flights occurred.
3. Evasion from helicopter disturbance is short-term with buck settling back into normal movement patterns soon thereafter and overall effect on daily movement patterns is minimal.

Chapter 4 – Resource Selection of White-tailed Deer (Odocoileus virginianus) Relative to Cattle Management

1. Days since grazing significantly influenced resource selection of bucks during the dormant season with bucks selecting pastures with intermediate values of days since grazing (i.e., 140–220 days).
2. In both seasons, resource selection of bucks relative to days since grazing was dependent on the preceding stocking rate of a pasture.
3. Bucks selected areas closer to non-forested wetlands in both seasons.
4. Bucks selected areas closer to feeders in both seasons.
5. Days since fertilizer and biosolids were considered uninformative predictors in both seasons and bucks selected pastures with higher values of days since fertilizer during the growing season.

MANAGEMENT IMPLICATIONS

1. Using surrogates of white-tailed deer to develop sightability models for helicopter surveys provides advantages over using collared animals including known locations, reduced cost and labor, a known population for model validation, and accurate records of covariates.
2. Helicopter surveys used to obtain population estimates of white-tailed deer do not displace or significantly affect movement patterns.
3. When establishing pastures, maintaining an interspersion of plant communities that can provide cover (i.e., non-forested wetlands) can increase pasture utilization by deer.
4. Understanding selection patterns of bucks relative to livestock management practices can be used to inform hunters of deer movements and ultimately increase hunter success and satisfaction.