WHITE-TAILED DEER CAMERA SURVEYS: DENSITY ESTIMATION AND SPATIO-TEMPORAL DYNAMICS

by

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(Under the Direction of KARL V. MILLER and RICHARD B. CHANDLER)

ABSTRACT

Reliable population estimates are needed to make informed wildlife management decisions. Baited camera surveys are a popular method for estimating densities of white-tailed deer (*Odocoileus virginianus*), however the commonly used baited survey invokes ecological, economic, analytical, and logistical concerns. I evaluated an unmarked spatial capture-recapture (SCR) model that does not require baiting to estimate deer densities and incorporates telemetry data from captured deer to estimate encounter rate parameters. I conducted camera surveys in 2014-2016 at four (~1000 ha) study sites in southwestern Georgia, USA and compared density estimates from the unmarked SCR model to estimates from the common baited camera survey protocol, distance sampling surveys, and SCR models applied to data on marked male deer. Estimates were similar between the unmarked SCR model, distance sampling, and the marked SCR model, however the baited camera survey consistently produced greater density estimates than all other surveys. The unmarked SCR model was less precise than SCR analyses with marked males. The unmarked SCR model could be a viable alternative for estimating deer densities without the need to use bait or identify individual deer. I used a SCR estimation framework to determine the effect of bait on male white-tailed deer resource selection and space use, before and after the 2015-2016 hunting season. I found little evidence bait affected the spatial distribution of home ranges and strong evidence that bait affected space use within home ranges. Shifts in core area use during times of baiting could enhance disease transmission and alter harvest susceptibility of deer. I compared spatial distributions of deer detections from September baited camera surveys to autumn passive camera surveys in 2014 to assess the baited camera survey's ability to guide management decisions. Spatial distributions were affected by sexual segregation during September surveys, and shifts in observed spatial distributions resulted in highly overlapped distributions of males and females during the autumn surveys. My results demonstrate that an unmarked SCR estimation protocol is a promising technique for estimating deer densities, the use of bait can alter core area use of deer, and the spatial distribution of deer can change drastically after pre-hunting season surveys.

INDEX WORDS: abundance estimation, camera traps, deer density, deer management, Georgia, *Odocoileus virginianus*, passive camera, resource selection, space-use, spatial capture-recapture

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DEDICATION

Dedicated to the memory of my aunt, Shirley Ruth Johnson. My passion for wildlife stems from my childhood adventures with her on horseback, and may her wisdom live on in all who followed her down the trail.

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CHAPTER 1

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

INTRODUCTION

White-tailed deer (*Odocoileus virginianus*) are an important ecological, recreational, and economic resource generating more than $800 million each year in hunting fees, sales of sporting goods, food, and land leases in Georgia (DNR-WRD 2004) and are considered North America's most popular game species (U.S. Fish and Wildlife Service 2011). Obtaining unbiased and precise estimates of white-tailed deer population parameters (e.g., recruitment, abundance, and age structure) are important components of responsible deer-management plans (Halls 1984, Moore 1995, Jacobson et al. 1997, Roberts et al. 2006, Curtis et al. 2009, Amos et al., 2014), and a wide variety of techniques have been developed to achieve this goal (Halls 1984, Jacobson et al. 1997, Buckland et al. 2001, Amos et al. 2014, Fryxell et al. 2014). These methods include, but are not limited to, browse surveys, pellet counts, harvest data reconstruction, spotlight surveys, track counts, helicopter counts, distance sampling, and camera surveys (Eberhardt and Van Etten 1956, Jenkins and Marchinton 1969, Halls 1984, Fuller 1991, Roseberry and Woolf 1991, Jacobson et al. 1997, Koerth et al. 1997, Tremblay et al. 2005, Kissell and Nimmo 2011, Collier et al. 2012). More work has been applied to the evaluation of population estimation methods for white-tailed deer than any other species (Collier et al. 2012), and yet the struggle to estimate reliable deer densities persists.

The current need for a method that produces precise estimates of population parameters in an economically and logistically reasonable manner is clear. In Georgia, deer populations in some urban and suburban areas are high, approaching or exceeding both social and ecological carrying capacity. Stakeholders of many rural properties are becoming increasingly interested in more intensive deer management practices such as quality deer management (i.e., the act of managing for desirable traits and healthy population structures) (DNR-WRD, 2004). In addition, past and ongoing studies in Georgia have identified coyotes (*Canis latrans*) as important fawn predators in some areas, leading to herds that may be sensitive to overharvest as a function of low recruitment (Howze et al. 2009, Gulsby et al. 2015, Nelson et al. 2015, Cherry et al. 2016, Conner et al. 2016). Obtaining adequate data to produce reliable estimates for guiding management decisions often involves logistically challenging and expensive sampling regimes, which is one reason why reliable parameter estimates are unavailable for many populations (Collier et al. 2007, 2012; Fryxell 2014).

Camera traps have increased in popularity as a non-invasive survey tool for obtaining data on wildlife populations (Caravaggi et al. 2017). The Jacobson baited camera survey (Jacobson et al. 1997) is widely employed by land managers and landowners for surveying white-tailed deer populations. However, this method is surrounded by a myriad of potential issues associated with the use of bait and biases associated with the estimates produced. In addition, this method has gone relatively unchanged for over 20 years. Relatively recent advancements in capture-recapture analytical techniques offer a unique opportunity to evaluate a novel method using camera traps to estimate deer abundance, and data obtained from baited and unbaited camera trap arrays provide an opportunity to address specific issues associated with the baited camera survey.

BACKGROUND

Common methods for estimating deer density

The two most common techniques for surveying populations of deer are distance sampling and the Jacobson baited camera survey (Jacobson et al. 1997, Buckland et al. 2001). Distance sampling is a relatively convenient and inexpensive method when attempting to survey deer populations (Mitchel 1986, Collier et al. 2007, Collier et al. 2012), and accounts for imperfect detection. Distance sampling is normally conducted at night by driving or walking transects, using a light to detect eye shine from deer, or deer cohorts, and counting individual occurrences (Mitchell 1986). Variants include using rangefinders and angular measurements (azimuths) to determine the distance from the observer to create density estimates within an area of interest based on calculated detection functions (Larue et al. 2007). Aerial surveys may also be utilized to conduct distance sampling surveys in open areas where closed canopies are not present (Potvin and Breton 2005)

Evaluations of distance sampling have focused primarily on biases associated with estimates and the violation of key assumptions (Koenen et al. 2002, Larue et al. 2007, Collier et al. 2012, Beaver et al. 2014). Distance sampling requires minimal disturbance of the animals and assumes that deer movement is minimized during sampling, which is rarely achieved because most distance sampling protocols involve surveying deer from vehicles (Collier et al. 2007, 2012). Road-based distance sampling protocols violate another key assumption of distance sampling: that individuals must be uniformly distributed with respect to the transect. The only way to guarantee that this assumption is met is by using random sampling designs (Collier et al. 2007, 2012). Detection probability and abundance estimates are often highly variable among sampling occasions, making it difficult to detect temporal trends (Collier et al. 2007, 2012). Independent detections of deer may also be difficult if deer move during the survey and transects must be spaced properly to avoid multiple detections of the same individual. In addition, distance sampling relies on accurate measurements of distance which can be troublesome at night when vegetation is present. These issues coupled with the inherent subjective observer-based variability of counting deer, create several concerns when considering distance sampling surveys for deer (Collier et al, 2007, 2012).

The most common technique used to estimate white-tailed deer abundance and density is likely the Jacobson et al. (1997) baited camera survey. This method employs remote, motion-triggered cameras (1 camera / 40-60 ha) placed over bait piles for 10-14 days, usually before or after the hunting season. Individual males are identified based on unique antler configurations, and it is assumed that all male deer in the study area are detected. The ratio of unique males identified to the number of total male images is used as a correction factor to estimate the number of does and fawns by multiplying the correction factor by the number of doe or fawn images, ultimately producing abundance indices and sex ratios. While the protocol is relatively easy to follow, the process of identifying individual males can be difficult and time consuming, the use of bait is illegal in some places and may be used only outside of hunting seasons in others, and consumption of bait by non-target species, such as feral swine (*Sus scrofa*) or bears

(*Ursus* spp), could impact survey results. These factors create several logistical concerns for those wishing to use the method.

Baited camera survey concerns

Several studies have raised concerns regarding the validity of results produced by the baited camera method (Rowcliffe et al. 2008, 2011; McCoy et al. 2011; 2013; Weckel et al. 2011; Beaver 2017). Perhaps the most important of these is the violation of the assumption of equal detectability between sexes and among age classes of deer (McCoy et al. 2011, Rowcliffe et al. 2011, Beaver 2017). Greater rates of male detections result in negatively biased estimates (Jacobson et al. 1997, Moore 2014), behavioral interactions at high deer densities could lower sightability of subordinate members (Donohue et al. 2013), and greater probability of photographing females results in positively biased estimates (Jacobson et al. 1997, Weckel 2011). Chitwood et al. (2014) also determined the Jacobson method lacks reliability when estimating recruitment parameters due to the low rates of detecting fawns at bait sites during summer months. Differences in detection rates also lead to biased estimates of sex ratios and fawn:doe ratios.

The use of bait may shift deer home ranges and activity patterns (Ozoga and Verme 1982, Schmitz 1990, Kilpatrick and Stober 2002 Brown and Cooper 2006, Cooper et al. 2006, Timmons et al. 2010), which can also be influenced by social status among deer cohorts (Stone, 2017), altering visitation rates leading to the biases described above. These shifts could ultimately influence the rate and quantity of photographic captures associated with baited camera surveys (Curtis et al. 2009, Weckel et al. 2011). Another concern with the Jacobson method is that the area surveyed is assumed to be known, even though home range size can strongly affect the effective area surveyed by camera traps (O'Connell et al. 2011, Royle et al. 2014). Density estimates produced by the Jacobson method, and other methods that assume the area surveyed is known, are highly sensitive to changes in the assumed sample area (Noss et al. 2012, Beaver et al. 2016). Lastly, the use of bait itself could enhance disease transmission (Eve 1981, Thorne and Herriges 1992, Schmitt et al. 1997, Brown and Cooper 2006, Sorensen et al. 2014) and potentially change hunter harvest success and satisfaction (Synatzke 1981, Langenau et al. 1985, Wisconsin BWM 1993, Michigan DNR 1999, Frawley 2000).

Apart from issues related to the use of bait, the baited camera survey method requires that all antlered males be uniquely identified, which is subject to observer error and is time-consuming. In addition, the Jacobson protocol does not provide error terms for parameter estimates, which is a cause of concern for biologists, landowners, and resource managers (White et al. 1982, Weckel et al. 2011). Without a measure of accuracy or precision, comparing deer populations across time and space has limited value. Modifications to the Jacobson method have been attempted to produce abundance confidence intervals via bootstrapping camera trap data. However, resulting confidence intervals are relatively large and the bias of higher trap success for females remains (Weckel et al. 2011).

Baiting and supplemental feeding defined

Baiting is defined as the act of providing a concentrated food source for a limited time at a specific location with the goal of attracting wildlife for harvest opportunities (Kilpatrick et al. 2010), increase viewing opportunities (Corcoran et al. 2013), and aid in achieving research objectives, such as capturing deer (Kilpatrick and Stober 2002). Supplemental feeding is the practice of providing a food resource for wildlife, typically for an extended period, with the goal of increasing the nutritional carrying capacity of the habitat to enhance survival, body condition, fecundity, and/or antler size (Ozoga and Verme 1982, Zaiglin and DeYoung 1989, Bartoskewitz et al. 2003, Page and Underwood 2006). Many indirect ecological impacts are associated with both practices, however a primary distinction is the length of time food resources are supplied.

Effects of baiting on disease transmission

Bait sites may artificially congregate deer, increasing the chance of transmission of diseases such as chronic wasting disease (CWD) and bovine tuberculosis (TB) through deer-deer contact (Eve 1981, Thorne and Herriges 1992, Schmitt et al. 1997, Garner 2001) as well as indirect contact from contaminated bait sites (Palmer et al. 2001, Schmitt et al. 2002). Direct contact between deer is not uncommon in natural settings where bait sites are not present, however these behaviors are typically associated with small social groups (Hawkins and Klimstra 1970, Marchinton and Hirth 1984), and increased concentrations of deer could increase direct and indirect contact of deer at higher rates than would normally occur (Eve 1981, Thorne and Herriges 1992, Schmitt et al. 1997, Garner 2001).

Bovine TB may remain active at bait sites, such as corn piles, for at least 28 days (Whipple and Palmer 2000). Chronic Wasting Disease (CWD) is a fatal transmissible spongiform encephalopathy currently spreading in white-tailed deer populations in the US and prions can remain active in the soil of bait sites for a minimum of 16 years (Georgsson et al. 2006), and are considerably more infectious when bound to soil particles (Johnson et al. 2007). Considering most bait sites consist of shelled corn placed directly on the soil's surface, this information alone should warrant careful consideration when deciding to allow baiting of white-tailed deer.

A comprehensive review of CWD and the science supporting a ban on baiting was compiled by Van Deelen (2003) for the Wisconsin Department of Natural Resources. Findings suggest a baiting and supplemental feeding ban would likely reduce disease outbreaks to smaller scales which could be managed or contained. Given the long incubation time and difficulty of detecting the disease, baiting likely increases the probability of a widespread outbreak, and increases the difficulty of controlling the spread of diseases like CWD.

Baiting is legal to some extent in 26 of the 48 contiguous states (Adams and Ross 2017). However, Best Management Practices for management of chronic wasting disease include elimination of "baiting and feeding of all wild cervids using regulatory mechanisms such as jurisdictional bans" (Gillin and Mawdsley 2018). Continued spread of CWD will likely lead to additional restrictions of the use of bait for hunting and surveying white-tailed deer.

Effects of baiting on deer activity patterns and movement

Activity patterns and home ranges of white-tailed deer are influenced by many factors (habitat quality, population density, landscape, etc.) and are highly variable among individuals (Nicholson et al. 1997, McLoughin et al. 2000, Relyea et al. 2000, Said and Servanty 2005, Walter et al. 2009, DeYoung and Miller 2011, Quinn et al. 2013). Typically, highly productive habitats result in smaller home ranges when compared to poorer quality habitats (Marchinton and Hirth 1984, Sargent 1992, Storm et al. 2007, Hellickson et al. 2008, Efford et al. 2015). While little evidence exists on whether baiting changes the location of a deer's home range (Kilpatrick and Stober 2002), activity patterns are almost certainly affected. Several studies suggest a shift in deer core areas and space use within a home range once bait sites are established (Darrow 1993, Williams and DeNicola 2000, Kilpatrick and Stober 2002, Campbell et al. 2006, Milner et al. 2014, Beaver 2017). Garner (2001) used VHF telemetry to monitor deer movement patterns and found that bait reduced average home range size, increased overlap of home ranges in space and time, and increased concentrations of deer around feeding sites.

Many of the negative effects of baiting result from altered movement patterns of deer (Synatzke 1981, Jacobson and Darrow 1992, Kilpatrick and Stober 2002, Garner 2001, Milner et al. 2014). Bait can affect space use within a home range by altering resource acquisition behaviors. Optimal foraging theory suggests that individuals should select resources to maximize energy intake and minimize energy expenditure (MacArthur and Pianka 1966, Schoener 1971, Brown et al. 1999). Bait allows individuals to maximize net energy gain by reducing the amount of time needed to search for native forages (Murden and Risenhoover 1993). Baiting has the potential to alter distributions of deer on the landscape (Milner et al. 2014), by means of altered core area use (Kilpatrik and Stober 2002, Campbell et al. 2006), however the resulting changes in home range use and distributions have also been reported to be unaltered by the presence of bait (Webb et al. 2010).

Baiting effects on hunter harvest success and satisfaction

Changes in space use by deer may lead to higher encounter rates near bait sites increasing harvest susceptibility. However, studies pertaining to harvest success associated with baiting have been equivocal. Following a ban on baiting in Wisconsin, declines in female deer harvest were minimal (Van Deelen et al. 2006). The Pennsylvania Game Commission reported no increase in harvest when temporary legalization of baiting was implemented (Fleegle and Rosenberry 2010). However, increased harvest has been reported in some instances of legalization (Frawley 2002, Kilpatrick et al. 2010). Several studies have also demonstrated baiting increases nocturnal activity of deer when visiting feeding sites (Synatzke 1981, Jacobson and Darrow 1992, Stone 2017), and the use of bait sites by male deer decreases dramatically during the breeding season (Stone 2017). However, the use of bait has been shown to increase female harvest in several instances (Ruth and Shipes 2005, Kilpatrick et al. 2010), and post-breeding season use of bait could lead to greater harvest rates of both sexes. In addition, hunter success and satisfaction for those using bait is generally very similar or even lower to those not hunting over bait (Langenau et al. 1985, Wisconsin BWM 1993, Michigan DNR 1999, Frawley 2000).

Timing of baited camera surveys

Another concern of the baited camera survey that has received little attention is the timing in which the survey is conducted and how well it represents the population available for harvest during the hunting season. During spring and summer, white-tailed deer populations typically are sexually segregated (Bowyer 2004). Sexual segregation is defined as the differential use of space and resources by males and females (Bowyer 1984, 2004; McCullough et al. 1989). Several hypotheses have been introduced to explain segregation such as differences in nutritional/foraging requirements, predation risk, social factors (Bowyer 1984, 2004; Kie and Bowyer 1999; McCullough et al. 1989). This period of sexual segregation includes the time frame when a typical baited survey would be conducted, creating a "snapshot in time" estimate of the segregated population prior to the hunting season. This snapshot, however, may lead managers to set harvest goals that may no longer be applicable once the hunting season commences after segregated populations dissolve.

Shortly after the baited surveys are concluded (typically late summer in the Southeast) and the hunting season begins (early fall into winter), many environmental and social changes occur which influence the distribution (and likely, local abundance) of males and females on the landscape. Home range size and location often shift as food resources change (Beier and McCullough 1990, McShea and Schwede 1993, Miller and Marchinton 1999, Walter et al. 2009, Olson 2014). Rut-related activities also can alter deer movement patterns as well as activity centers (Tierson et al. 1985, Beier and McCullogh 1990, Tomberlin 2007, Foley 2012). Additionally, fall dispersal of yearling males often coincides with rut-related behavior (Rosenberry et al. 2001), and many studies suggest ≥50% of yearlings disperse (Kammermeyer and Marchinton 1976, Nelson and Mech 1981, Nixon et al. 1991, Holzenbein and Marchinton 1992, Rosenberry et al. 1999). Thus, although late summer baited camera surveys may provide reasonable estimates of herd demographics at the time they are conducted, changes in deer distribution during the autumn hunting season may result in inappropriate deer harvest recommendations.

Spatial capture-recapture

Camera traps have become increasingly popular as the cost to purchase, operate, and maintain the devices has declined (Cutler and Swann 1999, O'Connell et al. 2011, Dougherty and Bowman 2012). However, many monitoring protocols continue to use judgment and convenient sampling to create population indices which are often biased

(O'Connel 2011, Weckel 2011). In addition to the continued use of relative abundance indices, traditional capture-recapture (CR) analysis has seen major improvements in the last 10 years.

A primary drawback of traditional CR estimation methods is that they discard the spatial component of the associated capture history data. Specifically, traditional CR models discard information about the location where each individual was detected. Consequently, the effective area sampled is unknown and likely varies through space and time, and it impossible to model spatial variation in density and capture probability (Efford 2004). Spatial capture-recapture models (SCR) (Efford 2004, Borchers and Efford 2008, Royle and Young 2008, Royle et al. 2014) make it possible to estimate density and abundance in specific spatial regions by adopting a spatial point process model for activity centers and modeling detection probability as a function of the distance between a trap location and an animal's activity center. Spatial capture-recapture models estimate the activity center based on the spatial coordinates of traps where each individual was detected.

Few studies have applied SCR estimation methods to camera trap data for white-tailed deer, partly because females are not individually identifiable, a requirement for most capture-recapture techniques. Chandler et al. (2018) used spot patterns of fawns detected on camera trap images to create individual-level encounter histories and to model abundance and recruitment over time. Beaver et al. (2016) compared male deer density estimates from the traditional Jacobson et al. (1997) camera survey method and from SCR approaches using unique antler characteristics. They found the SCR method to produce lower male deer density estimates than the traditional method and attributed the difference in estimates to result from the inability of traditional methods to properly define the area surveyed, causing upward bias in density estimates.

The major limiting factor of SCR models is the need for all individuals to be uniquely identifiable, which is not possible for many species, including female white-tailed deer. However, Chandler and Royle (2013) presented a model for drawing inferences about population size and density using spatially correlated count data on unmarked individuals. Their approach models the count data as a sum of the latent (i.e., unobserved) individual-level encounter histories. This model is known to yield imprecise estimates of abundance and density in the absence of ancillary information about detection probability, but information about detection probability can be acquired by marking a subset of the population, as is done in spatial mark-resight (SMR) models (Sollmann et al. 2013, Efford and Hunter 2017, Whittington et al. 2017) or through telemetry data.

Developing a model which integrates telemetry data from captured deer could produce estimates based on detection/non-detection data without the need for identifying unique individuals. In addition, placing unbaited camera traps on trails frequented by deer may allow for an unbiased survey approach and alleviate issues associated with using attractants (McCoy et al. 2011). This sampling and modeling approach would create an efficient, cost-effective, and ecologically sound means of estimating and predicting trajectories of deer population parameters.

OBJECTIVES

I conducted this research to address three primary objectives:

1. Evaluate an unmarked spatial capture-recapture model using data from passive cameras to estimate abundance and density of deer.
2. Estimate the effect of bait on male deer resource selection and space use during baited camera survey before and after a deer hunting season.
3. Assess the use of pre-hunting season baited camera surveys for white-tailed deer harvest management decisions during subsequent hunting seasons.

STUDY AREAS AND DESIGN

The study area included three properties with varying deer densities and management regimes (Figure 1.1). The properties were located in Southwest Georgia (USA) and ranged in size from ~1,600 hectares to ~12,000 hectares. I established 1000-ha sites within each property consisting of baited and passive cameras. Property 1 contained site A, property 2 contained site B, and property 3 contained sites C and D (Figures 1.2 – 1.4). Habitat types consisted primarily of longleaf pine (*Pinus palustris*) savannas, loblolly pine (*Pinus taeda*) savannas, scattered hardwoods, riparian zones, planted pine stands, and depressional wetlands. Property 2 and 3 had a long history of intensive habitat management for the primary objective of promoting high densities of northern bobwhite (*Colinus virginianus*), while property 1 was primarily focused on white-tailed deer habitat management and unlike the other two properties, had a long term supplemental deer feeding program in place. Typical landscape management for all three properties (varying to some degree between properties) included frequent prescribed fire, wildlife food plots, timber management, roller chopping, mowing, and seasonal disking.

DISSERTATION FORMAT

This dissertation is presented in manuscript format. Chapter 1 is an introduction and background of relevant studies related to my research subjects. Chapter 2 presents the results of an evaluation of an unmarked spatial capture-recapture model for estimating white-tailed deer abundance and density using un-baited cameras. Chapter 3 presents an investigation of the effect of bait on white-tailed deer space use and resource selection, during both pre-hunting and post-hunting season baited camera surveys. Chapter 4 is an evaluation of how well a pre-hunting season baited camera survey represents the spatial distribution of deer detections and the population of male deer available for harvest during the hunting season. And lastly, chapter 5 consists of conclusion and management implications of this research.

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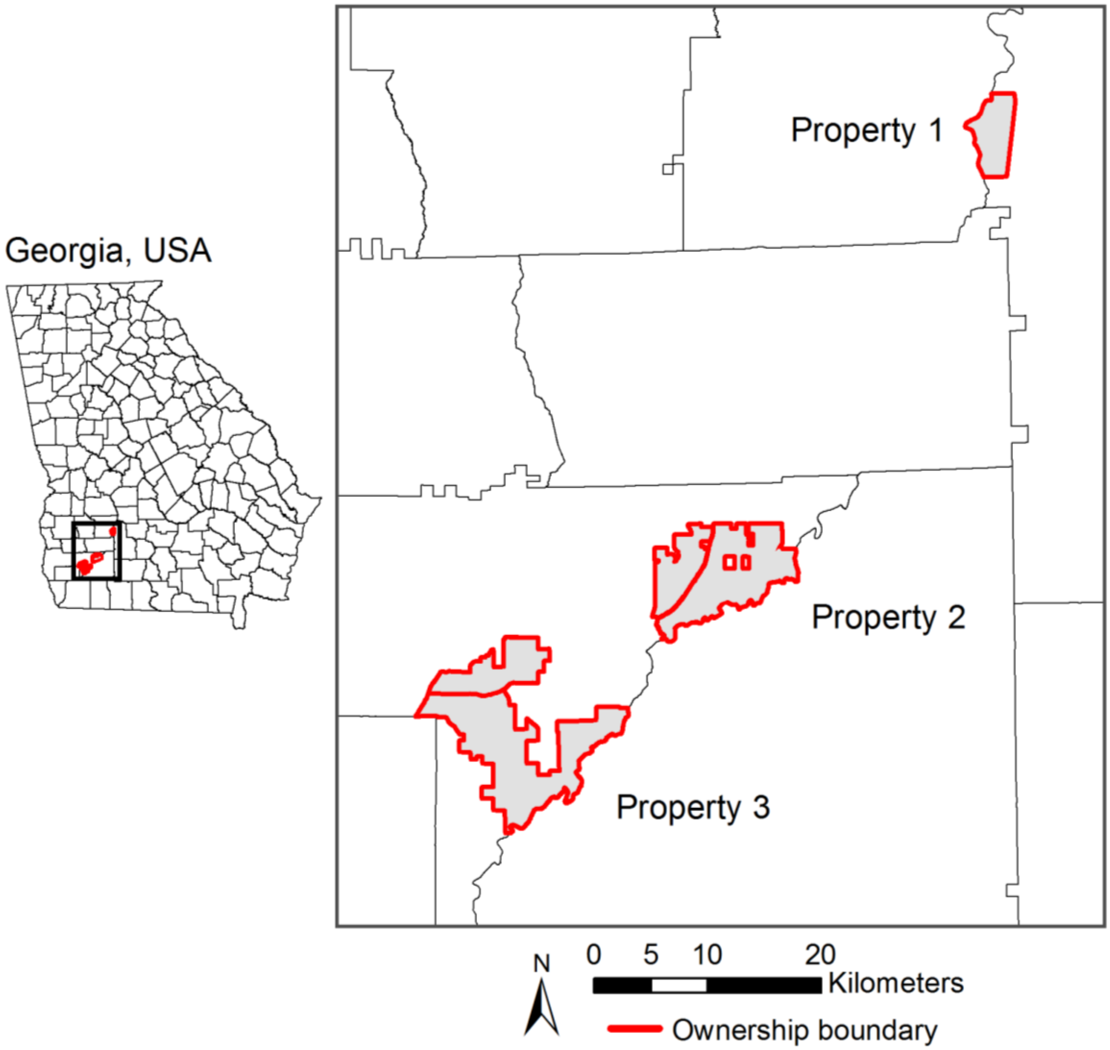

Figure 1.1. Location of three study properties containing camera array sites in southwestern Georgia, USA (2014 - 2016). Properties range in size from 1,600 ha to 12,000 ha.

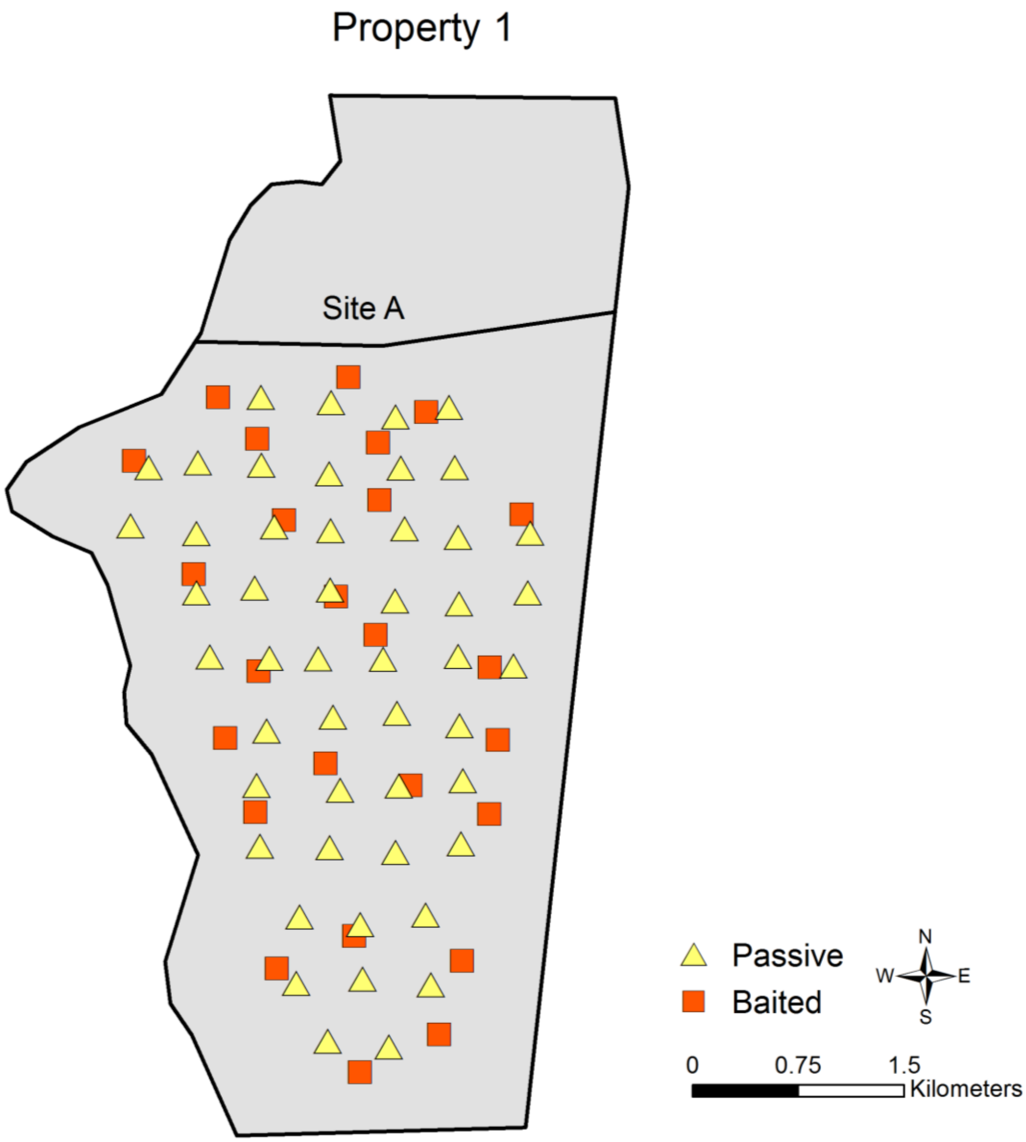

Figure 1.2. Distribution of passive (yellow triangles) and baited (orange squares) cameras of site A for property 1 (2014-2016).

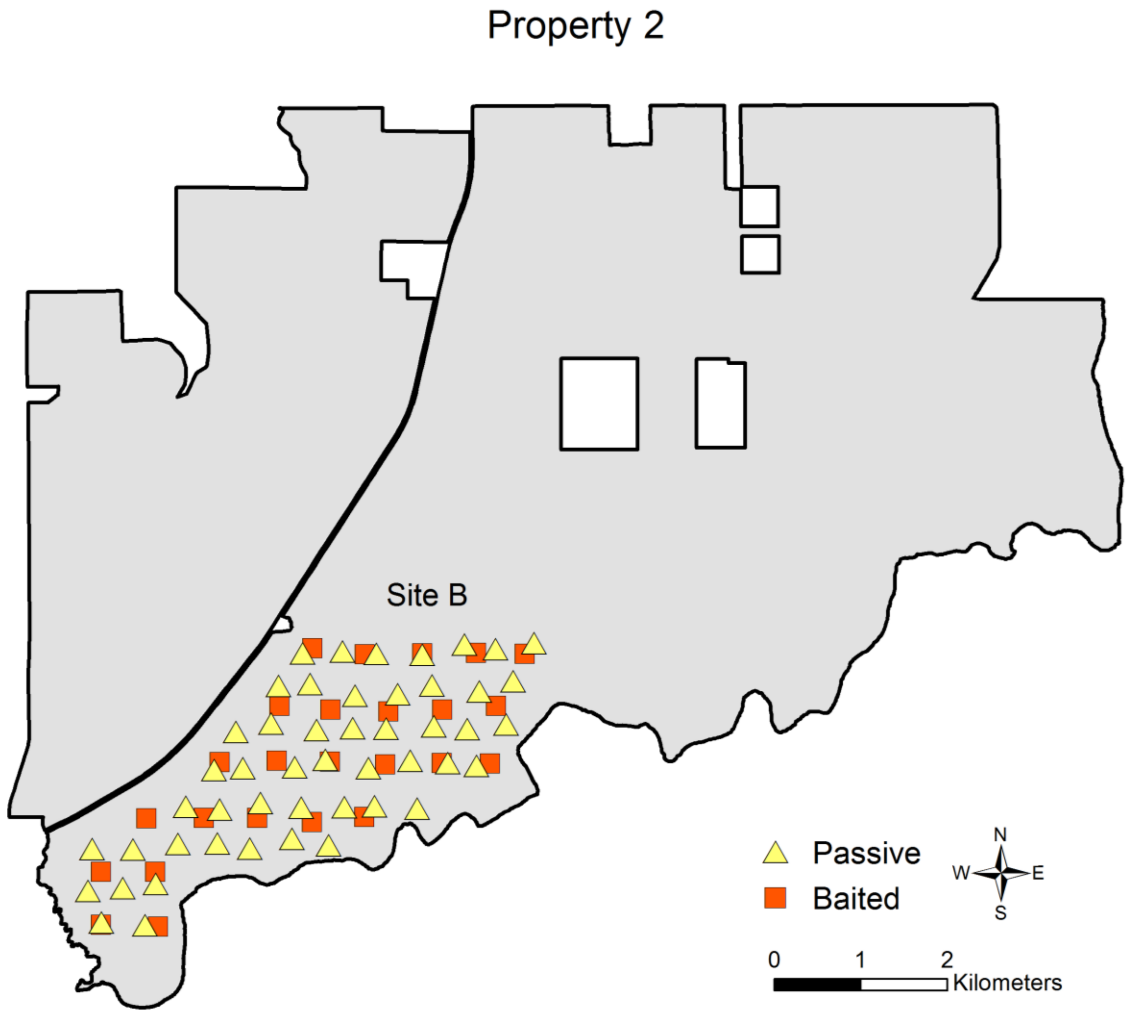

Figure 1.3. Distribution of passive (yellow triangles) and baited (orange squares) cameras of site B for property 2 (2014-2016).

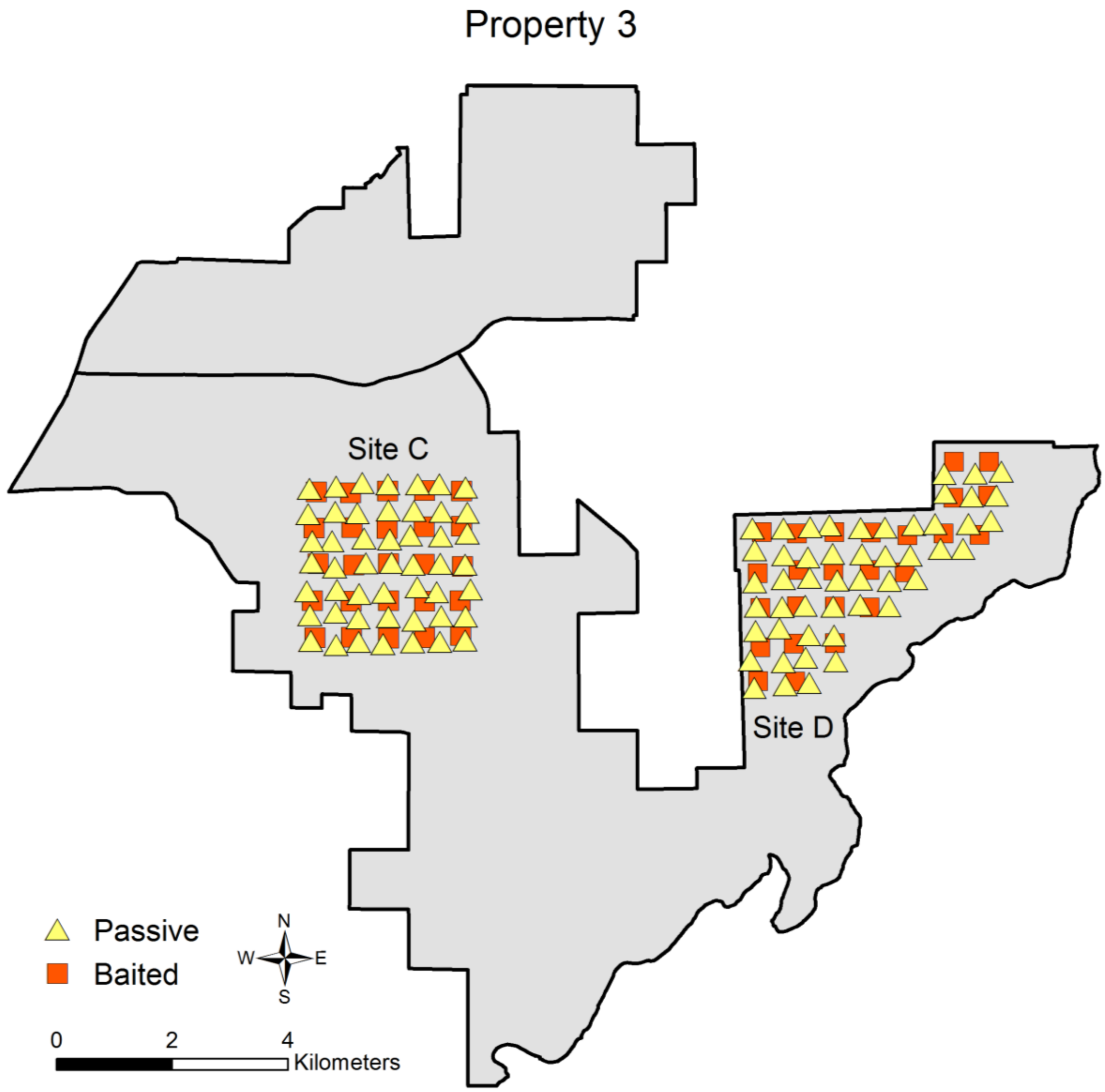

Figure 1.4. Distribution of passive (yellow triangles) and baited (orange squares) cameras at site C to the west and site D to the east for property 3.

CHAPTER 2

EVALUATION OF AN UNMARKED SPATIAL CAPTURE-RECAPTURE MODEL FOR ESTIMATING WHITE-TAILED DEER (*ODOCOILEUS VIRGINIANUS*) DENSITY

Johnson, J. T., R. B. Chandler, L.M. Conner, M. J. Cherry, and K. V. Miller. 2019. To be submitted to the *Journal of Wildlife Management.*

ABSTRACT

A common method for estimating white-tailed deer (*Odocoileus virginianus*) density from camera trap data involves a baited survey (Jacobson method) in which all males must be uniquely identified. The method does not produce estimates of uncertainty, and in addition to being expensive and time consuming, it assumes that: (1) all males in the region are detected, (2) the area of the surveyed region is known, and (3) males, females, and juveniles have equal encounter rates. We evaluated an alternative method based on spatial capture-recapture (SCR) models for unmarked or partially-marked populations that makes less restrictive assumptions and does not require bait or uniquely identifying males. We conducted unbaited camera surveys (1 camera per 20.4 ha) in 2014, 2015, and 2016 at four study sites (A, B, C, and D; approximately 1000 ha each) in southwestern Georgia, USA. We collected telemetry data from 20 collared individuals to provide additional information about the encounter rate parameters of the SCR model. We compared unmarked SCR model estimates to estimates from the Jacobson method for baited camera surveys, and to estimates from distance sampling conducted on two study sites, and SCR models applied to data on uniquely identified male deer. The methods produced similar rank orders of density estimates at the four study sites, however, density estimates produced by the Jacobson method were greater averaging over the three years 40.4, 22.7, 30.8, and 17.0 deer / km^2, when compared to estimates from the unmarked SCR model averaging 17.8 (95% CI: 12.1 – 25.0), 11.9 (95% CI: 8.1 – 16.8), 13.3 (95% CI: 8.8 – 38.3), and 11.5 (95% CI: 7.8 – 16.3) deer / km^2, respectively. Density estimates from distance sampling surveys for sites C and D were 16.7 km^2 (95% CI: 11.0 – 25.5) and 8.5 km^2 (95% CI: 5.8 – 12.3), respectively, which were similar to estimates from the unmarked SCR model. When applied to data on uniquely identified male deer for 2015, the unmarked SCR model was less precise than the standard SCR model which used individual-level encounter histories, however point estimates were often similar when comparing marked and unmarked surveys for males. Marked SCR density estimates (deer/km^2) for male deer at the four sites were 6.345 (95% CI: 5.993-6.843), 3.979 (95% CI: 3.560-4.450), 5.694 (95% CI: 4.767-6.693), and 3.063 (95% CI: 2.606-3.602) and male deer density estimates (deer/km^2) from the unmarked SCR model were 6.863 (95% CI: 3.602 – 12.559), 3.029 (95% CI: 1.672 – 4.911), 3.130 (95% CI: 1.425 – 6.089), and 5.284 (95% CI: 2.673 – 9.531), respectively. Sex specific estimates from the unmarked SCR model produced greater male density estimates than females for 3 of 4 sites, unlike the Jacobson method which consistently produced greater female estimates. Our results indicate that the unmarked SCR model alleviates many issues associated with the Jacobson method and may be an improvement for estimating deer densities when telemetry data or prior information is available about the SCR encounter rate parameters. However, the unmarked SCR model will produce less precise estimates of abundance than standard SCR models applied to encounter history data. Therefore, we recommend individually identifying males and spotted fawns when resources are available. Future research should investigate methods for increasing precision of the unmarked SCR model, possibly by jointly analyzing data on males, females, and juveniles.

KEY WORDS: bait, camera trap, distance sampling, Georgia, passive, survey, telemetry

INTRODUCTION

Obtaining accurate estimates of white-tailed deer population parameters is an important component of monitoring and development of management (Halls 1984, Moore 1995, Jacobson et al. 1997, Amos et al. 2014). Common methods for collecting data on white-tailed deer abundance include spotlight surveys, track counts, helicopter counts, distance sampling, and camera surveys (Jenkins and Marchinton 1969, Jacobson et al. 1997, Koerth et al. 1997, Collier et al. 2011, Kissell and Nimmo 2011). However, many of these methods can be difficult to implement and may not yield data that can be used to generate statistically rigorous estimates of abundance.

The Jacobson et al. (1997) baited camera survey is commonly used by state agencies and private landowners to estimate deer abundance (Koerth and Kroll 2000, Heilbrun et al. 2006, Rowcliffe et al. 2008). The Jacobson method involves placing remote, motion triggered cameras over evenly spaced bait piles (typically ranging from 600-1000m apart) for 10-14 days, usually before and/or after the hunting season. Individual adult males are identified based on unique antler configurations, and the ratio of unique males to the number of total male images is used as a correction factor to estimate the number of adult females and juveniles. Density is computed by dividing the abundance estimates by the area assumed to have been surveyed.

Several studies have raised concerns regarding the validity of results produced by the baited camera method (Rowcliffe et al. 2008, 2011, 2013; McCoy et al. 2011, Weckel et al. 2013, Beaver 2017). Perhaps the most important of these is the violation of the assumption of equal detectability between sexes and among age classes of deer (McCoy et al. 2011, Rowcliffe et al. 2011, Beaver 2017). Another concern is that the area surveyed is assumed to be known, even though many factors such as home range size can impact the effective area surveyed by camera traps (O’Connell et al. 2011, Royle et al. 2014). Density estimates produced by the Jacobson method, and other methods that assume the area surveyed is known, are highly sensitive to changes in the assumed sample area (Noss et al. 2012, Beaver et al. 2016). The use of bait raises additional concerns about altering natural activity patterns of deer and non-target species, and increasing disease transmission through elevated rates of deer-to-deer contact (Brown and Cooper 2006, Sorensen et al. 2014, Beaver 2017).

Spatial capture-recapture (SCR) is a recent extension of traditional mark-recapture methods that can be used in conjunction with camera data to estimate wildlife population parameters when animals can be individually identified (Efford 2004, Royle et al. 2014). SCR models use information about the locations of detection events and the detection histories of individuals to estimate encounter rate, density, and abundance in a region of interest. Recently, SCR models have been applied to encounter history data on male deer and fawns, which can be uniquely identified based on their antler characteristics and their spot patterns respectively (Beaver et al. 2016, Chandler et al. 2018). However, standard SCR models cannot be applied to data on adult female deer because they lack distinct natural markings. Furthermore, the process of uniquely identifying males and fawns may be prohibitively time consuming to be widely adopted by managers. Chandler and Royle (2013) extended the SCR framework to allow for inference about population size when animals cannot be uniquely identified. Instead of requiring spatially referenced encounter histories, the model can be fitted to spatially correlated count data or binary detection data. This model is known to yield imprecise estimates of abundance and density in the absence of ancillary information about detection probability, but information about detection probability can be acquired by marking a subset of the population, as is done in spatial mark-resight (SMR) models

(Sollmann et al 2013, Efford and Hunter 2017, Whittington et al. 2017). Telemetry data can be used to provide additional information about detection probability parameters (Ramsey et al. 2015, Whittington et al. 2017).

We evaluated the Chandler and Royle (2013) model (hereafter, the unmarked SCR model) applied to data from unbaited (herafter, passive) camera traps to determine if this model could be useful for agencies and landowners interested in estimating deer density without the need for individual identification or baiting. To evaluate the unmarked SCR model, we collected camera and telemetry data from several properties in southwestern Georgia and compared density estimates to estimates from the Jacobson method, marked SCR analysis from male antler characteristics, and road-based distance sampling.

METHODS

Study Area

The study area was located in southwestern Georgia (USA) and included three properties that ranged in size from ~12,000 ha to ~1,600 ha (Fig. 2.1). Habitat types consisted of pine savannas, scattered hardwoods, riparian zones, planted pines, and depressional wetlands. Properties 2 and 3 had a long history of intensive habitat management for the primary objective of promoting high densities of northern bobwhite (*Colinus virginianus*), while property 1 was primarily focused on white-tailed deer habitat management and unlike the other two properties, had a long-term supplemental deer feeding program in place. Typical landscape management for all three properties (varying to some degree between properties) included frequent prescribed fire, wildlife openings/food plots, timber management, roller chopping, mowing, and seasonal disking.

Sampling Design

We established four camera trapping sites within the three properties (Figure 2.1). In 2014, we deployed one array of camera traps at each of the three properties (sites A, B, and C). In 2015, an additional camera array was established on property 3 (site D). Within each site, 49 passive cameras and 25 baited cameras were distributed on an irregular grid with 451-m spacing for passive cameras and 632-m spacing for baited cameras within a region that was approximately 1,000 ha (Figure 2.2). This resulted in camera densities of approximately 0.025 baited cameras/ha and 0.049 passive cameras/ha at properties 2 and 3. However, property 1 had a long history (>10 years) of baited camera use, and we used 25 pre-established bait sites at this property (0.02 cameras/ha) and placed the same passive camera array (n=49) within the pre-establish baited camera array. Passive cameras were operated during October, and baited camera surveys were conducted in late August and/or early September prior to the onset of deer hunting season. Baited cameras were operated for two weeks with a week of pre-baiting without operational cameras, corresponding to the baited camera survey protocol. In 2016, only passive cameras during October were operated on sites A, C, and D where captured deer were located. October was chosen for passive camera surveys to avoid overlap with baited camera surveys and to avoid the onset of breeding season behavior, typically beginning in November for the survey region.

We placed passive cameras approximately 1.5 m from the ground, fixed to trees or a metal fence post when trees were not available. Each passive camera was within 200 m of each cell centroid on trails or other areas that appeared to have been used by deer to increase detection probability. We cleared vegetation in front of each camera to reduce vegetation-induced camera triggering. Baited cameras were placed at a similar height as passive cameras, fixed to trees, as close as possible to the center of each grid cell and shelled corn was placed approximately 5 m in front of each baited camera.

All cameras were operated 24 hr/day during the study period, and baited cameras were set with a 5-min delay between successive photographs where passive cameras were set to a 10-s delay between image captures. Baited cameras were visited on average twice a week to replenish bait if needed and check camera functioning, and passive cameras were checked a minimum of once per 31-day October survey. We used infrared cameras developed by HCO Outdoors (model Uway VH200HD, Duluth, GA, USA).

Jacobson Method

The Jacobson method for estimating deer abundance and density from baited camera surveys (Jacobson et al. 1997) involves dividing the number of uniquely identified antlered bucks (N_b) by the number of photographs of uniquely identified bucks (C_b) to obtain the ratio:

$$P_b = N_b / C_b$$

This ratio is used as a correction factor to estimate the abundance of females:

$$N_d = P_b \; x \; C_d$$

Where C_d is the number of photographs of females, and N_d is the estimated female abundance. A similar procedure is used to estimate fawn abundance:

$$N_f = P_b \; x \; C_f$$

Where N_f is the estimated fawn population and C_f is the total number of fawn occurrences in photographs. Total abundance is estimated by summing the abundance estimates for adult males, adult females, and fawns and density is calculated by dividing the total abundance estimate (or each estimated segment of the population) by the assumed area surveyed, which was calculated as the total area surveyed based on the number of cameras used at the specified camera density.

Distance Sampling

We conducted distance sampling surveys in October 2015 at sites C and D. We selected drivable routes that covered the study area and were a minimum of 400 m apart. Site C contained three transects with a combined transect length of 12.4 km and site D contained four transects with a total distance of 15.3 km (Figure 2.3). We sampled transects beginning at dusk by driving at < 16 km/hr and we used FLIR® TS32PRO thermal camera to detect deer. When a deer was detected, the thermal scouting camera and a spotlight were used to count the number of deer present. We measured distances using a range finder (Leupold® RX-1000i) and used a compass to measure the angle from the transect to each deer. We then calculated perpendicular distances from each transect to each detected deer. We altered starting points for each survey night until a minimum of 60 detections for each site was achieved. We used program DISTANCE 7.3 to estimate density (deer / km^2), and we selected detection functions using AIC for each site.

SCR for Individually Identifiable Males

We used unique antler characteristics from both baited and passive cameras to identify individual males within each site and to create capture histories of all male deer detected during the 2015 baited camera surveys. We recorded the detection or non-detection of unique male deer at each camera during each 24-hour sampling period of the two-week August-September surveys, and assumed population closure for this period. For the area of abundance estimation, we used a 1.5 km buffer surrounding the camera grids to create a two-dimensional state-space that defined the area of interest. In SCR models, density is characterized by a spatial point process for the activity centers of the N individuals in the population (Efford 2004, Borchers and Efford 2008, Royle and Young 2008, Royle et al. 2014). An activity center is the average location of an individual during the sampling period. For deer with stationary symmetric home ranges, the activity center is the home range center.

We used a Bernoulli model for encounter histories and modeled the encounter rate as a function of the distance between a deer's activity center and a camera trap location. We used the standard half-normal model for the encounter function:

$$\lambda_{ij} = \lambda_0 \exp\left(-\frac{d_{ij}^2}{2\sigma^2}\right)$$

where λ_0 is the encounter rate of an individual deer when the distance (d_{ij}) from its activity center to the camera trap is 0. The parameter σ is the spatial scale parameter describing how encounter rate (λ_{ij}) decreases with increasing distance from a camera site and a deer's home range center. We modeled binary detection histories instead of encounter frequencies, and were therefore converted the encounter rate to encounter probability using the equation:

$$p_{ijk} = 1 - \exp(-\lambda_{ijk})$$

We set detection probability to zero on days for which a camera wasn't operational. The model for the encounter histories was:

$$y_{ijk} \sim \text{Bernoulli}\ (p_{ijk} \times z_i)$$

We used Bayesian inference and parameter expanded data augmentation in which the dimensions of the parameter space are fixed by choosing M to be an integer much greater than N, and by including a set of latent binary variables indicating whether individual i is a member of the population:

$$z_i \sim Bernoulli(\psi); i = 1,2 \dots M.$$

where ψ is the proportion of the M individuals that were part of the population (Royle et al. 2014). We used vague prior distributions for all parameters. We fit the model in R (version 3.3.1) with the package rjags (Plummer 2016), which interfaces with the Gibbs sampler software JAGS (Plummer 2003).

Unmarked SCR Model

We used the unmarked SCR model (Chandler and Royle 2013) to estimate abundance for each age and sex class. This model extends the standard SCR model described above by treating the encounter histories as unobserved (latent) variables that determine the observed data on unmarked individuals at each camera. Specifically, instead of observing y_{ijk}, we observe n_{jk}, which is either the number of detections at camera *j* on occasion *k*, or it is a binary variable indicating if at least one deer was detected. For count data, the model is $n_{jk} = \sum_{i=1}^{M} y_{ijk}$, and for binary data, the model is $n_{jk} = I\left(\left\{\sum_{i=1}^{M} y_{ijk}\right\} > 0\right)$ where $I(\cdot)$ is the indicator function returning 1 if the argument is true and 0 otherwise. If the latent encounter history data are Poisson distributed, they can be marginalized out of the model to improve computational performance. In the case of count data, this results in $n_{jk} \sim \text{Poisson}(\Lambda_{jk})$ where $\Lambda_{jk} = \sum_{i=1}^{M} \lambda_{ijk} z_i$. If the observed data are binary, the model simplifies to $n_{jk} \sim \text{Bernoulli}(1 - \exp(-\Lambda_{jk}))$. The unmarked SCR model is known to yield imprecise estimates when there is no ancillary information available about the detection parameters (Chandler and Royle 2013). We therefore deployed GPS collars on deer at each of the study sites to collect direct information about the detection parameters (λ_0 and σ) as described below.

Telemetry Data and Estimation of Detection Probability Parameters

We captured 25 deer (15 males, 10 females) between March 2016 – June 2016. We fit each deer with a Lotek LifeCycle global positioning system (GPS) collar (Lotek Wireless Inc., Newmarket, Ontario, Canada) and applied uniquely numbered ear-tags to each ear. Collars were pre-programmed to record coordinate locations every 13 hours. We distributed capture locations throughout camera grids A, C, and D, and targeted deer of varying ages based on body morphology and/or antler characteristics. We followed all animal use protocols prescribed by the University of Georgia Animal Use and Care Committee (AUP Permit # A2014 02022, Georgia Scientific Collecting Permit # 29-WJH-13-169). Telemetry data from the captured and marked individuals provided a greater level of detail describing the spatial parameters of deer within our study area than camera re-sightings alone.

We created standard SCR encounter histories from the captured and marked individuals within our camera grids. We used the standard half-normal encounter function to model encounter rates as described above. We used the telemetry data of marked deer to improve estimates of λ_0 and σ. The telemetry data were modeled conditional on the activity center and the spatial scale parameter:

$$u_{i,t} \sim \text{Norm}(s_i\, , \sigma^2)$$

The posterior distribution for λ_0 and σ from the analysis of the data on GPS-collared deer was used as an informative prior in the unmarked SCR model. We fit the unmarked model in R (version 3.3.1) using a custom MCMC sampling algorithm. We generated two Markov chains each representing 30,000 posterior samples, and we discarded the first 1000 as burn-in. Convergence was graphically assessed and evaluated using the Gelman-Rubin statistic (Gelman and Rubin 1992).

RESULTS

Jacobson Method

We collected 108,479 images and identified 825 unique males from the two-week August – September baited camera surveys in 2014 and 2015 (Tables 2.1 and 2.2). In both years, the Jacobson method indicated that density was highest at site A (2014: 42.8 deer / km^2; 2015: 38.0 deer / km^2), followed by sites C (2014: 28.3 deer / km^2; 2015: 33.3 deer / km^2) and B (2014: 19.7 deer / km^2; 2015: 25.7 deer / km^2) (Figure 2.4). Density was lowest at site D in 2015 (17.0 deer / km^2), the only year this site was surveyed with baited cameras. The Jacobson method produced greater density estimates of females than males for each year and all sites (Figures 2.5 and 2.6).

Distance Sampling

In October 2015, we observed 96 deer in 67 groups for site C during three survey nights and 93 deer in 60 groups for site D during 6 survey nights. The Hazard-rate model and the Half-normal model produced the lowest AIC values for sites C and D, respectively (Table 2.3). Site C produced a mean density estimate of 16.7 deer / km^2 (95% CI: 11.0 – 25.5), which was nearly twice the density estimate produced for site D with a mean of 8.5 deer / km^2 (95% CI: 5.8 – 12.3) (Figure 2.4). Distance surveys produced lesser density estimates than the Jacobson method for both sites surveyed.

SCR for Individually Identifiable Males

We collected 19,904 photographs of 470 uniquely identified males for the two-week marked SCR baited survey in September 2015 from all camera grids combined (Table 2.2). Density estimates were greatest at site A (6.4 deer / km^2; 95% CI: 6.0 – 6.9), followed by sites C (5.7 deer / km^2; 95% CI: 4.8 – 6.7), B (4.0 deer / km^2; 95% CI: 3.6 – 4.5), and D (3.1 deer / km^2; 95% CI: 2.6 – 3.6), respectively (Figure 2.5; Table 2.4). The marked SCR results had the greatest precision, producing the narrowest confidence intervals (95% CI) compared to all other surveys.

Unmarked SCR

We collected 19,747 images of deer during the October passive surveys from 2014, 2015, and 2016 (Table 2.2). Binary detections at each site for each 24-hour sampling occasion resulted in sites A and C producing 2,078 and 978 detections in 4,557 camera-days, respectively, and sites B and D producing 755 and 494 detections in 3,038 camera-days, respectively (Figure 2.7). Across all years, site A produced the highest averaged density estimate (deer / km^2) of 17.8 (95% CI: 12.1 – 25.0), followed by site C with 13.3 (95% CI: 8.8 – 38.3), site B with 11.9 (95% CI: 8.1 – 16.8), and site D with 11.5 (95% CI: 7.8 – 16.3) (Figures 2.5; Table 2.5). In 2015 we experienced large amounts of camera malfunctions (>50%) in sites B and C relative to other sites, likely resulting in the observed drop in density compared to 2014 for both sites, and 2016 for site C.

We collected more images of female than male deer in all sites and years from October passive camera surveys (Table 2.2). For male deer, site A produced the highest average density estimates (deer / km^2) across all years with 6.7 (95% CI: 3.6 – 12.0), followed by site D with 6.2 (95% CI: 3.2 – 10.7), site B with 5.9 (95% CI: 3.2 – 10.0), and site C with 3.8 (95% CI: 1.9 – 6.9) (Figures 2.5; Table 2.6). For female deer, site C produced the highest averaged density estimates (deer / km^2) across all years with 5.0 (95% CI: 3.1 – 7.6), followed by site A with 4.5 (95% CI: 2.9 – 6.6), site B with 4.4 (95% CI: 2.7 – 6.8), and site D with 3.4 (95% CI: 2.0 – 5.2) (Figures 2.6; Table 2.7). Site C was the only site to consistently produce greater density estimates of females compared to males for all years surveyed (Figures 2.5 and 2.6; Tables 2.6 and 2.7).

Detection Probability Parameters from Captured Deer

We recorded 452 locations for the 25 GPS-collared deer during the 31 days of October 2016. Eleven (7 females and 4 males) of the 25 GPS-collared deer were detected on cameras in a total of 45 photographs during October 2016 (Figure 2.8). Five captured deer were excluded from the analysis due to malfunctioning GPS collars, therefore 20 captured deer with telemetry data were used to estimate detection probability parameters. Posterior mean estimates for the spatial scale parameter (σ) and the baseline encounter rate (λ_0) of all deer with collars were 0.407 km (95% CI: 0.389 – 0.426) and 0.029 (95% CI: 0.020 – 0.041), respectively (Figure 2.9; Table 2.8 and 2.9). Male deer with collars produced the largest mean estimate of σ (0.432 km; 95% CI: 0.410 – 0.456) and lowest λ_0 (0.017; 95% CI: 0.009 – 0.027), and females produced a lesser mean estimate of σ (0.328 km; 95% CI: 0.299 – 0.359) and the highest λ_0 (0.067; 95% CI: 0.041 – 0.099) (Figure 2.9; Table 2.8 and 2.9). Spatial parameters estimated from collared/marked male deer were similar to male deer of the marked SCR surveys (Tables 2.4 and 2.8)

DISCUSSION

Our evaluation of the unmarked SCR model for white-tailed deer indicated that the method can yield density estimates that are similar to estimates from standard SCR models and to estimates from distance sampling. Moreover, the unmarked SCR model alleviates all of the limitations of the Jacobson method, which is currently the most widely used method for estimating deer density using camera data. Limitations of the Jacobson method include the need to make assumptions about the area sampled, the need to assume equal visitation rates of sexes and age classes, the need to detect and identify all antlered males, the lack of measures of precision, and the need to use bait.

Eliminating the use of bait when surveying deer has many benefits. The use of bait may enhance disease transmission (Eve 1981, Thorne and Herriges 1992, Schmitt et al. 1997, Brown and Cooper 2006, Sorensen et al. 2014), impact non-target species (Bowman et al. 2015), potentially altering activity rates and patterns of deer (Jacobson and Darrow 1992, Kilpatrick and Stober 2002), create legal concerns when and where baiting is prohibited, and create conflicts with non-target species such as feral swine (*Sus scrofa*) or bears (*Ursus* spp). In addition to avoiding these issues, an unbaited technique such as the unmarked SCR model could reduce the cost associated with baited camera surveys.

The Jacobson method assumes that the area being sampled is known when in reality the effective sample area is influenced by many factors, including home range size, and may vary through space and time. The Jacobson method assigns a survey area based on the number of cameras used at a specified camera density. Density estimates could be inflated by deer using bait sites on the periphery of camera arrays when home ranges overlap the boundary of the assigned area being surveyed. The SCR models we used estimate home range centers and spatial parameters based on the distribution of deer detections at camera traps, and do not rely on informal approaches for estimating survey area extents. Therefore, the state-space assigned for density estimation is assumed to encompass all deer available for detection within the camera arrays and that activity centers are distributed randomly. In addition, SCR models assume there is no permanent emigration or immigration from the state-space during the survey period and allows for temporary movements around the state-space, resulting in variable exposure to encounter by a camera trap (Royle et al. 2014). Nearly all density estimates from our SCR analyses were lesser than the Jacobson method estimates. Beaver et al. (2016) also compared an SCR approach for estimating male deer densities to estimates produced by the Jacobson method and found the spatially explicit approach to produce lesser density estimates. In addition, Noss et al. (2012) analyzed data from 13 camera trap surveys involving jaguar (*Panthera once*), puma (*Puma concolor*), ocelot (*Leopardus pardalis*), and lowland tapir (*Tapirus terrestris*) with SCR likelihood-based and Bayesian approaches and found, in general, SCR approaches produced lesser density estimates than non-spatial analyses that use informal estimations of the effective survey area.

The Jacobson method relies on the assumption of equal visitation rates of deer, and biases associated with this assumption have been presented by many studies, including greater rates of male detections resulting in low-biased estimates (Jacobson et al. 1997, Moore 2014), behavioral interactions at high deer densities could lower sightability of subordinate members (Donohue et al. 2013), and greater probability of photographing females which results in high-biased estimates (Jacobson et al. 1997, Weckel et al. 2013). SCR models directly estimate encounter rates based on the distance between an individual's estimated activity center and the camera trap, providing the ability to account for differences in sexes and age classes when estimating abundance.

Jacobson et al. (1997) reported higher capture rates of females when compared to males at high camera densities, which they attributed to larger home range sizes of males, as is the case within our study sites. Baited cameras within core areas of smaller female home ranges would inflate detections relative to males. Our baited camera density was greater (1 camera per 40 ha) than that suggested by Jacobson et al. (1997) (1 camera per 65 ha), and may have led to greater detectability of females within our study, inflating overall density estimates of the Jacobson method results relative to other methods.

Unlike the Jacobson method, SCR models produce estimates of uncertainty. Without a measure of precision (sampling variance), abundance or density estimates are not very useful (White et al. 1982). Confidence intervals indicate a level of uncertainty associated with point estimates, providing a way to compare estimates or detect population fluctuations across years. The unmarked SCR model approach uses statistical inference to draw conclusion about uncertainty of the estimates produced and provide an inherent advantage for those seeking to make informed management decisions.

We are unable to compare any of our estimation methods to a known density of deer within each site, therefore we cannot conclude which technique produced the most realistic estimates of abundance. However, the Jacobson method tended to produce much greater density estimates than all other methods. While the Jacobson method is faced with justifiable criticism, the unmarked SCR model is not free of limitations. The unmarked model we used requires ancillary data, or prior information, concerning the spatial parameters specific to the deer of the region surveyed before proceeding to using unmarked detection/non-detection camera trap data. We overcame this hurdle by capturing deer to obtain telemetry data in conjunction with camera trap data of marked individuals at our sites to develop prior probability distributions of detection parameters for the unmarked model. Capturing and marking deer is not a simple solution, and certainly adds a layer of logistical complications.

Estimates from the unmarked SCR model are not as precise as models fitted to data on marked individuals. All estimates of males from the unmarked SCR model contained higher degrees of uncertainty when compared to estimates from the marked SCR method. The marked SCR method uses more information contained in the camera trap data, while time consuming to produce, the estimates are generally more precise. The unmarked SCR model also produced greater estimates of males than females in some cases which contradicts results from the Jacobson method, however we have no way of knowing the true sex ratios for each site. We also have no way to currently account for clustering of deer at camera sites which can result in erroneous outcomes of the unmarked model estimates. Clustering of family groups may be responsible for our low estimates of females from the unmarked model, given binary data cannot account for female clusters of deer at a camera site on a given occasion. If males are primarily solitary during October, the binary data would account for single male observations in the same manner it would account for female group observations. Camera trap data alone do not provide adequate information about female group size, and further research is needed to refine the model to account for this phenomenon.

During 2015, sites B and C experienced high rates of camera failures, and the unmarked SCR model produced large shifts in density estimates from the year prior. It is likely the sparse camera data did not provide enough information for accurate estimates and that camera reliability was not consistent from one year to the next. It is apparent that not all manufactured camera models are the same, and the reliability of within camera model replicates can vary significantly. Weingarth et al. (2013) tested six models of cameras and found considerable differences in trigger speed, image quality, and reliability between and within camera models, all of which could affect the outcome of detection rates of cameras within a site over a given period of time. It is intuitive then that camera reliability should be a primary concern when using a spatial model sensitive to changes in spatial parameters that could be affected by camera design.

We found similar estimates between the unmarked SCR survey and distance sampling surveys. Road-based distance sampling surveys have become a mainstream addition to many deer monitoring programs (Mitchell 1986, Buckland et al. 2001), and the use of thermal imagers have enhanced the method's reliability (Gill et al. 1997, Morelle et al. 2012). However, the use of road-based distance sampling has been criticized because it is often difficult to meet the assumption that deer are uniformly distributed with respect to the road (Buckland et al. 2001, Koenen et al. 2002, McShea et al. 2011, Collier et al. 2012; Beaver et al. 2014). The uniformity assumption can be violated if roads are not randomly placed with respect to habitat, or if deer avoid (or are attracted to) the road before being detected (Collier et al. 2007, 2012). In addition, repeatable detection rates are difficult to achieve which could bias estimates, and the technique isn't reliable when thick vegetation is present (Collier et al. 2007, 2012). However, we used private unpaved and low-use roads within the pine savannas of our sites, which contained low understory and minimal midstory vegetation within a relatively homogenous habitat, and it is unlikely our estimates were heavily biased by the common criticisms.

The unmarked SCR model produced similar density estimates to the standard SCR model we applied for male deer. All 95% confidence intervals from the unmarked survey for males contained the point estimates from marked SCR surveys. However, the marked SCR approach resulted in smaller confidence intervals that did not contain the unmarked survey point estimates, indicating a greater level of precision. Mark-recapture studies have been widely employed across numerous taxa for decades when detection of individuals is imperfect (McCrea and Morgan 2015). While often laborious to conduct, standard marked SCR surveys contain greater levels of information than other methods we compared and were likely the most reliable estimates produced.

Juvenile specific estimates were excluded from our results due to the lack of spatial data associated with juveniles. Further research is needed to estimate these spatial parameters as they are likely different than the adult male or female spatial parameters we estimated from our capture efforts. Considering the importance of estimating recruitment within managed deer populations, and the lack of reliability when using the Jacobson method to estimate juvenile abundance (Chitwood et al. 2016), a statistical approach such as the unmarked SCR survey using passive cameras could provide the necessary means for user friendly fawn estimation without the need for individual spot-pattern identification (Chandler et al. 2018).

Our evaluation of the various methods presented indicate the unmarked SCR model will produce similar estimates to distance sampling surveys and standard SCR methods. However, given the high degree of uncertainty of the unmarked SCR model when compared to standard SCR models, efforts to uniquely identify individuals, such as antlered males or spotted fawns, should be pursued when resources allow. In general, camera spacing should be approximately twice the estimated spatial scaling parameter (σ), and our study design could be refined to reduce passive camera density to 1 camera per 64 ha. Future research should investigate methods for increasing precision of the unmarked SCR model, possibly by jointly analyzing data on males, females, and juveniles.

MANAGEMENT IMPLICATIONS

The unmarked SCR approach resulted in relatively consistent estimates when compared to other approaches, however estimates produced were typically 50% lower than the Jacobson method. Additional research with known populations would provide insight into the accuracy of the methods we evaluated. While we have no way of determining accuracy at this time, the unmarked SCR model could provide many advantages over the Jacobson method surveys for deer, including measures of precision lacking with the Jacobson method. Using an unmarked and unbaited survey technique would provide an economic relief for many deer management programs as well as simplifying sampling processes and data collection. The use of unbaited survey techniques should also be considered given the prevalence of diseases such as CWD. Using unbaited camera surveys would give managers an alternative method for surveying deer when baiting bans are in place.

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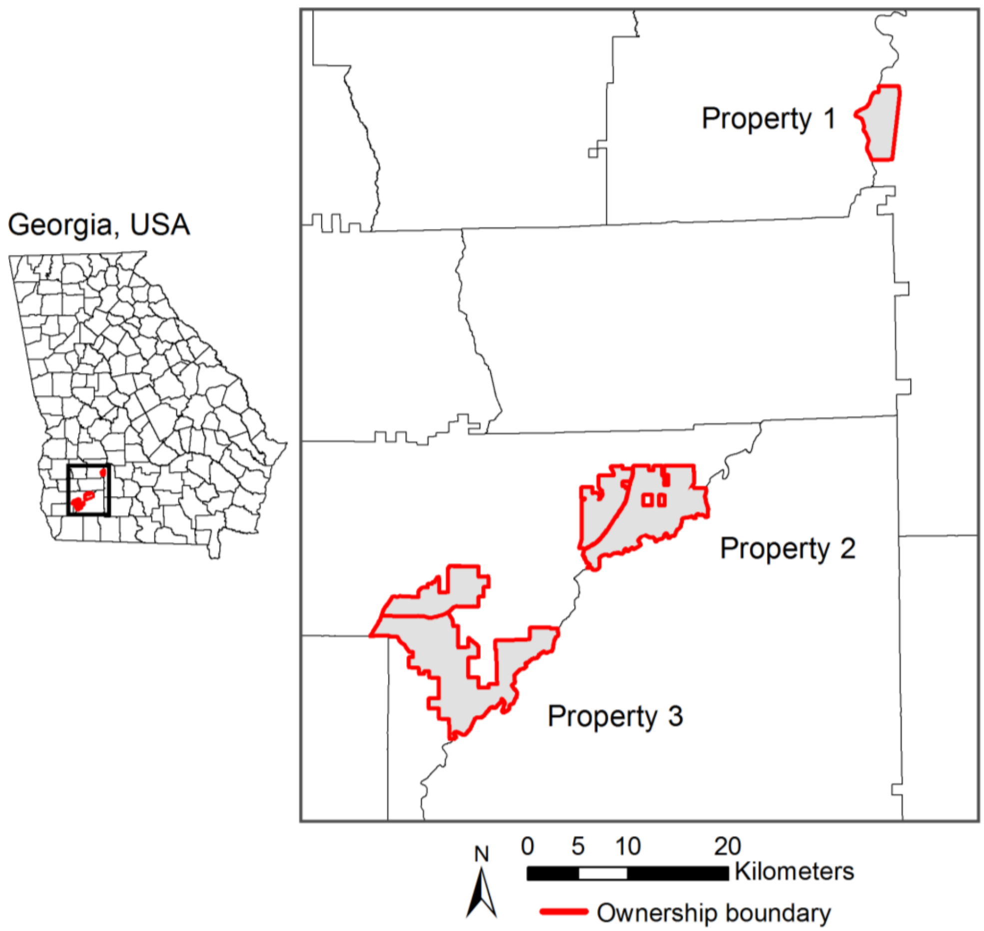

Figure 2.1. Property locations in southwestern Georgia, USA, where study sites containing camera arrays for white-tailed deer (*Odocoileus virginianus*) were located during 2014, 2015, and 2016. Property 1 contained site A, property 2 contained site B, and property 3 contained sites C and D.

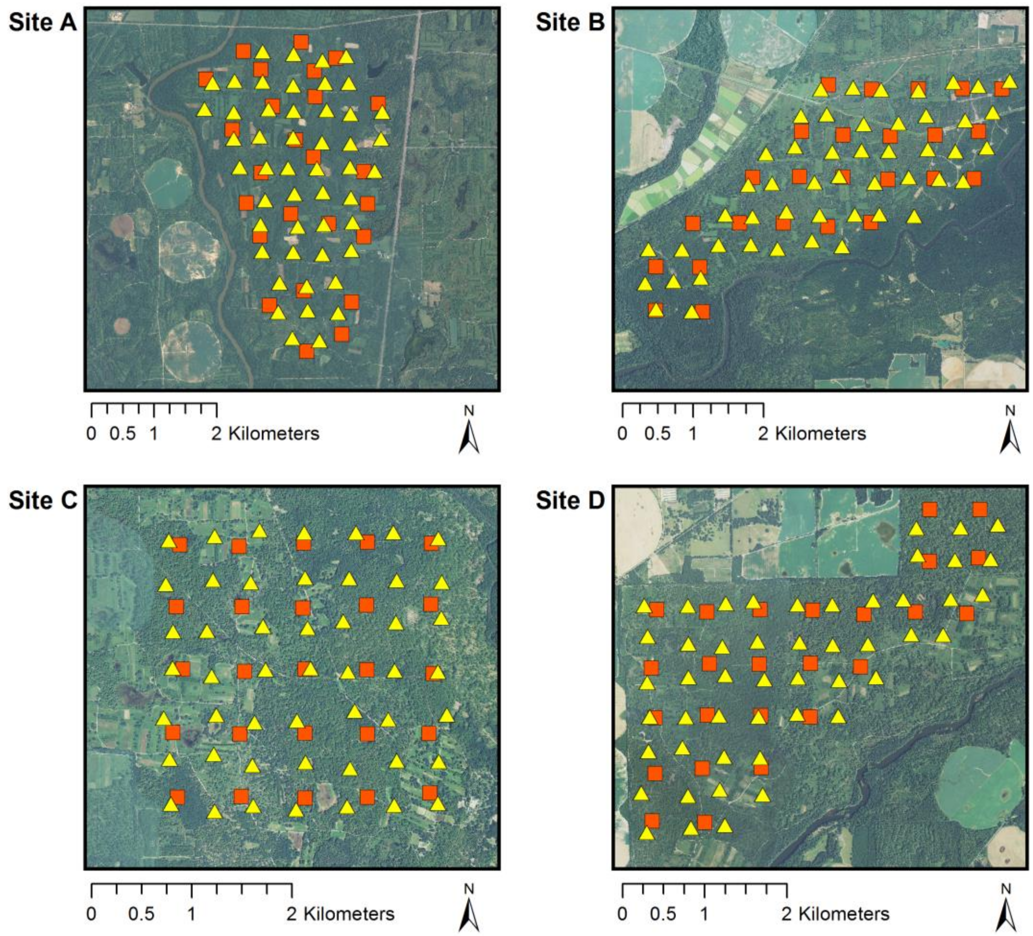

Figure 2.2. Camera array sites A, B, and C used for white-tailed deer (*Odocoileus virginianus*) surveys in southwestern Georgia, USA (2014, 2015, and 2016). Orange squares represent baited cameras and yellow triangles represent unbaited passive cameras.

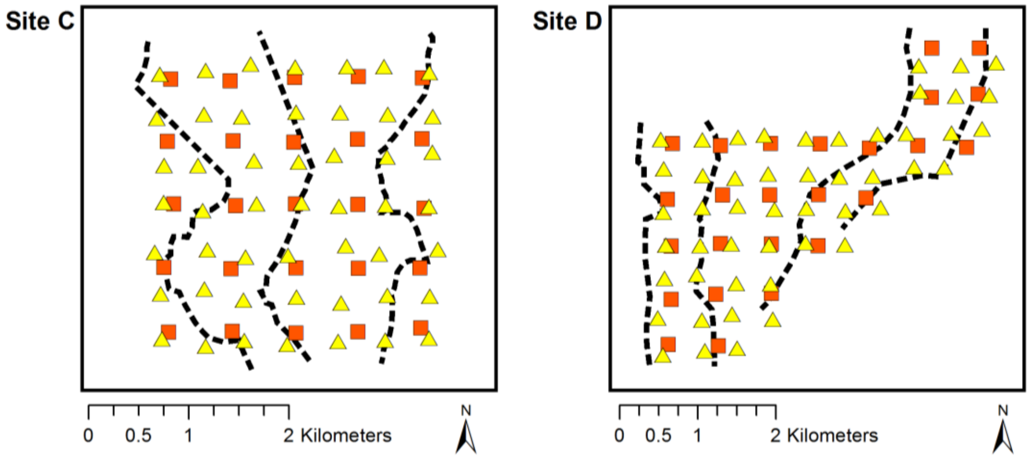

Figure 2.3. Road-based distance sampling transects (dashed lines) for sites C and D in southwestern Georgia, USA, used to conduct distance sampling surveys for white-tailed deer (*Odocoileus virginianus*) in 2015.

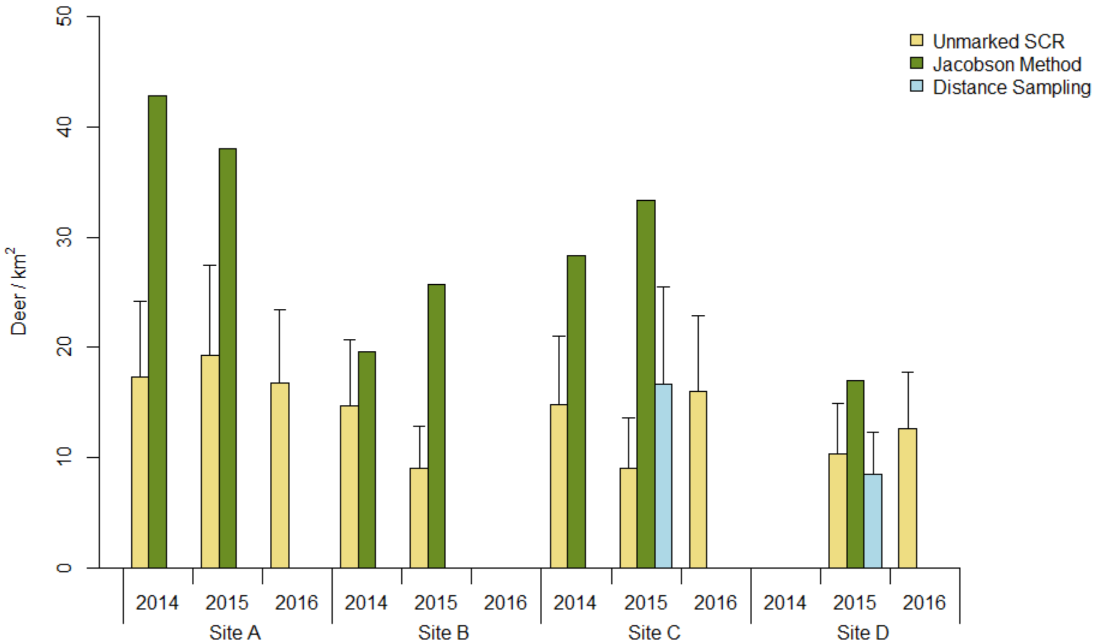

Figure 2.4. Total population density estimates (deer/km^2) for white-tailed deer (*Odocoileus virginianus*) from 2014, 2015, and 2016 for each site in southwestern Georgia, USA, comparing the unmarked SCR survey, distance sampling, and the Jacobson baited survey.

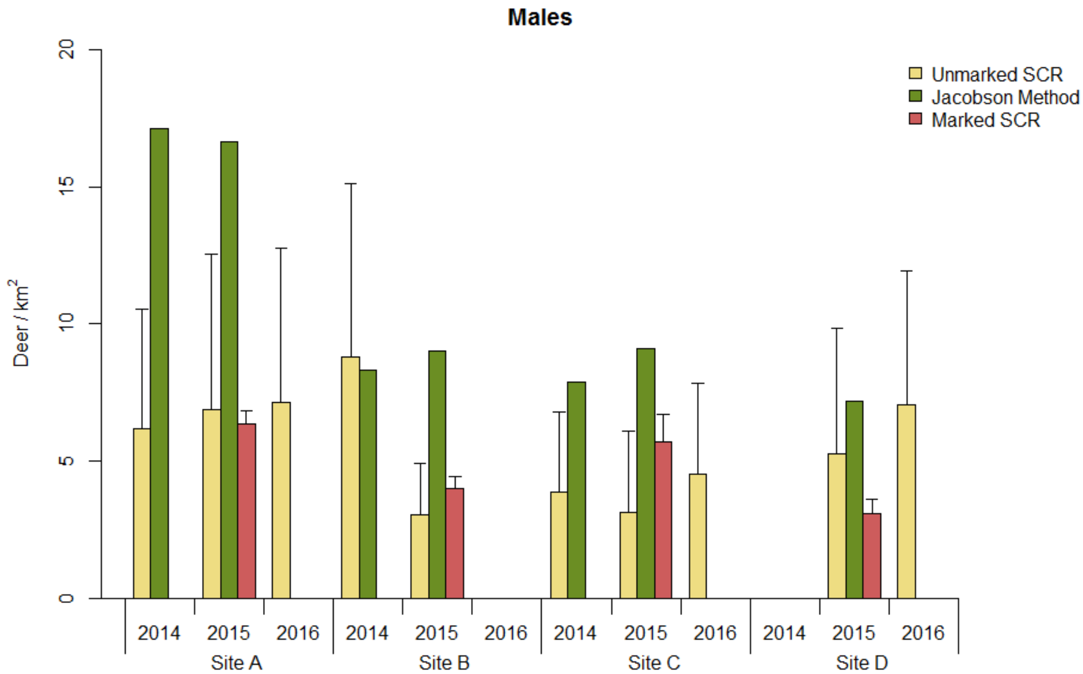

Figure 2.5. Male white-tailed deer (*Odocoileus virginianus*) density (deer/km^2) estimates from 2014, 2015, and 2016for each site in southwestern Georgia, USA, comparing the unmarked SCR survey, the Jacobson baited survey, and the marked SCR survey.

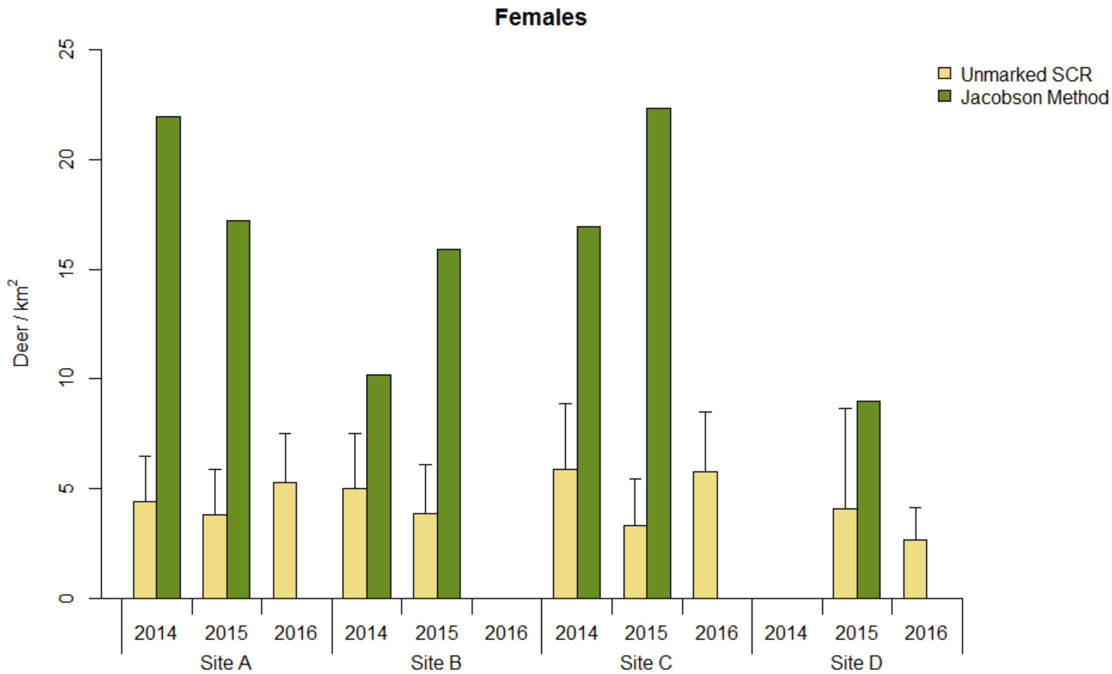

Figure 2.6. Female white-tailed deer (*Odocoileus virginianus*) density (deer/km^2) estimates from 2014, 2015, and 2016 for each site in southwestern Georgia, USA, comparing the unmarked SCR survey, the Jacobson baited survey, and the marked SCR survey.

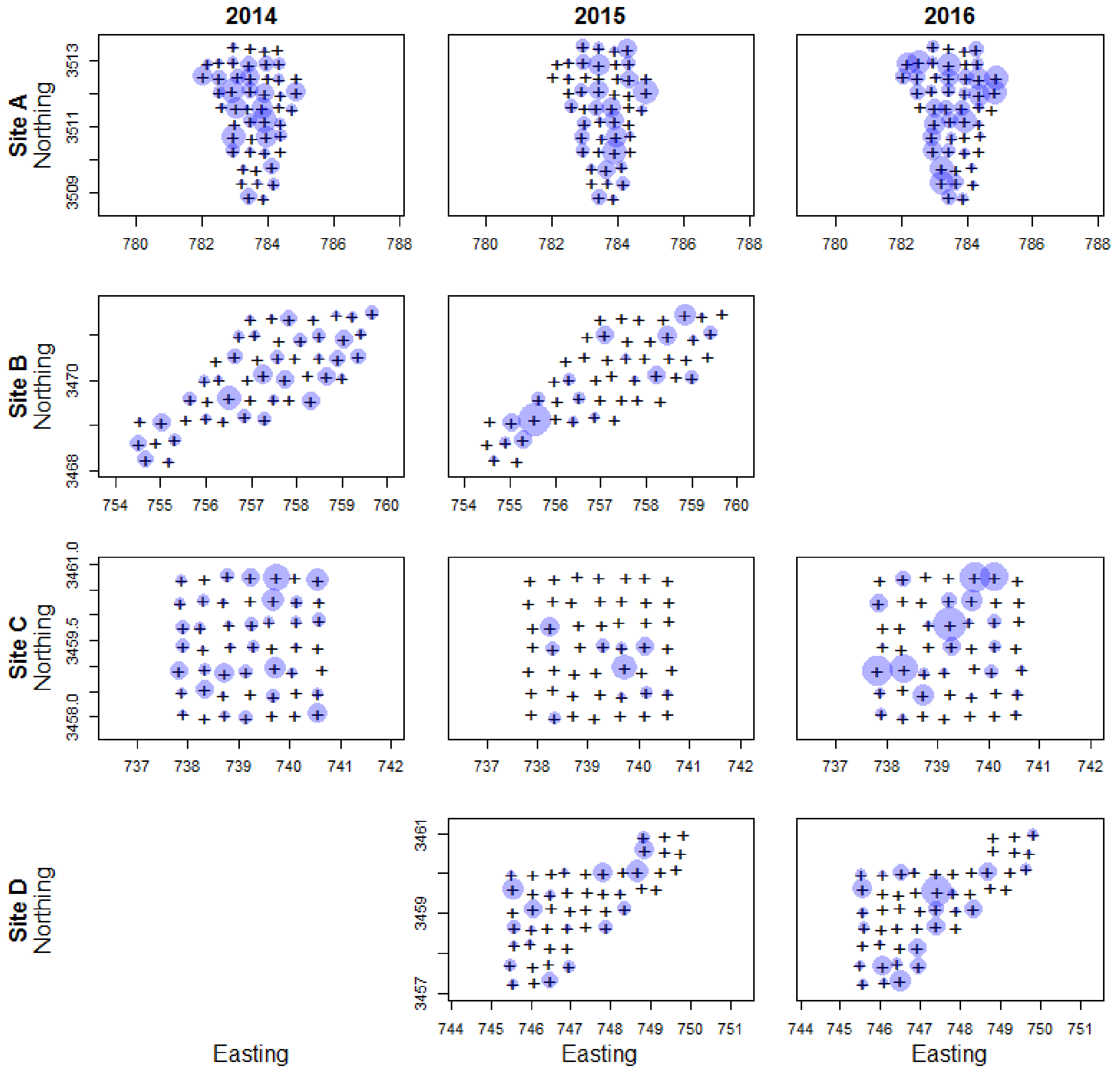

Figure 2.7. Passive camera (+) detections for all white-tailed deer (*Odocoileus virginianus*) at sites A-D during October 2014, 2015, and 2016 in southwestern Georgia, USA. Circle size is proportional to the number of detections. A detection event was defined as at least one photograph of a deer during a 24-hr sampling occasion.

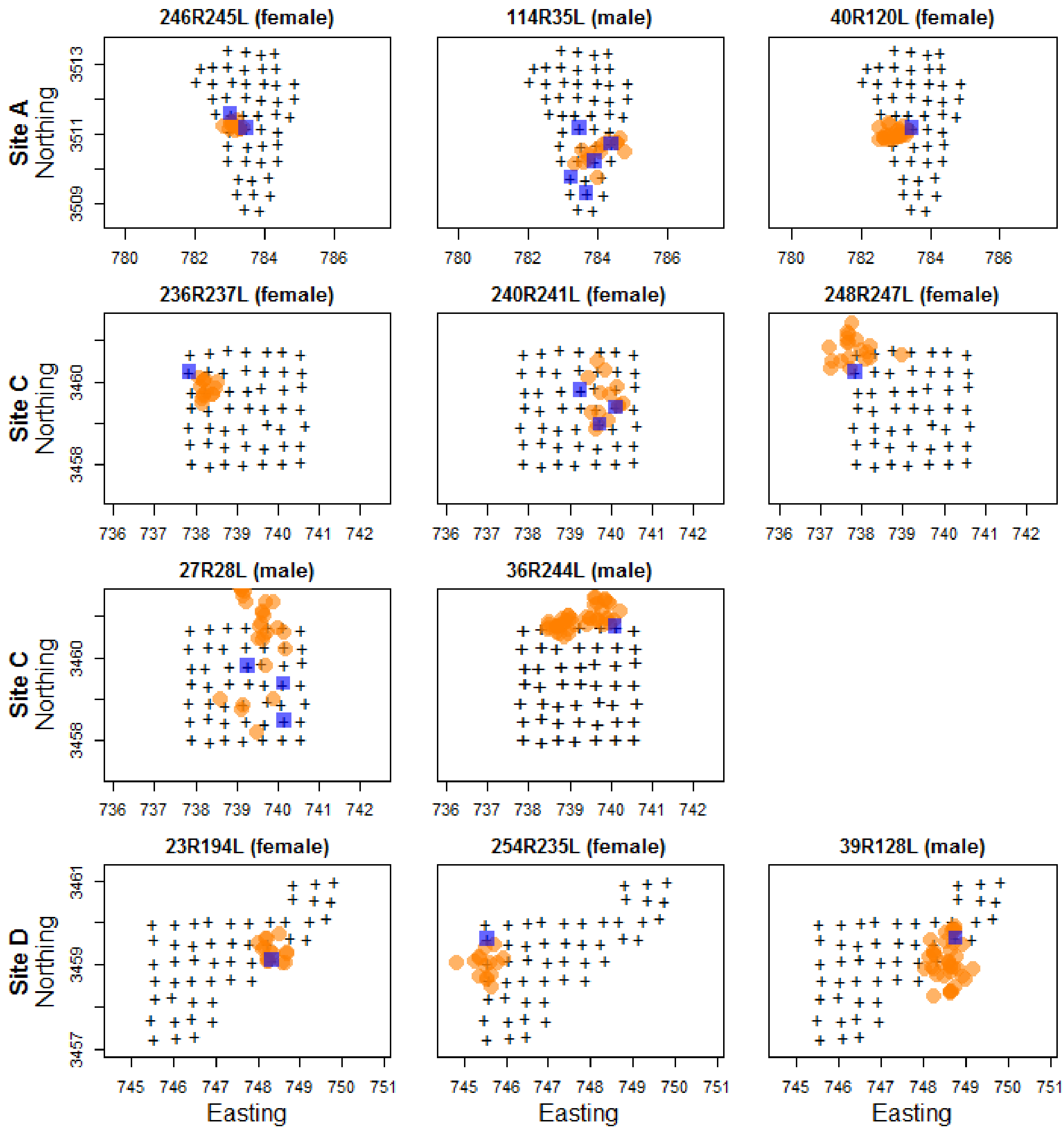

Figure 2.8. Telemetry locations of white-tailed deer (*Odocoileus virginianus*) (orange circles) and camera (+) detections (blue squares) for deer 246R245L, 114R35L, and 40R120L at site A, deer 236R237L, 240R241L, 248R247L, 27R28L, and 36R244L at site C, and deer 23R194L, 254R235L, and 39R128L at site D in southwestern Georgia, USA (2016).

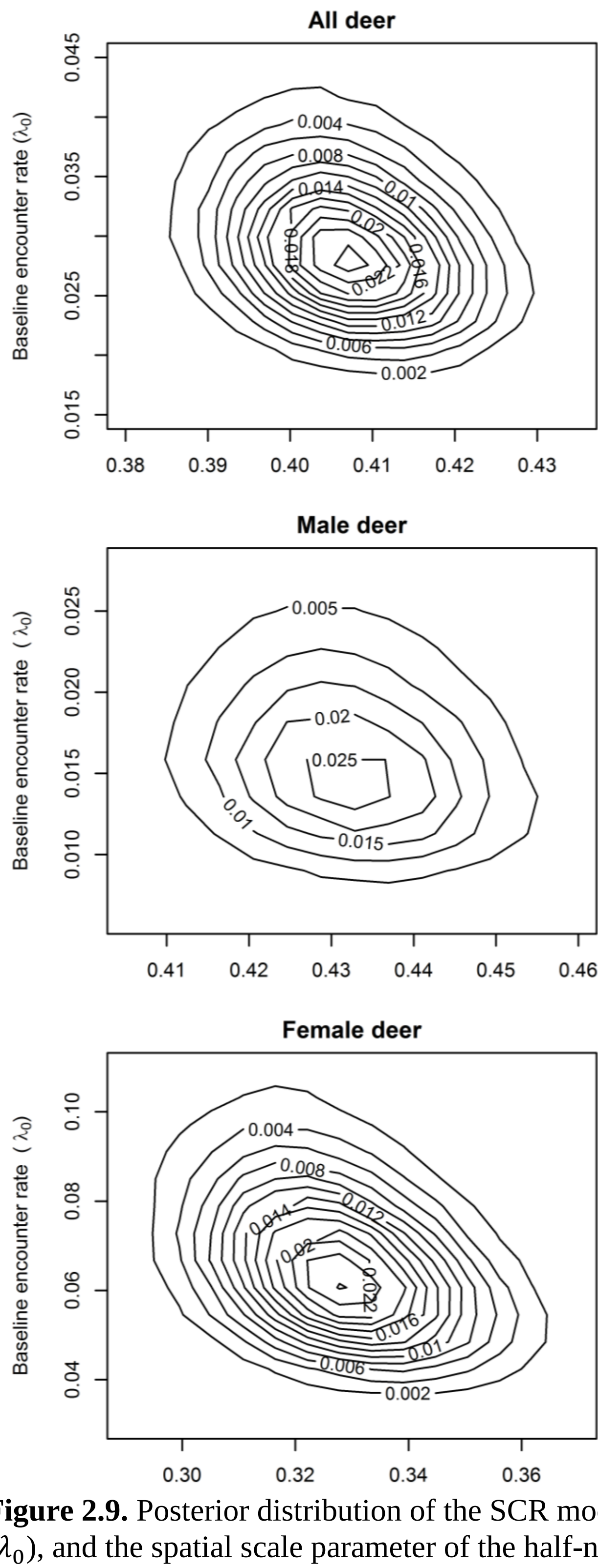

Figure 2.9. Posterior distribution of the SCR model parameters (baseline encounter rate (λ_0), and the spatial scale parameter of the half-normal detection function (σ)) from the analysis of data from GPS-collared male, female, and all captured white-tailed deer (*Odocoileus virginianus*) in southwestern Georgia, USA (2016). The posterior distribution was used as a prior in the analysis of the data on unmarked individuals.

Table 2.1. Jacobson baited survey density (deer/km^2) estimates of total population, female, and male white-tailed deer (*Odocoileus virginianus*) for 2014, 2015, and 2016 from study sites in southwestern Georgia, USA.

Site / Year	Unique Males	Total *D* (km2)	Female *D* (km^2)	Male *D* (km2)
A / 2014	208	42.8	22.0	17.1
A / 2015	202	38.0	17.2	16.6
B / 2014	83	19.6	10.1	8.3
B / 2015	90	25.7	15.9	9.0
C / 2014	79	28.3	17.0	7.9
C / 2015	91	33.3	22.3	9.1
D / 2015	72	17.0	9.0	7.2

Table 2.2. Number of photographs collected for male, female, and all white-tailed deer (*Odocoileus virginianus*) during baited and unbaited (passive) camera surveys in 2014, 2015, and 2016 from study sites in southwestern Georgia, USA.

	Site A	Site B	Site C	Site D
All deer				
2014 baited (September)	21087	10503	13843	N/A
2014 passive (October)	3237	1419	1413	N/A
2015 baited (September)	26522	12010	18059	6455
2015 passive (October)	3565	1166	366	517
2016 passive (October)	5618	N/A	1252	1194
Male deer				
2014 baited (September)	8007	3986	3521	N/A
2014 passive (October)	988	383	181	N/A
2015 baited (September)	10364	4054	4299	2531
2015 passive (October)	1099	221	47	148
2016 passive (October)	1221	N/A	193	187
Female deer				
2014 baited (September)	10253	4875	7598	N/A
2014 passive (October)	1091	687	768	N/A
2015 baited (September)	10722	7164	10543	3148
2015 passive (October)	1103	716	222	246
2016 passive (October)	2107	N/A	744	583

Table 2.3. Distance sampling estimates for white-tailed deer (*Odocoileus virginianus*) in 2015 from two study sites in southwestern Georgia, USA.

Site / Year	Model	Density (km^2)	LCL	UCL	AIC	Delta AIC
C / 2015	Half-normal	17.9	11.7	27.5	598.820	1.640
	Hazard-rate	16.7	11.0	25.5	597.180	0.000
D / 2015	Half-normal	8.5	5.8	12.3	495.410	0.000
	Hazard-rate	9.4	5.2	16.9	496.810	1.400

Table 2.4. Estimates of the posterior means for a marked SCR analysis of male white-tailed deer (*Odocoileus virginianus*) including abundance (*N*), density (*D*), baseline encounter probabilities for both passive (p_0 [passive]) and baited cameras (p_0 [baited]), and the scaling parameter of the half-normal detection function (σ) from summer (2015) camera surveys in southwestern Georgia, USA.

Site	Parameter	Mean	SD	2.5%	97.5%
A	*N*	261.474	8.925	247.000	282.000
	D (km^2)	6.345	0.217	5.993	6.843
	p_0[passive]	0.028	0.002	0.023	0.033
	p_0[baited]	0.673	0.017	0.641	0.707
	σ	0.338	0.004	0.331	0.345
B	*N*	138.577	8.041	124.000	155.000
	D (km^2)	3.979	0.231	3.560	4.450
	p_0[passive]	0.020	0.003	0.014	0.027
	p_0[baited]	0.370	0.021	0.331	0.411
	σ	0.375	0.009	0.358	0.394
C	*N*	168.446	14.598	141.000	198.000
	D (km^2)	5.694	0.494	4.767	6.693
	p_0[passive]	0.028	0.004	0.022	0.036
	p_0[baited]	0.420	0.023	0.378	0.467
	σ	0.487	0.012	0.463	0.510
D	*N*	104.585	8.606	89.000	123.000
	D (km^2)	3.063	0.252	2.606	3.602
	p_0[passive]	0.022	0.004	0.015	0.030
	p_0[baited]	0.457	0.025	0.409	0.506
	σ	0.443	0.012	0.421	0.467

Table 2.5. Estimates of the posterior means for white-tailed deer (*Odocoileus virginianus*) abundance (N), baseline encounter rate (λ_0), the scaling parameter of the half-normal detection function (σ), and density (D) from an unmarked spatial capture-recapture analysis from study sites in southwestern Georgia, USA (2014, 2015, and 2016).

Site / Year	Parameter	Mean	SD	2.5%	97.5%
	N	553.479	98.646	382.000	772.000
A / 2014	λ_0	0.041	0.007	0.036	0.057
	σ	0.399	0.010	0.380	0.418
	D (km^2)	17.335	3.090	11.964	24.179
	N	616.492	122.815	526.000	875.000
A / 2015	λ_0	0.035	0.007	0.024	0.052
	σ	0.401	0.010	0.382	0.420
	D (km^2)	19.309	3.847	12.622	27.405
	N	535.399	96.388	370.000	748.00
A / 2016	λ_0	0.056	0.010	0.039	0.079
	σ	0.395	0.009	0.377	0.413
	D (km^2)	16.769	3.019	11.589	23.428
	N	554.676	101.027	382.000	779.000
B / 2014	λ_0	0.029	0.005	0.020	0.040
	σ	0.410	0.010	0.388	0.425
	D (km^2)	14.725	2.682	10.141	20.680
	N	338.724	66.644	226.000	483.000
B / 2015	λ_0	0.039	0.007	0.027	0.054
	σ	0.401	0.009	0.384	0.421
	D (km^2)	8.992	1.769	6.000	12.822
	N	342.343	67.209	231.000	487.000
C / 2014	λ_0	0.031	0.006	0.021	0.045
	σ	0.404	0.010	0.385	0.423
	D (km^2)	14.783	2.902	9.975	21.029
	N	208.162	47.913	127.000	315.000
C / 2015	λ_0	0.035	0.001	0.028	0.050
	σ	0.402	0.009	0.384	0.422
	D (km^2)	8.989	2.069	5.484	13.602
	N	370.998	70.778	251.000	529.000
C / 2016	λ_0	0.036	0.007	0.025	0.050
	σ	0.402	0.010	0.384	0.421
	D (km^2)	16.020	3.056	10.838	22.843
	N	375.135	73.623	251.000	541.000
D / 2015	λ_0	0.032	0.006	0.022	0.045
	σ	0.405	0.009	0.387	0.424
	D (km^2)	10.334	2.028	6.914	14.903
	N	458.825	83.879	314.000	643.000
D / 2016	λ_0	0.029	0.005	0.021	0.040
	σ	0.406	0.010	0.388	0.425
	D (km^2)	12.639	2.311	8.650	17.712

Table 2.6. Estimates of the posterior means for male white-tailed deer (*Odocoileus virginianus*) abundance (N), baseline encounter rate (λ_0), the scaling parameter of the half-normal detection function (σ), and density (D) from an unmarked spatial capture-recapture analysis from study sites in southwestern Georgia, USA (2014, 2015, and 2016).

Site / Year	Parameter	Mean	SD	2.5%	97.5%
	N	196.846	59.163	109.000	337.000
A / 2014	λ_0	0.044	0.013	0.023	0.072
	σ	0.417	0.012	0.394	0.441
	D (km^2)	6.165	1.853	3.414	10.555
	N	219.133	72.507	115.000	401.000
A / 2015	λ_0	0.035	0.011	0.017	0.061
	σ	0.420	0.012	0.397	0.444
	D (km^2)	6.863	2.271	3.602	12.559
	N	227.337	76.369	120.000	407.000
A / 2016	λ_0	0.048	0.015	0.024	0.081
	σ	0.418	0.011	0.396	0.441
	D (km^2)	7.120	2.392	3.758	12.747
	N	331.181	99.564	179.000	570.000
B / 2014	λ_0	0.016	0.005	0.009	0.027
	σ	0.431	0.016	0.408	0.454
	D (km^2)	8.792	2.643	4.752	15.132
	N	114.087	31.556	63.000	185.000
B / 2015	λ_0	0.039	0.010	0.024	0.062
	σ	0.425	0.011	0.404	0.448
	D (km^2)	3.029	0.838	1.672	4.911
	N	90.004	29.734	47.000	157.000
C / 2014	λ_0	0.023	0.007	0.012	0.039
	σ	0.427	0.012	0.404	0.450
	D (km^2)	3.887	1.284	2.030	6.780
	N	72.491	27.840	33.000	141.000
C / 2015	λ_0	0.017	0.005	0.009	0.027
	σ	0.431	0.019	0.408	0.455
	D (km^2)	3.130	1.202	1.425	6.089
	N	104.460	33.205	55.000	181.000
C / 2016	λ_0	0.032	0.009	0.018	0.053
	σ	0.426	0.012	0.403	0.449
	D (km^2)	4.511	1.434	2.375	7.816
	N	191.813	64.904	97.000	346.000
D / 2015	λ_0	0.019	0.006	0.010	0.032
	σ	0.430	0.012	0.408	0.454
	D (km^2)	5.284	1.788	2.672	9.531
	N	255.868	76.091	136.000	434.000
D / 2016	λ_0	0.016	0.005	0.009	0.026
	σ	0.431	0.012	0.409	0.459
	D (km^2)	7.048	2.096	3.746	11.955

Table 2.7. Estimates of the posterior means for female white-tailed deer (*Odocoileus virginianus*) abundance (N), baseline encounter rate (λ_0), the scaling parameter of the half-normal detection function (σ), and density (D) (km^2) from an unmarked spatial capture-recapture analysis from study sites in southwestern Georgia, USA (2014, 2015, and 2016).

Site / Year	Parameter	Mean	SD	2.5%	97.5%
	N	140.590	30.438	90.000	207.000
A / 2014	λ_0	0.132	0.029	0.084	0.193
	σ	0.294	0.014	0.267	0.324
	D (km^2)	4.403	0.953	2.819	6.483
	N	121.767	28.636	75.000	188.000
A / 2015	λ_0	0.198	0.045	0.116	0.296
	σ	0.267	0.013	0.244	0.293
	D (km^2)	3.814	0.897	2.349	5.888
	N	168.097	32.420	113.000	240.000
A / 2016	λ_0	0.195	0.037	0.131	0.275
	σ	0.277	0.012	0.254	0.302
	D (km^2)	5.265	1.015	3.539	7.517
	N	188.348	42.615	116.000	283.000
B / 2014	λ_0	0.078	0.017	0.050	0.117
	σ	0.312	0.015	0.283	0.341
	D (km^2)	5.000	1.131	3.079	7.513
	N	145.596	36.833	86.000	229.000
B / 2015	λ_0	0.081	0.019	0.050	0.122
	σ	0.311	0.015	0.283	0.342
	D (km^2)	3.865	0.978	2.283	6.080
	N	136.495	30.505	88.000	206.000
C / 2014	λ_0	0.088	0.020	0.054	0.129
	σ	0.312	0.015	0.285	0.343
	D (km^2)	5.894	1.317	3.800	8.895
	N	77.219	21.613	43.000	126.000
C / 2015	λ_0	0.095	0.021	0.061	0.141
	σ	0.315	0.014	0.288	0.344
	D (km^2)	3.334	0.933	1.857	5.441
	N	133.032	28.683	85.000	196.000
C / 2016	λ_0	0.127	0.027	0.084	0.189
	σ	0.296	0.014	0.270	0.325
	D (km^2)	5.744	1.239	3.670	8.463
	N	148.444	34.972	90.000	226.000
D / 2015	λ_0	0.062	0.013	0.040	0.091
	σ	0.327	0.015	0.298	0.357
	D (km^2)	4.089	0.963	2.479	6.226
	N	95.771	24.1132	55.000	150.000
D / 2016	λ_0	0.062	0.013	0.040	0.092
	σ	0.327	0.015	0.299	0.358
	D (km^2)	2.638	0.665	1.515	4.132

Table 2.8. Estimates of the posterior means, standard deviations (SD), and 95% confidence intervals, for captured white-tailed deer (*Odocoileus virginianus*) baseline encounter rate (λ_0), and the scaling parameter of the half-normal detection function (σ) from male, female, and all captured deer combined using a spatial capture-recapture framework from study sites in southwestern Georgia, USA (2016).

	Parameter	Mean	SD	2.5%	97.5%
All deer	λ_0	0.029	0.005	0.020	0.041
	σ	0.407	0.010	0.389	0.426
Male	λ_0	0.017	0.005	0.009	0.027
	σ	0.432	0.012	0.410	0.456
Female	λ_0	0.067	0.015	0.041	0.099
	σ	0.328	0.015	0.299	0.359

Table 2.9. Variance-covariance matrix for the baseline encounter rate (λ_0) and the scaling parameter of the half-normal detection function (σ) from male, female, and all captured white-tailed deer (*Odocoileus virginianus*) combined using a spatial capture-recapture framework from study sites in southwestern Georgia, USA (2016).

		σ	λ_0
All deer	σ	0.0005454336	-0.0010916870
	λ_0	-0.0010916870	0.0312614260
Male	σ	0.0007460860	-0.0014846300
	λ_0	-0.0014846300	0.0831066700
Female	σ	0.0021118550	-0.0039268920
	λ_0	-0.0039268920	0.0508729230

APPENDIX: JAGS model for estimating probability of detection parameters of captured white-tailed deer (*Odocoileus virginianus*).

All captured deer combined:

```
model {
lam0 ~ dunif(0,1)
sigma ~ dunif(0,2)
for(i in 1:nDeer) {
  s[i,1] ~ dunif(xlim[1], xlim[2])
  s[i,2] ~ dunif(ylim[1], ylim[2])
   for(k in 1:nTelemLocs[i]) {
     u[k,1,i] ~ dnorm(s[i,1], 1/sigma^2)
     u[k,2,i] ~ dnorm(s[i,2], 1/sigma^2)}
  for(j in 1:nTraps) {
    d[i,j] <- sqrt((s[i,1]-x[j,1])^2 +
               (s[i,2]-x[j,2])^2)
    lam[i,j] <- lam0*exp(-d[i,j]^2/(2*sigma^2))
    p[i,j] <- 1-exp(-lam[i,j]))
    for(k in 1:nOcc) {
      y[i,j,k] ~ dbern(p[i,j]*oper[j,k])}}
  inBuff[i] <- 1-prod(d[i,]>buffer)
  ones[i] ~ dbern(inBuff[i])}}
```

Sex specific captured deer deer:

```
model {
lam0[1] ~ dunif(0,1) # Males
lam0[2] ~ dunif(0,1) # Females
sigma[1] ~ dunif(0,2) # Males
sigma[2] ~ dunif(0,2) # Females
for(i in 1:nDeer) {
  s[i,1] ~ dunif(xlim[1], xlim[2])
  s[i,2] ~ dunif(ylim[1], ylim[2])
  for(k in 1:nTelemLocs[i]) {
     u[k,1,i] ~ dnorm(s[i,1], 1/sigma[sex[i]]^2)
     u[k,2,i] ~ dnorm(s[i,2], 1/sigma[sex[i]]^2)}
  for(j in 1:nTraps) {
    d[i,j] <- sqrt((s[i,1]-x[j,1])^2 +
               (s[i,2]-x[j,2])^2)
    lam[i,j] <- lam0[sex[i]]*exp(-d[i,j]^2/(2*sigma[sex[i]]^2))
     p[i,j] <- 1-exp(-lam[i,j])
    for(k in 1:nOcc) {
      y[i,j,k] ~ dbern(p[i,j]*oper[j,k]) }}
  inBuff[i] <- 1-prod(d[i,]>buffer)
  ones[i] ~ dbern(inBuff[i])}}
```

CHAPTER 3

EFFECTS OF BAIT ON MALE WHITE-TAILED DEER RESOURCE SELECTION

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ABSTRACT

The use of bait can alter movement patterns of white-tailed deer (*Odocoileus virginianus*), typically with the desired outcome of increased harvest susceptibility, viewing opportunities, or detection probability for camera surveys. The effect of baiting on deer space use has been studied using telemetry-based methods, with varying results. Although telemetry studies allow for inferences about resource selection within home ranges (third-order selection), they provide no information about spatial variation in density, which is the result of second-order selection. Recent advances in spatial capture-recapture (SCR) techniques allows exploration of second and third-order selection simultaneously using non-invasive methods such as camera traps. We fit SCR models to data from baited and un-baited cameras in Southwestern Georgia to assess the effects of bait on second and third order selection. We found little evidence of second order selection during late summer or early winter surveys, when baited camera surveys are typically conducted. However, we found strong evidence for third order selection when bait was present, indicating that resource selection within home ranges is affected by bait. Changes in space use when concentrated resources are present could enhance disease transmission, change harvest susceptibility by concentrating space use to a specific area, and potentially bias the outcome of baited camera survey results.

KEY WORDS: camera survey, Georgia, *Odocoileus virginianus*, space-use, spatial capture-recapture

INTRODUCTION

The use of bait for attracting white-tailed deer (*Odocoileus virginianus*) is a complex issue encompassing potential risks and benefits. The use of bait may enhance disease transmission (Eve 1981, Thorne and Herriges 1992, Schmitt et al. 1997, Brown and Cooper 2006, Sorensen et al. 2014), impact non-target species (Bowman et al. 2015), and potentially change rates of hunter harvest success and satisfaction (Langenau et al. 1985, Wisconsin BWM 1993, Michigan DNR 1999, Frawley 2000). Many of the negative effects associated with baiting result from altered movement patterns of deer (Synatzke 1981, Jacobson and Darrow 1992, Kilpatrick and Stober 2002, Garner 2001).

Several studies have concluded baiting has little effect on the home range size of white-tailed deer (Darrow 1993, Williams and DeNicola 2000, Kilpatrick and Stober 2002, Beaver 2017), but baiting can affect space use and resource selection (Murden and Risenhoover 1993). These studies have used various methods to assess the effects of bait on resource selection, but most have focused on a single spatial scale. Resource selection, however, is a hierarchical process, often involving the selection of home ranges within a landscape (second order), and then the (third order) selection of resources within a home range (Johnson 1980). Ignoring either of these levels of selection inhibits the ability to assess the effects of bait on deer spatial distribution.

Baiting likely congregates deer in closer proximity than would normally occur under natural foraging conditions, increasing the chance of transmission of diseases such as chronic wasting disease and bovine tuberculosis through deer-deer contact (Eve 1981, Thorne and Herriges 1992, Schmitt et al. 1997, Garner 2001) as well as indirect contact from contaminated bait sites (Palmer et al. 2001, Schmitt et al. 2002). Baiting is legal to some extent in 26 of the 48 contiguous states (Adams and Ross 2017). However, Best Management Practices for management of chronic wasting disease include elimination of "baiting and feeding of all wild cervids using regulatory mechanisms such as jurisdictional bans" (Gillin and Mawdsley 2018). Continued spread of CWD will likely lead to additional restrictions of the use of bait for hunting white-tailed deer.

The baited camera survey (Jacobson et al. 1997) is a widely used method to survey deer population, despite apparent violation of the assumption of equal detectability between sexes and among age classes of deer (McCoy et al. 2011, Rowcliffe et al. 2011, Weckel et al. 2011, Beaver 2017). Baiting effects on the spatial distributions of home ranges or within home range space use would lead to downstream biases associated with the methodology. Density estimates would be inflated if bait concentrates home ranges into a smaller area (second-order selection) than when bait is absent. Similarly, differential use of bait sites between the sexes (third-order selection) would violate assumptions of equal visitation rates and impact density estimates. Given these potential biases, further investigations into second and third-order selection of deer in the presence of bait sites is warranted.

Spatially explicit capture-recapture models (hereafter: SCR) allow for simultaneous inference about second-order selection and third-order selection (Royle et al. 2013). In the SCR framework, second order selection is assessed by modeling spatial variation in density. If density is uniform across a landscape, then the distribution of home ranges is not the result of selection. Conversely, departures from spatial uniformity in density provide evidence of second-order selection. Third-order selection is assessed by modeling encounter probability as a function of trap-specific covariates while accounting for the distance between home range centers and trap locations (Royle et al. 2013). If animals are not exhibiting resource selection within home ranges, encounter rates at traps should not be affected by trap-level covariates. In addition to providing assessments of both second and third order selection, SCR models yield estimates of home range size as well as abundance, which is a primary objective of many camera surveys.

Our objective was to assess the impacts of bait on second- and third-order selection of white-tailed deer. Our assessment was used to evaluate how bait might affect disease transmission, harvest availability, and camera-based survey methods used to estimate population parameters. We also evaluated how the effect of bait on resource selection changes seasonally because the seasonal variation in selection could impact inferences from camera-based surveys.

STUDY AREA

The study area included three properties in Southwestern Georgia, USA, in Worth (31.5282° N, 83.8897° W) and Baker Counties (31.2816° N, 84.4803° W) (Figure 2.1). The properties ranged in size from approximately 1,600 to 12,000 ha with varying deer densities and management regimes. Habitat types consisted of longleaf pine (*Pinus palustris*) savannas, scattered hardwoods (primarily oaks; *Quercus* spp.), riparian zones, planted loblolly pine (*Pinus taeda*) stands, wildlife openings, and depressional wetlands. Properties 2 and 3 had a long history of intensive habitat management for the primary objective of promoting high densities of Northern Bobwhite (*Colinus virginianus*). Property 1 was managed intensively for white-tailed deer, and unlike the other two properties, had a long-term supplemental deer feeding program. Typical landscape management for all three properties (varying to some degree) included frequent prescribed fire, wildlife food plots, predator trapping, timber management, roller chopping, mowing, and seasonal disking.

METHODS

We conducted camera surveys in the summer (August – September) of 2015 and winter (January – February) of 2016, which included both baited and un-baited (hereafter: passive) cameras. We used unique antler configurations to identify males and a SCR analytical approach to investigate the seasonal effects of baiting on second and third order selection. We established four 1000 ha camera trapping sites within the three properties. Property 1 contained site A, property 2 contained site B, and property 3 contained sites C and D. Within each site, 49 passive cameras (1 camera per approximately 20 ha) and 25 baited cameras (1 camera per approximately 40 ha) were designated within a systematic grid approach. Baited cameras were operated and distributed according to the methodology commonly associated with a baited camera survey array (Jacobson et al. 1997), however we did not assess the baited camera survey estimation approach and instead evaluated space use and resource selection using a spatial capture-recapture framework. Property 1 had a long history (>10 years) of baited camera use, therefore, we opted to use the pre-established 29 baited camera locations for this property (1 camera per approximately 50 ha) and placed the same passive camera array (n=49) within the pre-establish baited camera array. Unlike the other properties, the majority of baited camera locations were associated with long term tripod gravity feeders, containing corn or protein pellet supplements, however, feeders remained empty while the baited camera surveys were conducted.

We secured baited cameras on trees ~1.5 m from ground level near the center of each grid cell and placed shelled corn approximately 5 m from each baited camera for all sites. Baited cameras were operated for two weeks following a 1-week pre-baiting period, simulating the baited camera survey protocol of Jacobson et al. (1997). We placed the passive cameras within 200 m of the centroid of each grid cell, on trees or metal fence posts at the same height as baited cameras. To place passive cameras, we searched a 200-meter buffer surrounding the centroid of each cell for the highest level of deer activity, such as deer trails and movement corridors, to optimize the chances of capturing images of deer.

We sampled for two weeks in August-September 2015 (late summer), prior to the onset of deer season, and again for two weeks in January-February 2016 (early winter), immediately following the conclusion of the 2015-2016 Georgia deer season. All cameras operated for 24-hours per day during the study period. Baited cameras were set with a 5-min delay between successive photographs while passive cameras were set to a 10-sec delay between image captures. We checked passive camera sites once during the two-week period and visited the baited cameras twice per week to replenish bait if needed. We used the infrared camera model Uway VH200HD (HCO, Duluth GA, USA).

Spatial Model

We used unique antler characteristics from both baited and passive cameras to identify individual males within each site and generate capture histories of all identified male deer. We defined each occasion within the study period as one 24-hour period. We generated a spatial raster layer representing distance to bait (Figure 2.2). Each raster cell measured 180 x 180 m and the extent was defined by a 1.5-km buffer surrounding each camera array. The 1.5-km buffer was chosen to define a state-space for each site such that the probability of detecting an individual near the border of the region was negligible. This is standard practice in SCR models (Royle et al. 2014). The areas of the four regions were: 41.21 km^2, 34.83 km^2, 29.58 km^2, and 34.15 km^2 for sites A-D respectively.

To assess second-order selection, we modeled spatial variation in density using distance to bait as a spatial covariate. In SCR models, density is characterized by a spatial point process for the activity centers of the N individuals in the population (Efford 2004, Borchers and Efford 2008, Royle and Young 2008, Royle et al. 2014). An activity center is the average location of an individual during the sampling period. For deer with stationary symmetric home ranges, the activity center is the home range center. We modeled density of activity centers at location $\boldsymbol{s}$ with a log-linear function:

$$\mu(\boldsymbol{s}) = \exp(\beta_0 + \beta_1 \text{DISTBAIT}(\boldsymbol{s}) \times w) \times \text{ pixelArea}$$

This effect of bait (β_1) can be interpreted in the same way as in standard GLM approaches (Royle et al. 2014). We predicted that β_1 would be less than zero, indicating deer density decreases as distance to bait increases. We did not assess the unrealistic scenario of positive correlation between distance to bait and density. In addition to estimating the effect of bait, we computed the probability that bait had no effect by including an indicator variable w, which would equal 1 if the data strongly suggest that a bait effect is present. Therefore, an effect of bait was considered significant if $Pr(w = 0) < 0.05$, similar to the frequentist p-value approach.

We used a Bernoulli model for encounter histories and modeled the encounter rate as a function of the distance between a deer's activity center and a camera trap location. We used the standard half-normal model for the encounter function:

$$p_{ij} = p_0 \exp\left(-\frac{d_{ij}^2}{2\sigma^2}\right)$$

where p_0 is the encounter probability when the distance (d_{ij}) between an activity center and a camera trap is 0. We estimated separate p_0 parameters for baited and passive cameras to determine if bait affected third-order selection. Detection probability was set to 0 on occasions for which a camera was not operational due to camera malfunctions. We predicted that p_0 would be greater at baited cameras than passive cameras because deer actively select sites with bait within their home ranges. The parameter σ is the spatial scale parameter describing how encounter probability decreases with increasing distance from a camera site and a deer's home range center. The scale parameter can be used as a measure of home range size because deer with larger home ranges can be detected further from their home range centers than deer with smaller home ranges.

We used data augmentation and a Bayesian approach for statistical inference (Royle et al. 2014). We used vague prior distributions for all parameters (Appendix 1). We fit the model in R (version 3.3.1) with the package rjags (Plummer 2016), which interfaces with the Gibbs sampler software JAGS (Plummer 2003). We generated two Markov chains each representing 30,000 posterior samples, and we discarded the first 1000 as burn-in. Convergence was graphically assessed and evaluated using the Gelman-Rubin statistic (Gelman and Rubin 1992).

RESULTS

We collected 19,904 photographs of 470 uniquely identified males for the summer survey, and 20,019 photographs of 423 unique males during the winter survey with a mean number of sampling occasions of 13 (24-h periods) for both seasons (Table 2.1). Summer baited cameras produced 40 times more images of antlered males than cameras operated during the summer passive period, and winter baited cameras produced 50 times more images as winter passive cameras. We found little evidence that baiting affected second-order selection of male white-tailed deer (Figure 2.3 and 2.4). The only site at which an effect of bait was observed was at site A, and the effect was only evident during the summer survey. The effect size at this site was more than three times greater than any of the other effects (Figure 2.3). Overall, the effect of bait on second order selection was weaker during the winter than during the summer (Figures 2.3 and 2.4).

The encounter probability (p_0), a measure of third order selection, varied among sites and between seasons (Figure 2.5 and Table 2.2). Encounter probabilities were greatest in summer for both baited and passive cameras, and we found strong evidence for third order selection within our study sites. Male deer were 19.6 times more likely to be encountered at a baited site within their home range than passive sites during the summer survey and 23.5 times more likely to be encountered at baited sites than passive sites during the winter surveys. In addition, we found males were 1.6 times more likely to be encountered at baited sites during the summer surveys when compared to winter surveys, and twice as likely to be encountered at passive sites during the summer when compared to passive sites in the winter (Figure 2.6).

Estimates of σ, the spatial scale parameter associated with home range size, were smallest in the summer averaging 0.411 km (95% CI: 0.393 – 0.429) and nearly doubled in the winter to 0.720 km (95% CI: 0.700 – 0.753), suggesting an expansion in home range size during the winter surveys at our study sites. Additionally, while not a primary objective for our study, our SCR analysis did produce estimates of *N*. For all sites, we found a decrease in abundance of antlered males after the hunting season as expected (Table 2.2).

DISCUSSION

Our results suggest that baited camera surveys have little influence on spatial variation in antlered male density within our study sites and did not appear to affect the spatial distribution of home ranges on the landscape. However, we did find strong evidence of third-order selection, with deer selecting baited sites within their home ranges at a much higher rate than unbaited passive sites. To our knowledge, this is the first attempt to simultaneously assess the effects of bait on multiple orders of selection within a deer population.

The only evidence of a relationship between male deer spatial distributions (second-order selection) and baited camera sites occurred within the property with a long history of deer management, including spring and summer supplemental feeding programs. However, this association was only apparent during the summer survey of this site, and the effect was significantly reduced during the winter survey after intensive feeding programs were stopped in September, four months prior. Altered spatial distributions of home ranges occurs in agricultural regions when abundant resources are available for prolonged periods (Vercauteren and Hyngstrom 1998, Walter et al. 2009), and the five-month supplemental feeding program during spring and summer associated with baited camera sites likely explains our findings of altered spatial distributions on site A.

Although the effect of bait on spatial variation in density was minimal, we did find strong evidence for third order selection, which is consistent with other studies (Kilpatrick and Stober 2002, Beaver 2017). Beaver (2017) reported that bait affected core area use by radioinstrumented male deer more than other spatial variables such as canopy cover during a 12-day baited camera survey. Similarly, Kilpatrick and Stober (2002) found that radioinstrumented deer did not alter spatial distributions of home ranges after bait was applied, but did alter space use when bait was present inside of pre-existing home ranges. Therefore, our findings are consistent with other studies and the use of cameras and SCR applications may simplify the ability to determine second and third order selection simultaneously without the need for telemetry-based studies.

Greater use of bait sites in the winter is likely the result of depleted fat reserves and reduced body condition from energy exertion associated with rutting behavior (Moen 1976, Warren et al. 1981, Beier and McCullough 1990). Other studies have similarly documented an increase in bait use during the post breeding season when compared to summer or fall (Kilpatrick and Stober 2002, Stone 2017). The greater encounter rates during the summer compared to winter is likely due to smaller summer home ranges of deer within our study sites (Nixon et al. 1991, Brinkham et al. 2005). At all sites, our spatial model estimated the σ movement parameter to be larger in the winter compared to its summer survey, nearly double in all comparisons, indicating that the individuals of our study have smaller home ranges in the summer compared to winter consistent with the studies reviewed by Marchinton and Hirth (1984). From their work in agricultural landscapes, Nixon et al. (1991) and Brinkham et al. (2005) reported a more than doubling of deer home range size in the winter vs summer. This is consistent with our findings of the agricultural area of our study sites in southwestern Georgia, where cover and forage are abundant in the summer months, likely resulting in smaller summer ranges.

Seasonal changes in bait site use as well as home range sizes could lead to biases associated with the Jacobson et al. (1997) baited camera survey method. Accurate estimates derived from these baited camera surveys rely heavily on the assumption of equal visitation rates of the sexes. While we did not investigate the effects of bait on resource selection and space use of females, multiple studies have indicated differences in bait use among males and females (McCoy et al. 2011, Beaver 2017). Extending our SCR approach to include both females and males could enhance our understanding of these apparent biases. Our preliminary findings suggest that the long-term feeding stations at site A may have affected home range distribution, considering the effect of bait on second-order selection was not apparent after the fall/winter cessation of supplemental feeding. Density estimates could also be inflated by deer using bait sites on the periphery of the camera arrays by having home ranges that overlap the boundary of the area being surveyed based on the camera density used. In addition, larger home range sizes during our winter surveys would suggest using the same camera densities as summer surveys may not be practical, and larger spacing in the winter when home ranges expand should be considered.

Our findings of strong effects on third-order selection likely indicate deer increase space use at baited cameras, leading to higher instances of deer-to-deer contact when bait is present. The effect of bait on enhanced deer-to-deer contact and increased concentrations would be consistent with the findings of Garner (2001) and could ultimately lead to higher transmission rates of diseases in susceptible areas (Miller 2002, Williams et al. 2002). Direct contact between deer is not uncommon in natural settings where bait sites are not present, however these behaviors are typically associated with small social groups (Hawkins and Klimstra 1970, Marchinton and Hirth 1984), and increased concentrations of deer by means of altered second-order selection could increase direct and indirect contact of deer at greater rates than would normally occur (Eve 1981, Thorne and Herriges 1992, Schmitt et al. 1997, Garner 2001).

Changes in space use within home-range, leading to greater encounter rates at bait sites, would also suggest deer may be more susceptible to harvest when using bait. However, we did not compare diurnal vs nocturnal activity and our study was conducted outside of the hunting season. Several studies have demonstrated that baiting increases nocturnal activity of deer when visiting feeding sites (Synatzke 1981, Jacobson and Darrow 1992, Stone 2017). The use of bait by males during the breeding season is greatly reduced (Stone 2017), therefore when hunting is concurrent with the breeding season, baiting may not alter susceptibility. However, if baiting coincides with post-breeding season recovery of bucks, enhanced use of bait sites by males may increase susceptibility during this time period.

MANAGEMENT IMPLICATIONS

Our results indicate that bait does not strongly affect spatial variation in density, but it does cause deer to concentrate space use within home ranges where bait is present. Baiting likely has no effect on deer which have home ranges located outside of the baited areas, which should be taken into consideration when population control is a factor. In addition, increased bait site use by males could enhance harvest susceptibility during specific times of the hunting season when males are highly respondent to the presence of bait. When considering disease transmission, we found little evidence of an effect on second-order selection, other than one site with a long history of supplemental feeding during the spring and summer months. However, our findings of a strong effect on third-order selection could lead to greater transmission rates from increased visitation to a concentrated resource such as corn bait sites. Our results suggest banning practices associated with baiting and feeding of deer is an appropriate response to limit disease spread.

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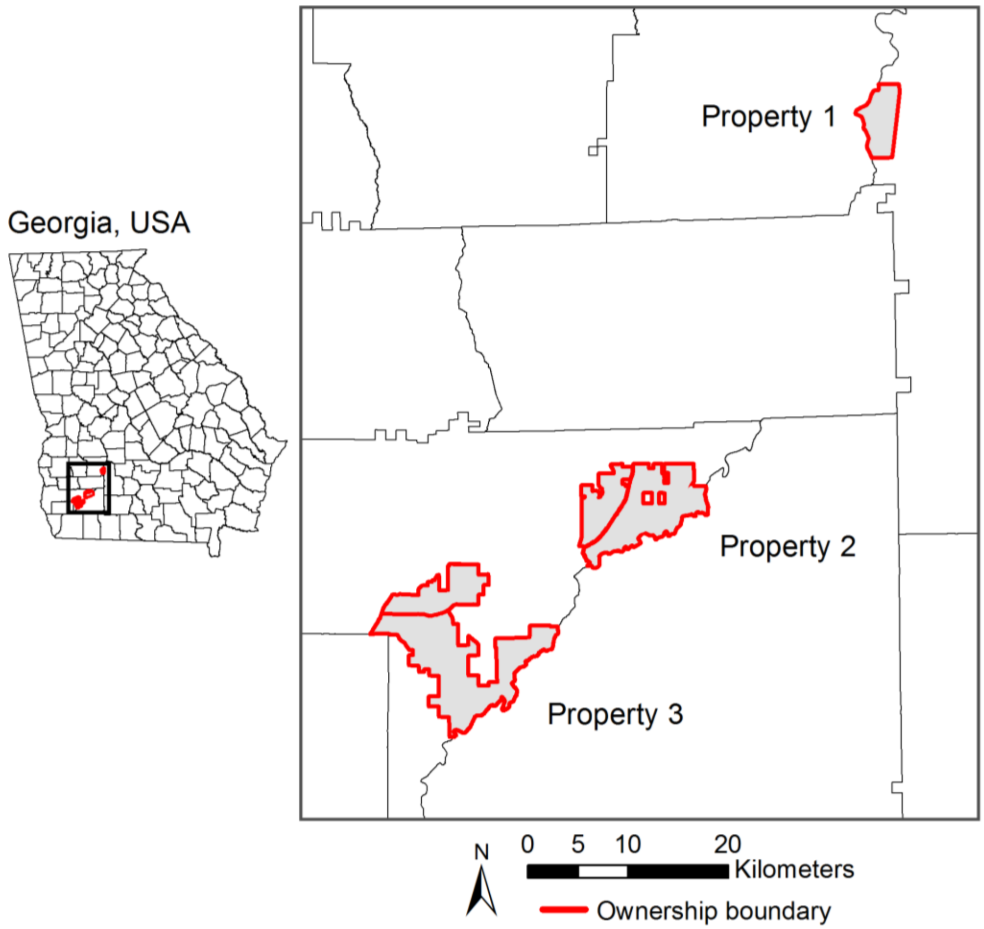

Figure 3.1. Properties in southwestern Georgia, USA, used to evaluate the effects of bait on male white-tailed deer (*Odocoileus virginianus*) resource selection in 2015-16. Property 1 contains camera array site A, property 2 contains site B, and property 3 contains sites C and D.

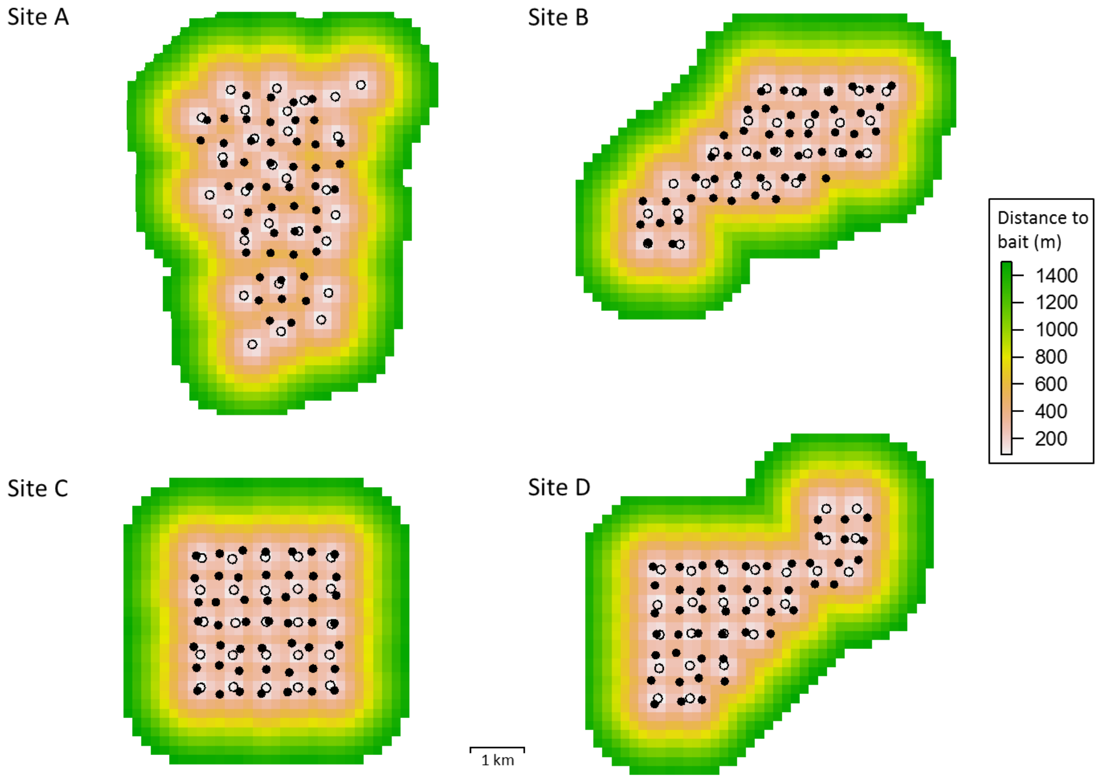

Figure 3.2. Raster density surfaces of each site (A, B, C, and D) located in southwestern Georgia, USA, indicating distance from the spatial covariate, bait. Cameras were operated in the summer 2015 and winter of 2016 to evaluate the effects of bait on male white-tailed deer (*Odocoileus virginianus*) resource selection. Open circles represent baited cameras and closed circles represent passive cameras.

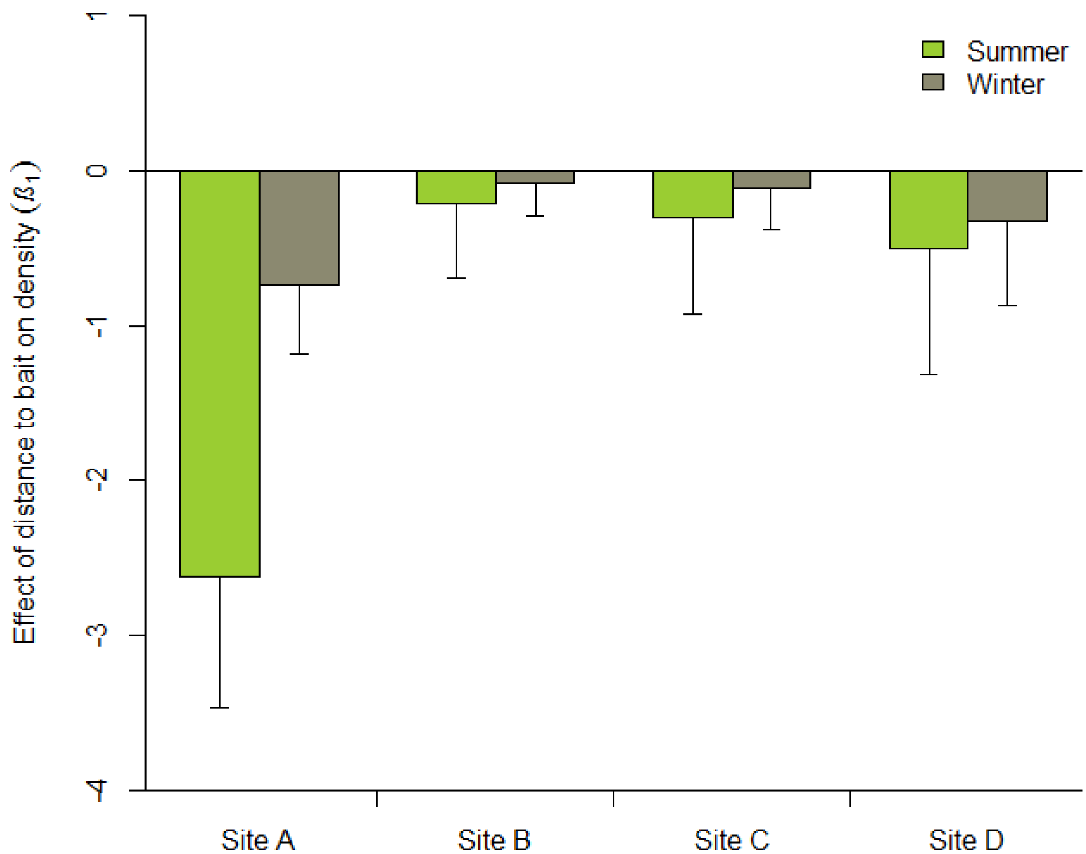

Figure 3.3. The effect of distance to bait on adult male white-tailed deer (*Odocoileus virginianus*) density distributions within four sites of summer 2015 and winter 2016 in southwestern Georgia, USA.

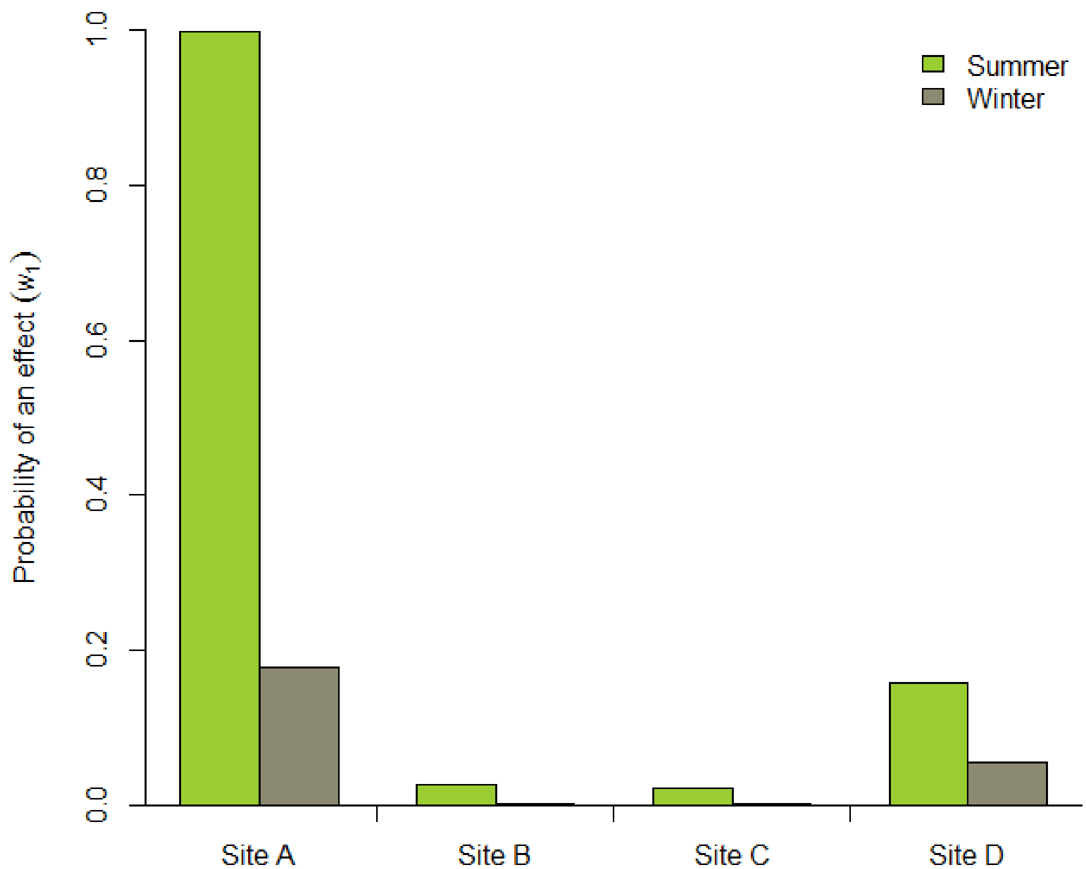

Figure 3.4. The probability that bait influenced second order selection (*w*) of male white-tailed deer (*Odocoileus virginianus*) in southwestern Georgia, USA, during summer (2015) and winter (2016) camera surveys.

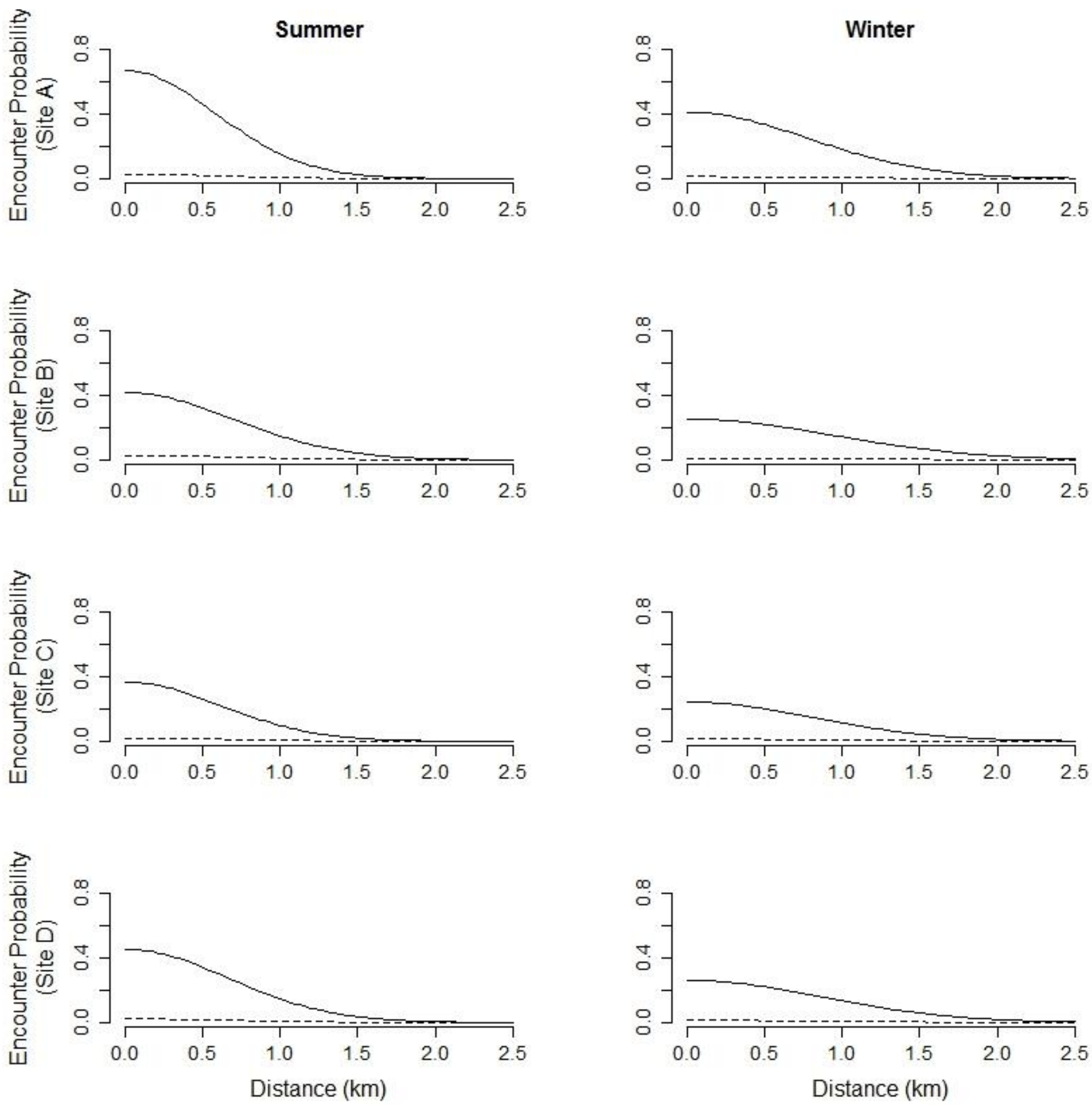

Figure 3.5. Half-normal detection functions of each baited (solid lines) and passive (dashed lines) camera array site, by season (summer 2015 and winter 2016), describing how the encounter probability of white-tailed deer (*Odocoileus virginianus*) changes as a function of distance (km) from camera at study sites in southwestern Georgia, USA.

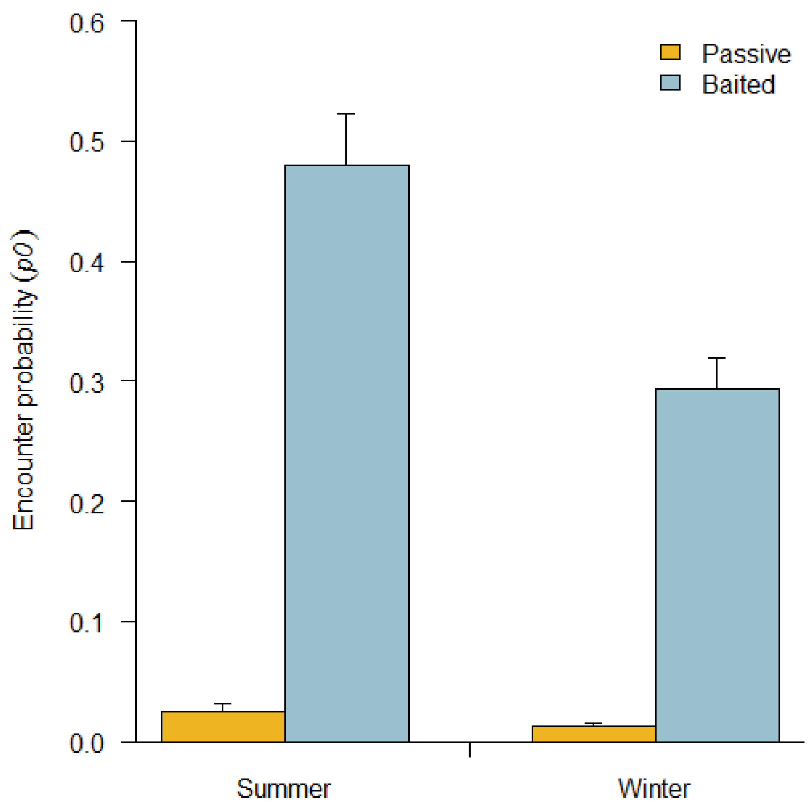

Figure 3.6. Encounter probabilities (95% CI) of male white-tailed deer (*Odocoileus virginianus*) captured on passive and baited cameras during summer 2015 and winter 2016 surveys in southwestern Georgia, USA.

Table 3.1. Total number of images and number of identified unique male white-tailed deer (*Odocoileus virginianus*) during summer (2015) and winter (2016) baited and passive camera surveys in southwestern Georgia, USA.

	Site A	Site B	Site C	Site D
Summer baited	10613	3609	3006	2188
Summer passive	240	143	57	48
Summer unique males	208	93	94	75
Winter baited	11318	3587	2222	2502
Winter passive	141	114	67	68
Winter unique males	177	85	89	72

Table 3.2. Estimates of the posterior means for male white-tailed deer (*Odocoileus virginianus*) abundance (N), intensity function intercept (β_0), the effect of bait on deer activity center density (β_1), baseline encounter probabilities for both passive (p_0 [passive]) and baited cameras (p_0 [baited]), and the scaling parameter of the half-normal detection function (σ) from summer (2015) and winter (2016) camera surveys in southwestern Georgia, USA.

Site / season	Parameter	Mean	SD	2.5%	97.5%
A / summer	N	261.474	8.925	247.000	282.000
	β_0	3.247	0.140	2.972	3.521
	β_1	-2.621	0.416	-3.456	-1.838
	p_0[passive]	0.028	0.002	0.023	0.033
	p_0[baited]	0.673	0.017	0.641	0.707
	σ	0.338	0.004	0.331	0.345
A / winter	N	213.980	5.167	205.000	225.000
	β_0	2.133	0.134	1.869	2.392
	β_1	-0.734	0.223	-1.182	-0.309
	p_0[passive]	0.012	0.001	0.010	0.015
	p_0[baited]	0.414	0.011	0.393	0.436
	σ	0.607	0.008	0.592	0.623
B / summer	N	138.577	8.041	124.000	155.000
	β_0	1.529	0.125	1.312	1.805
	β_1	-0.210	0.174	-0.651	-0.007
	p_0[passive]	0.028	0.004	0.022	0.036
	p_0[baited]	0.420	0.023	0.378	0.467
	σ	0.487	0.012	0.463	0.510
B / winter	N	100.302	1.180	99.000	103.000
	β_0	1.112	0.099	0.922	1.315
	β_1	-0.081	0.074	-0.275	-0.002
	p_0[passive]	0.011	0.001	0.009	0.014
	p_0[baited]	0.255	0.011	0.233	0.278
	σ	0.872	0.018	0.838	0.907
C / summer	N	168.446	14.598	141.000	198.000
	β_0	1.940	0.124	1.719	2.207
	β_1	-0.302	0.237	-0.874	-0.011
	p_0[passive]	0.020	0.003	0.014	0.027
	p_0[baited]	0.370	0.021	0.331	0.411
	σ	0.375	0.009	0.358	0.394
C / winter	N	108.200	4.387	101.000	118.000
	β_0	1.367	0.108	1.160	1.589
	β_1	-0.108	0.097	-0.358	-0.003
	p_0[passive]	0.014	0.002	0.010	0.018
	p_0[baited]	0.244	0.014	0.219	0.272
	σ	0.652	0.019	0.615	0.691
D / summer	N	104.585	8.606	89.000	123.000
	β_0	1.459	0.183	1.137	1.848
	β_1	-0.509	0.333	-1.263	-0.031
	p_0[passive]	0.022	0.004	0.015	0.030
	p_0[baited]	0.457	0.025	0.409	0.506
	σ	0.443	0.012	0.421	0.467
D / winter	N	85.474	2.349	82.000	91.000
	β_0	1.141	0.174	0.832	1.511
	β_1	-0.327	0.223	-0.838	-0.016
	p_0[passive]	0.013	0.002	0.009	0.018
	p_0[baited]	0.263	0.013	0.239	0.289
	σ	0.750	0.019	0.713	0.789

APPENDIX A. SCR JAGS model

```
model {
    p0[1] ~ dbeta(1,1)
    p0[2] ~ dbeta(1,1)
    sigma ~ dgamma(1,1)
    beta0 ~ dnorm(0, 0.1)
    beta1 ~ dunif(-100,0)
    w1 ~ dbern(0.5)
    for(g in 1:nPixels) {
      mu[g] <- exp(beta0 + beta1*bait.dist[g]*w1)*pixelArea
      pi[g] <- mu[g] / sum(mu)}
    EN <- sum(mu)
    psi <- EN / M
    for(i in 1:M) {
      z[i] ~ dbern(psi)
      s[i] ~ dcat(pi[])
      for(j in 1:J) {
     p[i,j] <- p0[bait[j]]*exp(-1*pow(d[s[i],j],2)/(2*sigma^2))
      for(k in 1:K) {
        y[i,j,k] ~ dbern(p[i,j]*z[i]*oper[j,k])}}}
    N <- sum(z)}
```

CHAPTER 4

ASSESSMENT OF BAITED CAMERA SURVEYS FOR WHITE-TAILED DEER HARVEST MANAGEMENT DECISIONS

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ABSTRACT

Baited camera surveys are commonly used to monitor white-tailed deer (*Odocoileus virginianus*) populations and establish harvest objectives. However, most surveys are conducted in late summer or early fall, prior to the hunting season, when sexual segregation is strongest. Therefore, these surveys may not accurately describe the population available during subsequent hunting seasons. To determine how well baited camera surveys reflect deer distributions and harvestable populations, we conducted a September baited survey (one camera/40 ha) followed with autumn passive camera surveys (one camera/20 ha) during the subsequent hunting season on three 1000-ha sites in southwestern Georgia. We collected 51,106 images of deer before and during the 2014 deer season from baited and passive cameras. Based on interpolated maps of camera detections, the populations within the camera arrays were highly segregated during the September baited surveys. Subsequent passive camera surveys indicated a high degree of overlap of males and females during the breeding months, with males demonstrating the most dramatic shift in distributions. Of the males identified during the September baited surveys, 12%, 28%, and 14% were not observed during subsequent passive camera surveys. However, an additional 21, 27, and 26 unique males were identified during the autumn passive surveys that were not observed in September. Our results suggest that late summer surveys may not accurately reflect deer distributions and the population available for harvest during the subsequent hunting season, potentially influencing management decisions.

KEY WORDS: camera survey, Georgia, interpolation, *Odocoileus virginianus,* passive camera, sexual segregation, spatio-temporal dynamics

INTRODUCTION

Management of game populations is dependent on accurate estimates of population abundance and distribution to guide harvest decision making (Halls 1984, Gibbs 2000). Although numerous methods of estimating or indexing white-tailed deer (*Odocoileus virginianus*) populations have been proposed and evaluated, the most commonly employed, and putatively most accurate, method of assessing local populations has been the Jacobson baited camera survey protocol (Jacobson et al. 1997). The Jacobson protocol employs motion-triggered cameras placed over systematically spaced bait piles (typically 600-1000 m apart) for 10-14 days, usually before and/or after the hunting season. Adult males are identified based on unique antler configurations and the ratio of unique males identified to the number of total male images is used to estimate the number of adult females and juveniles, ultimately producing abundance indices and sex ratios. However, accurate estimates rely on the assumption of equal visitation rates of age classes and sexes, as well as the assumption that deer only use the area which is determined by camera density.

Several studies have raised concerns regarding the validity of results generated by the baited camera method, particularly related to differences in use of bait sites between sexes and among age classes of deer during certain seasons (McCoy et al. 2011, Weckel et al. 2011, Rowcliffe et al. 2013, Beaver et al. 2016, Beaver 2017). An additional, although previously unevaluated, concern about the baited camera survey relates to deer sociobiology. Specifically, it is unclear how temporal changes in the distribution of the sexes affects inferences from camera surveys conducted during a single season. During spring and summer, white-tailed deer populations tend to segregate sexually (Bowyer

2004), with males forming loosely associated bachelor groups of unrelated individuals (Hirth 1977). Sexual segregation is manifested by differential use of space and resources by males and females due to differences in nutritional/foraging requirements, predation risk, and social factors (McCullough et al. 1989, Main and Coblentz 1990, Bowyer 2004). The period of sexual segregation includes the time frame when a typical baited survey would be conducted and may lead managers to set harvest goals that may be inappropriate once the hunting season commences after segregation dissolves.

Many management programs rely on late summer baited camera surveys to identify individual males for harvest prior to the hunting season and before the dissolution of bachelor groups. However, dynamic social and environmental factors can alter deer spatial dispersion during autumn, altering the actual huntable population. Home range size and location often shift as food resources change (Beier and McCullough 1990, McShea and Schwede 1993, Miller and Marchinton 1999, Walter et al. 2009, Olson 2014). Rut-related activities also can alter deer movement patterns and activity centers (Tierson et al. 1985, Beier and McCullogh 1990, Tomberlin 2007, Foley 2012). Additionally, fall dispersal of yearling males often coincides with rut-related behavior (Rosenberry et al. 2001), and many studies suggest ≥50% of yearlings disperse (Kammermeyer and Marchinton 1976, Nelson and Mech 1984, Nixon et al. 1991, Holzenbein and Marchinton 1992, Rosenberry et al. 1999). Thus, although late summer baited camera surveys may provide reasonable estimates of herd demographics at the time they are conducted, changes in deer distribution during the autumn hunting season may result in inappropriate deer harvest recommendations.

Passive camera traps have been widely used in wildlife occupancy studies with detection/non-detection data (Shannon et al. 2014) to evaluate species distribution (Long et al. 2010, Sollmann 2018) as well as habitat use (Betts et al. 2008). Detection data has been integrated into wildlife monitoring programs allowing managers to determine changes in distributions of species as well as a predictive tool for population dynamics studies (MacKenzie et al. 2003, Jones 2011, Noon et al. 2012). The basic form of detection data can describe patterns of species occurrence and distributions and could be used to track distribution of deer on the landscape over a given period.

We used unbaited (herafter: passive) camera detections to assess how well pre-hunting season, September baited camera surveys reflect distributions of deer on the landscape during the hunting season, and to determine how well they reflect male harvest availability. We used Kriging interpolation methods to predict monthly distributions of adult male and female deer based on camera detections, starting with baited camera surveys in September and then continual monitoring with autumn passive camera surveys from October through December. We also compared monthly observable unique male deer based on antler characteristics between September baited surveys to passive camera surveys during subsequent months. We used this information to compare initial observed distributions (baited survey) with subsequent passive surveys.

METHODS

The study area included three properties with varying deer densities and management regimes (Figure 1). The properties were located in Southwestern Georgia (USA) and ranged in size from ~1,600 hectares to ~12,000 hectares. Habitat types consisted primarily of longleaf pine (*Pinus palustris*) and loblolly pine (*Pinus taeda*) savannas, scattered hardwoods, riparian zones, planted pines, and depressional wetlands. Properties 2 and 3 had a long history of intensive habitat management for the objective of promoting high densities of northern bobwhite (*Colinus virginianus*), while property 1 was primarily focused on white-tailed deer habitat management and unlike the other two properties, had a long-term supplemental deer feeding program in place. Typical landscape management for all three properties (varying to some degree between properties) included frequent prescribed fire, wildlife openings/food plots, timber management, roller chopping, mowing, and seasonal disking.

In 2014, we established a 1000-ha site on each property (sites A, B, and C; Figure 2). Within each site, 49 passive cameras (1 camera/ ~20 ha) and 25 baited cameras (1 camera/ ~40 ha) were designated within a systematic fish net grid approach using ArcGIS 10.1 (Figure 2). However, property 1 had a long history (>10 years) of baited camera use, therefore, we opted to use 25 pre-established bait sites for this property (1 camera / ~50 ha) and placed the same passive camera array (n=49) within the pre-establish baited camera array. We operated passive cameras from October to December, and baited camera surveys were conducted in early September prior to the onset of deer hunting season. Baited cameras were operated for two weeks with a week of pre-baiting without operational cameras, and we followed the common methodology (Jacobson et al. 1997) for generating herd demographic estimates from the baited camera survey. Passive cameras were used to keep track of uniquely identified males and to observe shifts in male and female detections in autumn following the baited camera surveys

We placed passive cameras (Uway VH200HD, HCO Outdoors, Duluth GA, USA) approximately 1.5 m from the ground, fixed to trees or metal fence post when trees were not available. To place passive cameras, we created a buffer of 200 meters around the centroid of each grid cell. The buffer was searched for an optimal location for camera placement, typically facing a well-worn trail. Low impact vegetation clearing was conducted to clear the camera's view of the target area. We placed baited cameras at a similar height as passive cameras, fixed to trees, as close as possible to the center of each grid cell and shelled corn was placed approximately 5 m from each baited camera.

All cameras were operated for 24-hours per day during the study period. Baited cameras were set with a 5-minute delay between photographs where passive cameras were set to a 10-second delay between image captures. We visited baited cameras twice a week to replenish bait and check camera functioning; passive cameras were checked a minimum of once per month. Cameras that malfunctioned and resulted in loss of data during surveys were omitted from interpolation analysis.

We thinned passive camera detections to 2-minute intervals to reduce autocorrelation. We applied rank order or square root transformations to reduce the influence of outliers on interpolations. We used ArcGIS 10.6.1 to create a 250 m buffered polygon surrounding periphery cameras within each site, resulting in areas of 15.49, 15.02, and 13.46 km^2 for sites A-C respectively. Using ArcGIS we developed Kriging interpolations within each survey area polygon to create predictive surfaces of detections to observe spatial distributions of deer during the September baited camera surveys and for each subsequent month (October, November, and December) using the passive camera arrays. We identified unique males captured by photograph within each site and survey based on antler characteristics. This is typical for pre-hunting season surveys in which managers identify potential harvestable individual males during the subsequent hunting season. All identified males received a unique ID number when first encountered on September baited camera surveys and maintained the same ID when re-captured during subsequent monthly autumn passive camera surveys in October-December. This allowed us to quantify unique male re-capture success and to identify new unique males on passive cameras that were not detected during September baited surveys.

RESULTS

We collected 38,240 and 12,866 photographs from September baited and autumn passive camera surveys, respectively. November produced the highest number of deer detections on passive cameras with 4696 images, followed by October with 4098, and December with 4072. In addition, November produced the highest volume of male photographs (2236 captures) and October produced the highest volume of female photographs (2546 captures) (Table 4.1). September baited camera surveys indicated substantial differences in herd demographics on each of the three sites with densities ranging from 19.6-42.8 deer/km^2 and male:female sex ratios ranging from 0.47-0.80 (Table 4.2). The distribution of male and female detections during the baited camera surveys was spatially segregated at two sites (Figures 4.3 and 4.4) with little overlap of detections, whereas they were only moderately segregated on the third site (Figure 4.5). However, the spatial distribution of detections during the passive surveys drifted dramatically beginning in October, with eventual overlap of male and female detections during November and December. Spatial distributions of female detections remained relatively consistent across all survey months, whereas the distribution of male deer shifted towards areas with high doe density during November and December.

We identified 370 unique antlered males from the 2-week baited camera surveys and 385 unique males from the 3-month passive camera surveys. For passive camera surveys, we identified the most unique males in November and the fewest in October (Table 4.1). Following the September baited camera surveys, the autumn passive surveys did not recapture 25 (12%), 12 (14%), and 22 (28%) individual males from sites A, B, and C, respectively. However, we identified 21, 26, and 27 new individual males on passive cameras from sites A, B, and C (Figure 4.6), respectively. Of the 74 new individual males identified on passive cameras, we observed 18, 35, and 21 during October, November, and December, respectively. Therefore, across the 3-month autumn passive survey period, an average of 2.5 new individuals/km^2 were detected that were not observed on September baited camera surveys.

DISCUSSION

Our results demonstrate that sex-specific spatial distributions of deer shift during late summer through the autumn breeding season, and September baited camera surveys may not reflect male harvest availability during the hunting season. Sexual segregation is likely ubiquitous among dimorphic ungulate populations outside of the breeding season (McCullough et al. 1989, Bowyer 2004). The scale at which sexual segregation occurs varies among cervid species, and white-tailed deer are thought to segregate at finer scales when compared to other ruminants (McCullough et al. 1989, Kie and Bowyer 1999, Stewart et al. 2003). Detection of sexual segregation is likely dependent on several factors, primarily population density and habitat heterogeneity (Bowyer 2004).

At low densities, observations of sexual segregation could occur by random chance (Bowyer 2004), and higher habitat heterogeneity likely results in sexual segregation at smaller scales due to highly variable and diverse landscapes which are capable of accommodating the different requirements of the sexes resulting in smaller spatial scales of segregation (Bowyer 1984, Beier 1987, Barboza and Bowyer 2000). Densities of deer within our study sites were relatively high, and the resulting observations of sexual segregation during late summer baited surveys likely did not occur through random chance considering our robust sample size. Separation of the sexes based on camera detections appeared the strongest at our highest density site (A), with minimal mixing at lesser densities (B), and moderate mixing of detections at the lowest density site (C). In addition, our ability to detect sexual segregation at the large scale of our camera arrays (1000 ha) is likely due to the relatively uniform habitat which is a common characteristic of the pine dominant systems of our study sites, resulting in a lower chance of fine-scale separation of the sexes.

We observed shifts in spatial distributions of male detections during each month surveyed following the September baited camera surveys, with male detections eventually overlapping female detections in November and December. Female spatial distributions did not appear as dynamic and high detection areas of females remained consistent for each month for 2 of 3 sites. Baited camera surveys are typically conducted prior to the hunting season in late summer, such as September for the region of our study sites in Georgia, in order to guide harvest management decisions. Typical hunting leases in Georgia average ~380 ha (GON 2014), whereas our survey sites were 1000 ha. Considering the extent to which we observed shifts in deer spatial distributions, much larger than an average hunting lease, this may result in erroneous assessments in harvest availability of males for most hunters. Therefore, consideration should be made to conduct baited camera surveys later in autumn, where legally possible, or follow late summer baited surveys with continual monitoring with passive cameras in autumn to better guide management practices.

Peak breeding activity in southwestern Georgia, based on fetal measurements from the region, occurs in late November and early December (Biggerstaff 2018). Male deer typically expand their home ranges prior to and during the breeding season (Nelson and Mech 1981, Beier and McCullough 1990, Tomberlin 2007), likely due to different search strategies of males (Brown 1974, Schwagmeyer 1995, Foley et al. 2015), presumably undertaken to gain increased access to females. Our observations of changes in spatial distributions of male detections appear to support this presumption, with male deer detections overlapping female detections in November and December.

We identified new males on autumn passive cameras that were not detected on September baited camera surveys and males that were never re-captured following the baited surveys, even at the large spatial scales surveyed by our camera arrays. The largest influx of new males occurred in November, which is likely due to breeding season behavior, as well as seasonal shifts in home range size and location with respect to changing seasonal resources on the landscape (Marchinton and Hirth 1984, Nixon et al. 1991, Brinkham et al. 2005, Simoneaux 2012). In addition, yearling male dispersal often coincides with the breeding season (Rosenberry et al. 2001) which would result in newly identified males. However, we also recognize that some of the new male deer may have been present and gone undetected on September baited camera surveys, which has been documented from other baited camera survey studies with marked deer (Moore et al. 2014, Beaver 2017). It is also likely some portion of male deer that were never re-captured following the September baited survey remained within the sites but were not detected on passive cameras. Deer herds often use landscapes at spatial scale much larger than contiguous landholdings (DeYoung and Miller 2011) and generating management goals based on this “snapshot in time”, before hunting seasons begin could be cause for concern if baited surveys do not fully reflect the huntable population of deer and adjacent smaller properties differ in management practices and goals.

We also found differences in turnover of unique males among the three properties with site A having the highest number of males that were not recaptured following the September survey, and the lowest number of newly identified males during autumn surveys. Herd dynamics may have played a role in reducing the number of new males identified, considering site A had a greater density than other sites, and more than twice the number of identified males than other sites during the baited camera survey. At high deer densities, home ranges are typically smaller (Marchinton and Jeter 1967, Marshall and Whittington 1969, Ellisor 1969), which may explain why fewer new deer were detected at site A where movement distances were shorter. Site A also had lower connectivity to the surrounding landscape, being bordered by two highways (State Route 300 and 32) and a major river system (Flint River). Barriers such as roads and major rivers have been shown to hinder deer movement (Long et al. 2010, Stickles 2014), which likely reduce the ability of new males to enter or leave camera grid A. Deer would have more access to movement in and out of the surveyed area at sites B and C, which were not as isolated by barriers.

Our results demonstrate that male deer distributions are spatially and temporally dynamic throughout the late summer and fall. Female deer distributions appeared to be less dynamic relative to shifts in male deer distributions. Relying on results from a single "snapshot in time" survey, during periods of sexual segregation, may result in erroneous decision making during the hunting season. Passive cameras may be the best option for un-biased surveys during the autumn months when distributions are influenced by breeding activity. Studies have demonstrated male deer are less likely to visit bait stations during the breeding season (Kilpatrick and Stober 2002, McCoy et al. 2011, Stone 2017), which would result in biased baited camera survey estimates, and would likely not be a viable alternative for assessing deer distributions and composition.

MANAGEMENT IMPLICATIONS

Spatio-temporal dynamics of deer populations should be considered when establishing management goals based on pre-hunting season baited camera surveys. Sexual segregation during late summer affects the distribution of males and females on the landscape and management decisions should not be solely based on pre-hunting season surveys alone. Passive cameras could be used as an alternative for assessing deer distributions and male composition during the hunting season to improve management decision making and real-time analytical approaches could be developed with the use of cellular-based cameras. In addition, hunters may be able to concentrate efforts on areas of high female detections recognized from pre-hunting season surveys in order to anticipate male movement during the breeding season.

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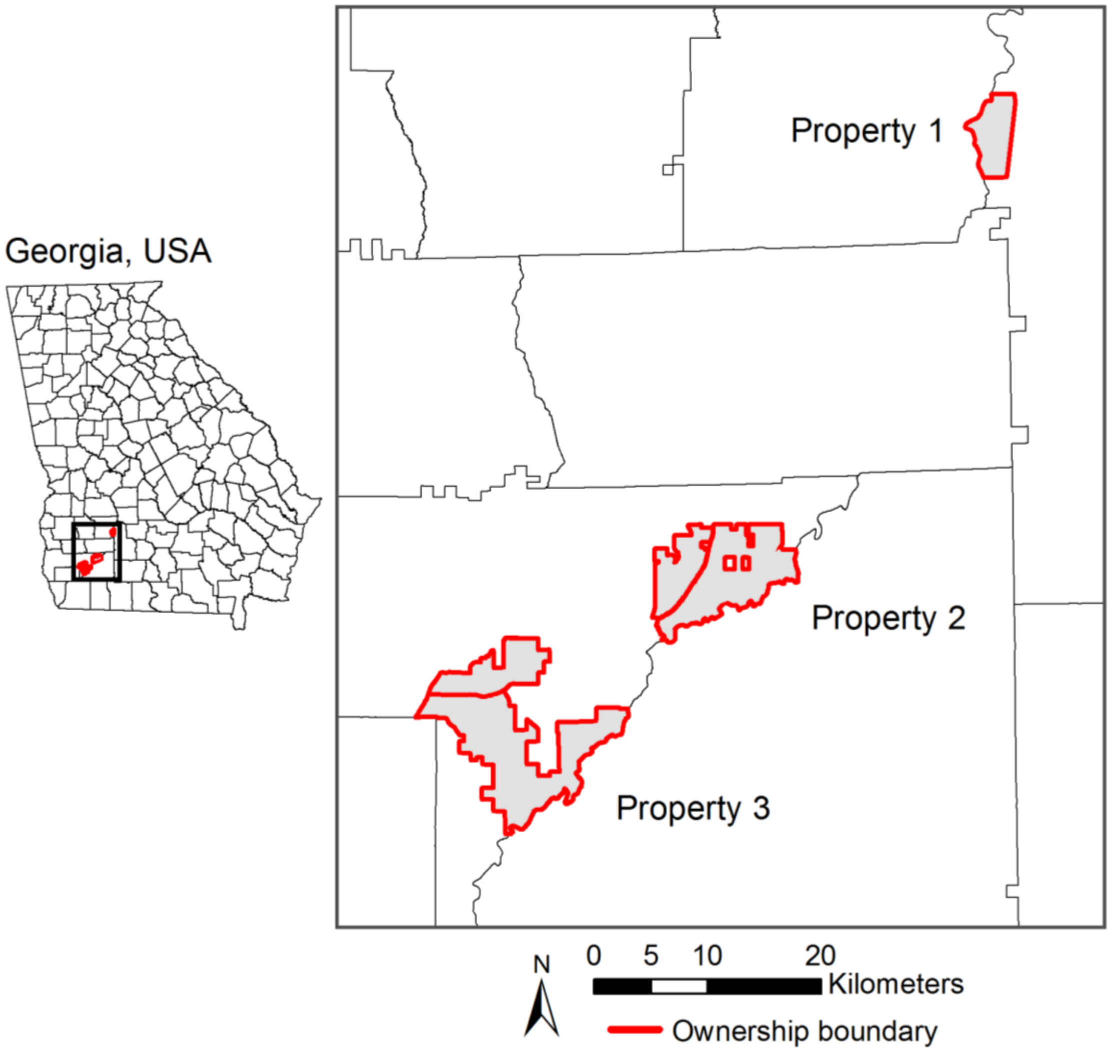

Figure 4.1. Properties (1, 2, and 3) where baited and unbaited passive camera arrays, used to investigate spatio-temporal dynamics of white-tailed deer (*Odocoileus virginianus*) were located in southwestern Georgia, USA (2014).

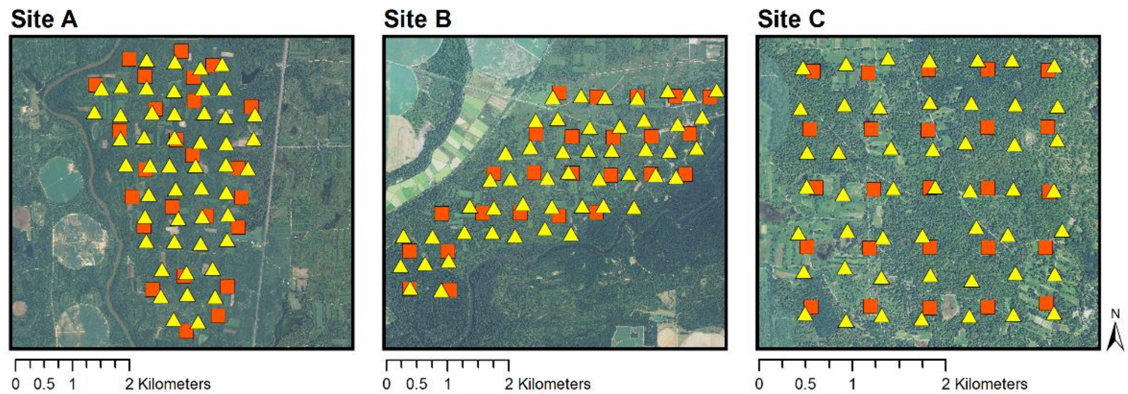

Figure 4.2. Camera array sites A, B, and C used for white-tailed deer (*Odocoileus virginianus*) surveys in southwestern Georgia, USA (2014). Orange squares represent baited cameras and yellow triangles represent unbaited passive cameras.

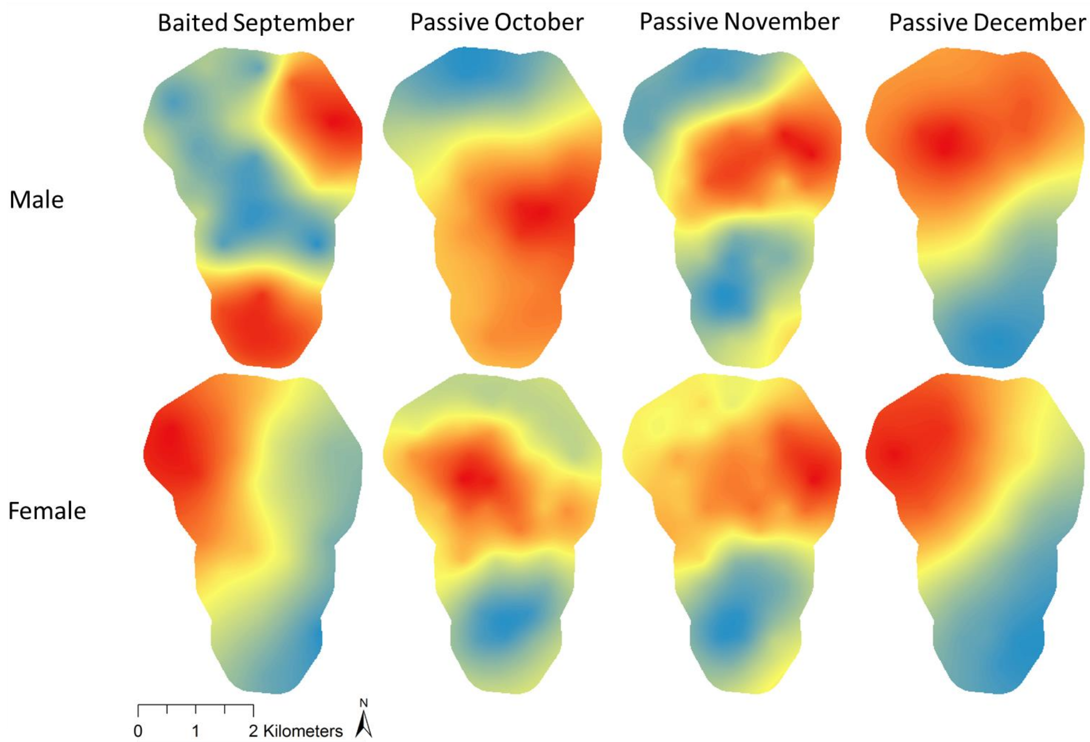

Figure 4.3. Kriging interpolated surfaces of male (top row) and female (bottom row) white-tailed deer (*Odocoileus virginianus*) from September baited camera surveys and October, November, and December unbaited passive cameras on property 1 (site A) in southwestern Georgia, USA (2014). Warmer colors indicate greater detections of deer and cooler colors indicate lesser detections of deer.

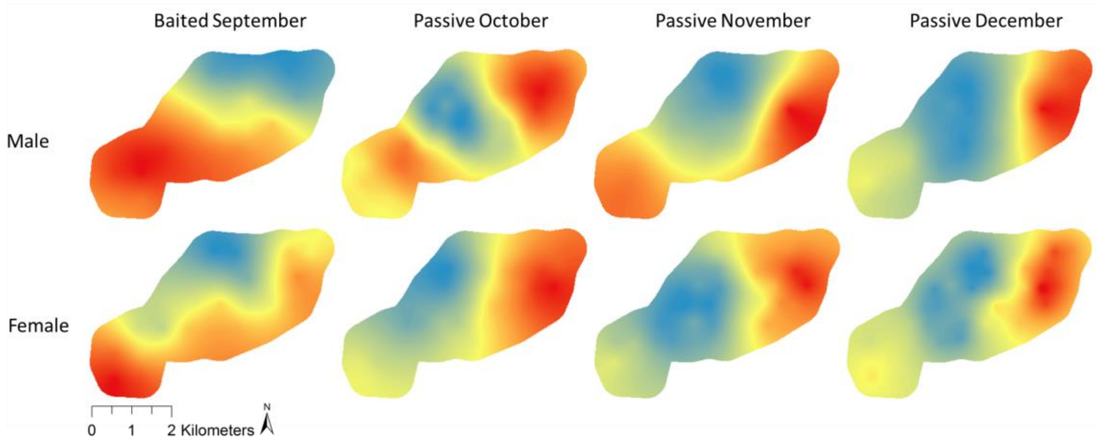

Figure 4.4. Kriging interpolated surfaces of male (top row) and female (bottom row) white-tailed deer (*Odocoileus virginianus*) detections from September baited camera surveys and October, November, and December unbaited passive cameras on property 2 (site B) in southwestern Georgia, USA (2014). Warmer colors indicate greater detections of deer and cooler colors indicate lesser detections of deer.

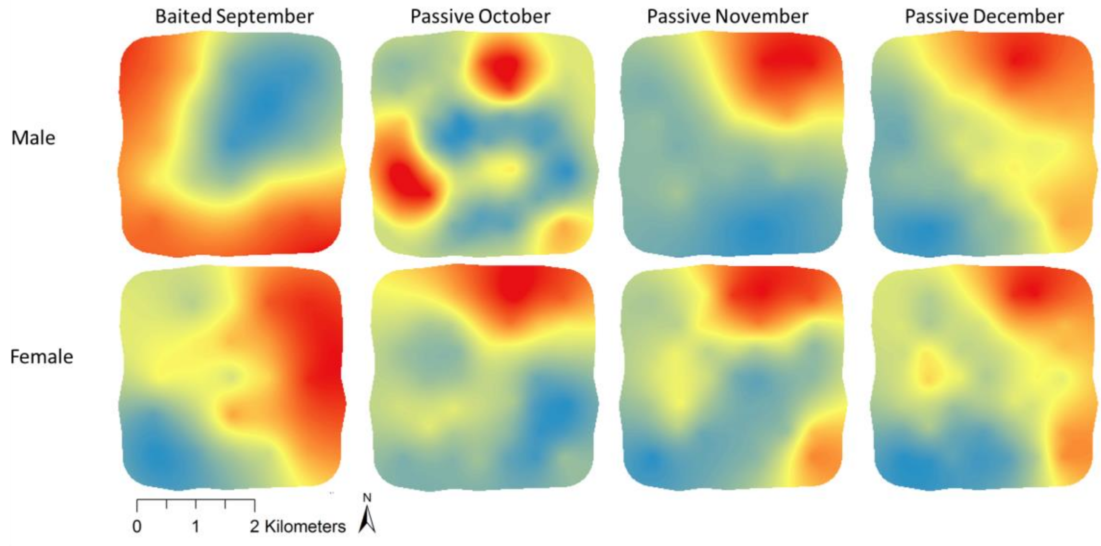

Figure 4.5. Kriging interpolated surfaces of male (top row) and female (bottom row) white-tailed deer (*Odocoileus virginianus*) detections from September baited camera surveys and October, November, and December unbaited passive cameras on property 3 (site C) in southwestern Georgia, USA (2014). Warmer colors indicate greater detections of deer and cooler colors indicate lesser detections of deer.

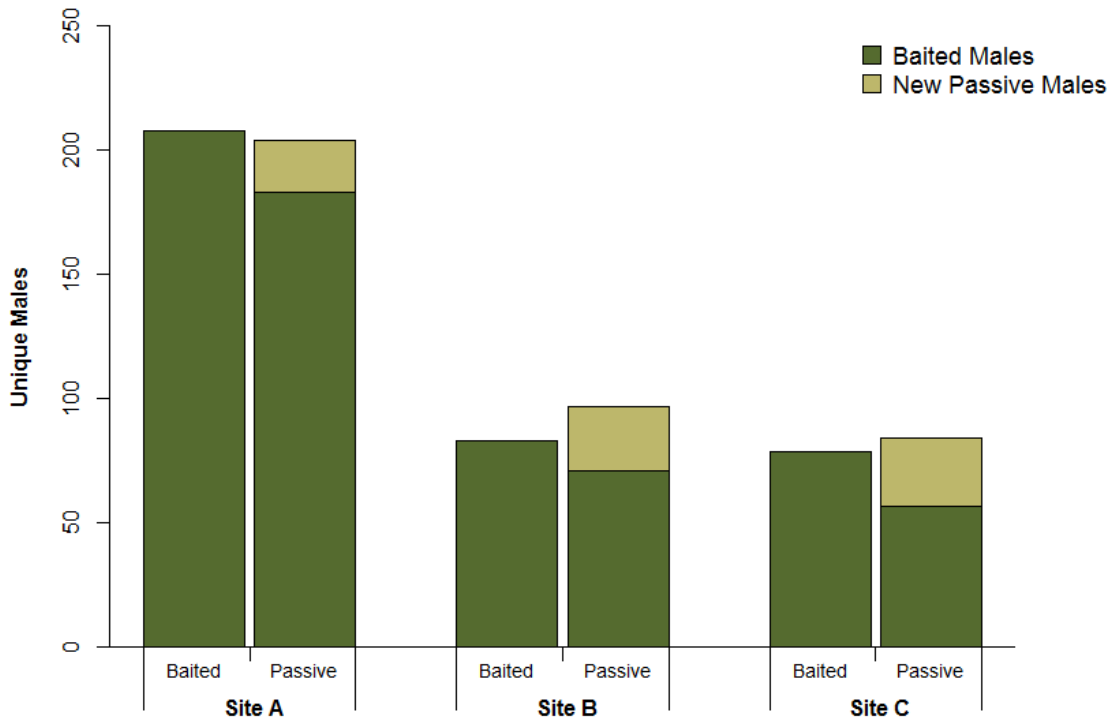

Figure 4.6. Uniquely identified individual male white-tailed deer (*Odocoileus virginianus*) from pre-hunting season baited camera surveys in September and male deer identified from unbaited passive cameras operated from October to December in southwestern Georgia, USA (2014). Green portions represent the number of unique males identified on the baited surveys and tan colors represent unique males identified only on passive cameras.

Table 4.1. Images collected of white-tailed deer (*Odocoileus virginianus*) and unique male deer identified (unique IDs) for each survey (Baited and Passive) and site (A, B, and C) with summed totals for camera surveys in southwestern Georgia, USA (2014).

	Site A	Site B	Site C	Totals
September (baited)				
Male captures	8007	3986	3521	15514
Female captures	10253	4875	7598	22726
Unique IDs	208	83	79	370
October (passive)				
Male captures	988	383	181	1552
Female captures	1091	687	768	2546
Unique IDs	128	50	35	213
November (passive)				
Male captures	1225	548	463	2236
Female captures	851	875	734	2460
Unique IDs	146	71	52	269
December (passive)				
Male captures	739	766	571	2076
Female captures	853	560	583	1996
Unique IDs	120	73	53	246

Table 4.2. Baited camera survey white-tailed deer (*Odocoileus virginianus*) density estimates (km^2) for adult males, females, and combined adults for three 1000-ha sites (A, B, and C) in southwestern Georgia, USA (2014).

Site	Total *D* (km2)	Female *D* (km^2)	Male *D* (km2)	Male:Female
A	42.8	21.9	17.1	0.77
B	19.6	10.2	8.3	0.80
C	28.3	17.0	7.9	0.47

CHAPTER 5

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

CONCLUSIONS

The results from this research suggest the following conclusions:

Chapter 2 – Evaluation of an Unmarked Spatial Capture-Recapture model for Estimating White-tailed deer Abundance and Density

1. Estimates from the unmarked SCR model produced similar estimates to distance sampling surveys and to estimates from SCR models applied to data on uniquely identified males.
2. Estimates from the unmarked SCR survey were less precise than the estimates from SCR models applied to data on uniquely identified male deer.
3. The unmarked SCR model did not perform well when estimating female density as evidenced by greater male density estimates at some sites. The low female density estimates may have resulted from clustering of female deer at camera sites, which was not accounted for by the unmarked SCR model.
4. The Jacobson method produced greater density estimates than all other survey methods.
5. The unmarked SCR model provides many advantages over the Jacobson method, including an estimate of uncertainty associated with point estimates, a defined survey extent, and the exclusion of baiting and the need to identify individual deer. In addition, further refinement could increase the precision of estimates.

Chapter 3 – Effects of Bait on Male White-tailed Deer Resource Selection

1. Bait did not strongly affect spatial variation in density (second-order selection) of male white-tailed deer.
2. The only site where we detected an effect of bait on second-order selection had a long-term supplemental feeding program.
3. Bait had a strong effect on within home range space use (third-order selection)
4. Male deer had greater bait site use in the winter relative to summer when comparing the probability of detection at baited versus passive cameras.

Chapter 4 – Assessment of Relying on Baited Camera Surveys for Harvest Management Decisions

1. The distribution of male and female deer detections from September pre-hunting season baited camera surveys were highly segregated within our 1000 ha study sites.
2. Distributions of male deer detections shifted over the three months (October, November, and December) of the passive camera surveys. Female deer distributions shifted to a lesser extent.
3. Distributions of male and female detections were highly overlapped in November and December, during the breeding season months.
4. New males were identified each month of the autumn passive camera surveys with the largest influx occurring during November.
5. The lowest turnover of new males occurred on the site with the highest deer density and lowest recognized landscape connectivity.

MANAGEMENT IMPLICATIONS

1. An unmarked and unbaited camera survey protocol would simplify sampling and data collection processes, reduce cost and ecological impacts associated with baited camera surveys, and provide managers with an estimate of uncertainty for making informed management decisions.
2. Managers should seek to apply marked SCR models to data on individually identified males and fawns when more precise estimates are required and when resources allow, as these models will produce the most reliable estimates when considering the methods we compared.
3. The strong effect of bait on within-home range resource selection could lead to greater rates of deer-to-deer contact leading to increased transmission rates of diseases and greater harvest rates during certain periods of the hunting season.
4. Spatial distributions of deer may be affected by sexual segregation during late summer surveys, and managers should be aware of the potential changes to local deer densities and unique individuals as the deer season progresses.