Current and Spatially Explicit Capture-recapture Analysis Methods for Infrared Triggered Camera Density Estimation of White-tailed Deer

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Abstract: Population monitoring of wildlife species requires techniques that produce estimates with low bias and adequate precision. Use of infrared-triggered camera (hereafter; camera) surveys for white-tailed deer (*Odocoileus virginianus*; deer) population density estimation is popular among land managers. However, current camera surveys do not provide an estimate of precision critical for accurate density estimation. We believed that incorporating spatial aspects of sampling into the analytical process would allow for both estimates of precision associated with density and an ability to calculate effective sample area. We conducted camera surveys for deer in Units 1 (1,385 ha) and 2 (1,488 ha) at Arnold Air Force Base, Tennessee, in August 2010. We used 1 camera per 53 and 62 ha in Units 1 and 2, respectively, and identified individual male deer based on antler criteria. We used spatially explicit capture-recapture (SECR) data with Program DENSITY to fit a spatial detection function ($g0$; probability of detecting an individual on a single occasion when the distance between their home range center and a trap is zero) and sigma (the scale parameter that determines the rate at which detection probability decreases with distance between a home range center and a trap) to estimate antlered male density. Density estimates were similar between camera surveys (based on recaptures of recognizable antlered males from camera images) using traditional sampling techniques (without spatial information on capture) and spatially explicit density estimation (with a record of location for each individual camera capture). Antlered male density estimates obtained via traditional sampling for Units 1 and 2 were 2.0 and 2.6 males/km^2, respectively. Density estimates based on SECR models were 1.6 males/km^2 (SE = 0.33, $g0$ = 0.24) for Unit 1 and 2.5 males/km^2 (SE = 0.56, $g0$ = 0.14) for Unit 2. Both estimation methods indicated lower deer density in Unit 1 versus Unit 2. Analysis of camera surveys using SECR modeling uses the data from the spatial distribution of cameras and does not require the assumption of equal detectability. Use of SECR modeling can improve current camera survey methods by providing both a measure of precision that is currently lacking from traditional camera analysis methods and including spatial distribution of captured deer. Spatial modeling should be explored further to enhance our understanding of potential biases associated with behavioral responses to the use of bait as an attractant.

Key words: density estimates, infrared-triggered cameras, *Odocoileus virginianus*, spatial modeling, Tennessee, white-tailed deer.

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Population monitoring is an important consideration when managing wildlife (Gibbs 2000). White-tailed deer (*Odocoileus virginianus*; hereafter deer) are an important big game species in North America (Miller et al. 2003), and elevated deer density can alter the structure and composition of the forest understory and affect other wildlife species (Tilghman 1989, Waller and Alverson 1997, Miller et al. 2003, Rossell et al. 2005). Managers need reli-

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able and cost-effective tools for population monitoring (Jenkins and Marchinton 1969, Jacobson et al. 1997, Heilbrun et al. 2006, McKinley et al. 2006). Techniques that not only estimate density (Lancia et al. 1994) but also allow detection of changes in density over time are needed (Gibbs 2000, Murray and Fuller 2000, Peterson et al. 2003).

Remote photography surveys have a long history in wildlife research and have surged in popularity since the advancement and commercialization of infrared-triggered camera (hereafter; camera) systems (Jacobson et al. 1997, Cutler and Swann 1999, Koerth and Kroll 2000). Camera surveys have been used for population estimation of many wildlife species and are popular among land managers for deer population monitoring (Jacobson et al. 1997, Koerth and Kroll 2000, Heilbrun et al. 2006, Rowcliffe et al. 2008). Camera surveys can be cost-effective (Kucera and Barrett 1993, Rowcliffe et al. 2008), less invasive (Franzreb and Hanula 1995, van Schaik and Griffiths 1996, Cutler and Swann 1999, Rowcliffe et al. 2008), and less labor intensive (Seydack 1984, Cutler and Swann 1999, Rowcliffe et al. 2008) compared with other techniques, such as direct observations or live-capture studies (Cutler and Swann 1999, Larrucea et al. 2007). Cameras allow continuous detection in a variety of vegetation types and during various weather conditions with limited human attention thus reducing human influence or observer bias (Cutler and Swann 1999, Larrucea et al. 2007, Rowcliffe et al. 2008). Many count techniques (spotlighting and ground forward-looking infrared imaging) that use distance sampling may not be representative of the entire area because they are often limited to using roads as transects (Beaver et al. 2014).

Traditional approaches to camera surveys estimate abundance (*N*) based on recaptures of recognizable individuals from camera images (Karanth and Nichols 1998, Rowcliffe et al. 2008). The photographic capture rate of identified adult males is assumed to be the equal to that for adult females and fawns (Jacobson et al. 1997, McKinley et al. 2006). However, this assumption of equal detectability has not been investigated in detail (Jacobson et al. 1997, Karanth and Nichols 1998, Cutler and Swann 1999, McCoy et al. 2011). Another source of potential bias that hasn't been adequately investigated is the potential error rate in identifying antlered bucks. Although several sources provide information about identifying individual bucks (Richards and Brothers 2003), we are not aware of any studies that have evaluated the potential error rate of identification of individual males using antler characteristics and body size. Also, traditional approaches to camera surveys and other conventional capture-recapture techniques ignore the spatial component of such data (Efford et al. 2004, Borchers and Efford 2008, Efford et al. 2009).

Spatially explicit capture-recapture (SECR) analysis incorporates spatial encounter history and location of each capture, creating an explicit account of the spatial nature of the sampling process (Efford et al. 2004, Borchers and Efford 2008, Efford et al. 2009). With traditional analysis, the effective sample area for each camera survey must be estimated based on assumed home range or arbitrary or judicial boundaries, which can lead to biased estimates (Efford et al. 2004, Borchers and Efford 2008). Effective sample area is D = n/ESA where D is density and n is the number of individuals detected. However, with the traditional analysis approach, the number of individuals that are identified during a survey period may not all be found within the pre-determined effective sample area at any given time. Thus, density estimates using traditional camera surveys may be biased high. However, with SECR, the effective sample area is estimated using maximum-likelihood methods based on capture-recapture data of individual antlered males. However, it also lets you estimate *N* for any region in the state space, and density across the entire state space is D = *N*/A(S), where A(S) is the area of the state space. Given the data and statistical model, this analysis method selects parameters that maximize agreement of the model with the observed data.

Numerous studies have utilized camera-trap data for capture-recapture abundance estimation for a variety of terrestrial mammals (Foster and Harmsen 2012). To our knowledge, however, none have done so for white-tailed deer. Prior research has also shown that SECR modeling can be used as an effective density estimation technique for other terrestrial mammals (Noss et al. 2012, Tobler and Powell 2013, Chandler and Clark 2014). Again, to our knowledge this has never been done for white-tailed deer. Thus, our objectives were to determine if SECR models can improve upon the traditional approach of using infrared cameras for white-tailed deer density estimation by providing density estimates with a measure of precision and estimate capture heterogeneity which may occur because of the use of bait.

Study Area

We conducted our study at Arnold Air Force Base (15,815 ha; AAFB), located in Coffee and Franklin counties Tennessee, within the Eastern Highland Rim physiographic province (U.S. Department of Defense 2006). Arnold Air Force Base was approximately 112 km southeast of Nashville, positioned among the towns of Manchester, Tullahoma, and Winchester, and within the Duck River and Elk River watersheds. The deer population on AAFB was managed jointly by Department of Defense and the Tennessee Wildlife Resources Agency. A majority of the area on AAFB was open to public hunting and was managed as six Wildlife Management Areas (WMA) by the Tennessee Wildlife Resource Agency (U.S. Department of Defense 2006).

Cultivated loblolly pine (*Pinus taeda*) plantations or hardwood forest dominated by southern red oak (*Quercus falcata*), scarlet oak (*Quercus coccinea*), post oak (*Quercus stellata*), black oak (*Quercus velutina*), white oak (*Quercus alba*), willow oak (*Quercus phellos*), water oak (*Quercus nigra*), and blackjack oak (*Quercus marilandica*), covered 12,673 ha. Midstory and understory species included dogwoods (*Cornus* spp.), maples (*Acer* spp.), sassafras (*Sassafras albidum*), sourwood (*Oxydendrum arboreum*), blueberries (*Vaccinium* spp.), hickories (*Carya* spp.), and blackgum (*Nyssa sylvatica*). Grasslands and early-successional vegetation in utility rights-of-way occupied 108 ha. The remaining 2,134 ha of the installation was occupied by buildings and structures, mowed areas, wildlife food plots, and other open areas (e.g., landfills, roads; U.S. Department of Defense 2006).

Methods

Camera Design

We conducted camera surveys over approximately 2,900 ha of deer habitat in WMA Units 1 (1,385 ha) and 2 (1,488 ha). We defined deer habitat as any area other than reservoirs, buildings, parking lots, or roads. We overlaid these two tracts with 48.6-ha grid cells in GIS (ArcGIS 9.2; Environmental Systems Research Institute Inc., Redlands, California) and placed cameras near the center of each grid as described in Jacobson et al. (1997). However, exact placement varied based on topography, likelihood of visitation by deer, and ease of access (Jacobson et al. 1997). We used Cuddeback Expert digital cameras (Non Typical, Inc., Green Bay, Wisconsin), and followed Tennessee Wildlife Resource Agency baiting regulations (all bait was removed at least 10 days prior to any hunting seasons).

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

Traditional Camera Analysis

We analyzed camera images using methods described by Jacobson et al. (1997). We identified individual males based on antler configuration and body characteristics. We divided total number of unique males by total number of male images to get a ratio (unique-to-total males). We used these numbers with our effective sample area, which was determined by administrative boundaries (Unit 1, 1,385 ha; Unit 2, 1,488 ha), to obtain traditional camera survey estimates of antlered male density (male/km^2). We only used antlered male density estimates for comparison with SECR modeling because they were individually identified. It should be noted that any error in identifying antlered individuals will bias the density estimate. This is true whether you use traditional methods or SECR, and to our knowledge, no source has evaluated the potential error rate in identifying individual bucks.

Spatially Explicit Capture-Recapture Analysis

We used encounter histories of individual males and their associated locations with program DENSITY (Efford 2007) to estimate antlered male density. SECR is a class of models that can be analyzed using either likelihood-based or Bayesian approaches to estimate population density, based on detection probability ($g_{0;}$ probability of detecting an individual on a single occasion when the distance between their home range center and a trap is zero; modeled as half-normal function) and sigma (σ; scale parameter that determines the rate at which detection probability decreases with distance between a home range center and a trap; Efford et al. 2004, Borchers and Efford 2008, Efford et al. 2009). We generated six models *a priori* for both WMA Unit 1 and 2. We modeled capture heterogeneity (h2) using two finite mixtures (Pledger 2000). We also considered behavioral (b) effects (based on previous capture experience for each animal) on detection probabilities and the spatial scale parameter. We applied a habitat mask, or what is known as state space, to specify which areas actually were included for density estimation based on suitable deer habitat boundaries. For example, we identified the downtown city limits of Tullahoma adjacent to both WMA Units 1 and 2 as non-habitat. We used minimum Akaike Information Criterion corrected for small sample size (AIC_c; Hurvich and Tsai 1989) for model selection of each site. We ranked models according to $\Delta_i AIC_c$ ($\Delta_i AIC = AIC_{ci} - AIC_c min$) and used AIC_c weights (w_i) to determine the relative importance of potential sources of variation within the models (Posada and Buckley 2004). We used model averaging to estimate population density (Buckland et al. 2001).

Results

We removed four camera sites from analysis for Unit 2 because of camera malfunctions, resulting in 24 camera sites included in analysis instead of 28. Consequently, we had a camera site for every 53 ha for Unit 1 and 62 ha for Unit 2 (Figure 1). We obtained 1,933 and 2,642 photographs containing male deer and identified 27 and 38 individual antlered males for Units 1 and 2, respectively. Antlered male density calculated via traditional analysis of camera data was 2.0 and 2.6 males/km^2 for Units 1 and 2, respectively.

Using the habitat mask, our total trapped area for both units using 50 usable camera trap locations (26 and 24 for Units 1 and 2; respectively) was 23 km^2. Thus, we effectively surveyed approximately 12.0 km^2 in Unit 1 and 11.1 km^2 in Unit 2. Models that included a behavioral effect for detection were consistently supported, receiving 95% and 100% of AIC$_c$ weights for Units 1 and

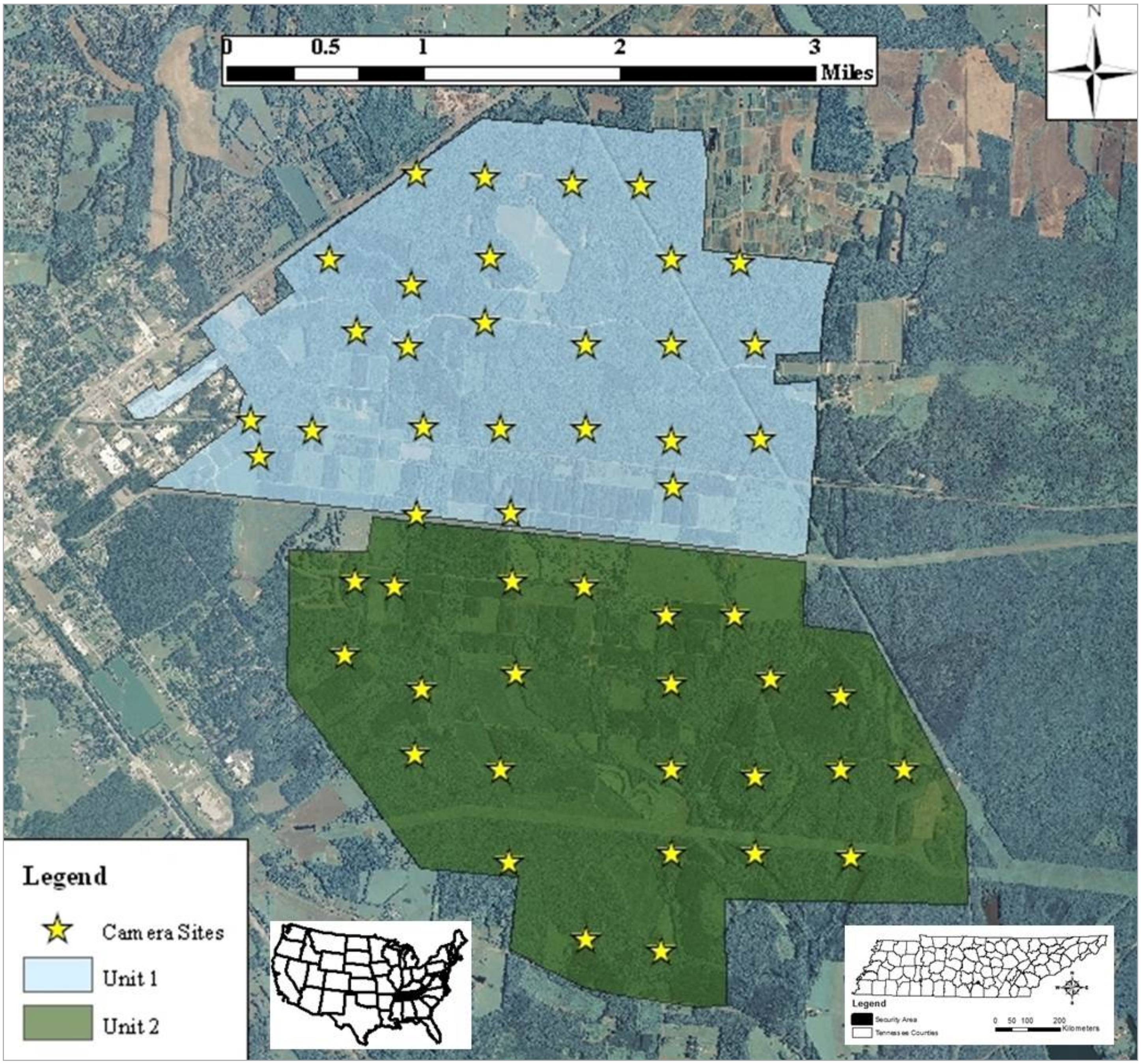

Figure 1. Infrared-triggered camera site locations for Wildlife Management Area Units 1 and 2 at Arnold Air Force Base in Tullahoma, Tennessee, July–August 2010. Wildlife Management Area Unit 1 contained 26 usable camera sites and Wildlife Management Area Unit 2 contained 24, creating a systematic spacing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

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

Model and unit	AIC_c [a]	ΔAIC_c	w_i [b]	D [c]	SE	g0 [d]	SE	σ [e]	SE
Unit - 1									
Half-normal g0[*b*] σ[.]	993.06	0.00	0.49	1.68	0.34	0.27	0.08	351.43	15.99
Half-normalg0[*b*] σ[*b*]	993.17	0.11	0.46	1.58	0.33	0.20	0.07	410.53	42.36
Half-normal g0[*h2*] σ[.]	997.61	4.55	0.05	1.55	0.31	0.30	0.06	347.78	14.06
Half-normal g0[.] σ[*b*]	1004.30	11.24	0.00	1.63	0.33	0.55	0.07	314.27	21.17
Half-normal g0[*h2*] σ[*b*]	1004.31	11.25	0.00	1.53	0.32	0.18	0.08	360.38	26.78
Half-normal g0[.] σ[.]	1005.86	12.80	0.00	1.50	0.29	0.56	0.07	350.24	15.83
Model average				1.63	0.33	0.24	0.07	378.38	28.05
Unit - 2									
Half-normal g0[*b*] σ[.]	963.80	0.00	0.66	2.56	0.56	0.15	0.05	334.93	14.44
Half-normal g0[*b*] σ[*b*]	965.14	1.34	0.34	2.47	0.57	0.12	0.05	372.50	38.44
Half-normal g0[.] σ[*b*]	986.22	22.42	0.00	2.26	0.40	0.45	0.05	269.13	19.26
Half-normal g0[*h2*] σ[*b*]	986.74	22.94	0.00	2.21	0.40	0.30	0.07	281.37	16.87
Half-normal g0[*h2*] σ[.]	987.37	23.57	0.00	2.80	1.38	0.50	0.05	342.42	15.52
Half-normal g0[.] σ[.]	997.76	33.96	0.00	1.84	0.31	0.45	0.05	333.91	14.75
Model average				2.53	0.56	0.14	0.05	347.65	22.56

a. Akaike's Information Criterion adjusted for small *n*
b. Akaike wt.
c. Density (number of antlered deer/km^2)
d. Probability of detecting an individual on a single occasion when the distance between their home range center and a trap is zero (g0)
e. Scale parameter that determines the rate at which detection probability decreases with distance between a home range center and a trap (σ)

2, respectively (Table 1). Model-averaged density estimates based on SECR models were 1.63 (SE = 0.33; C.I. 1.03–2.58) and 2.53 (SE = 0.56; C.I. 1.71–3.75) males/km^2 for Units 1 and 2, respectively (Table 1). Model-averaged detection probability (g0) was 0.24 for Unit 1 and 0.14 for Unit 2 (Table 1).

Discussion

Our results indicate that SECR modeling can be used with camera survey data to directly estimate antlered male density and obtain a measure of precision that is lacking in traditional closed-population analyses of camera surveys. White et al. (1982) indicated a population estimate without a measure of precision (sampling variance) and an assessment of related assumptions is not reliable. The model average of the 95% confidence intervals for the density estimates indicate an adequate measure of precision and a measure by which to evaluate for consistency across years. Thus, SECR modeling allows wildlife managers to make more informed decisions. Biased but precise estimates can be used to monitor population change provided detection rates are relatively constant over time (White et al. 1982, Diefenbach 2005, Beaver et al. 2014).

We obtained similar density estimates for the traditional camera method and SECR modeling (Table 1). However, both traditional camera survey estimates were higher than SECR estimates. It should be noted that our study was based on an open population of an unknown number of deer. Therefore, we do not know if the estimates are accurate, but only that the SECR modeling approach added a measure of precision currently lacking from traditional camera survey estimates. However, previous studies that have used SECR modeling in coordination with the jaguar (*Panthera onca*), puma (*Puma concolor*), ocelot (*Leopardus pardalis*), lowland tapir (*Tapirus terrestris*), and threatened Louisiana black bear (*Ursus americanus luteolus*) for density estimation have reported that SECR models provide estimates that are more accurate (Tobler and Powell 2013), precise (Chandler and Clark 2014), and unbiased because they don't rely on an informal estimation of the effective survey area (Noss et al. 2012).

The traditional camera surveys use a buffer around the trapping zone based on assumed home range size. Therefore, a male deer could be recorded as using the trapping zone but its range center may not be in the trapping zone. With SECR methods, we estimated the range center based on the distribution of locations and therefore were able to better determine which deer had range centers actually in the area surveyed.

We believe the use of a habitat mask used in our SECR analysis to reflect actual habitat boundaries was justified because we did not observe crossover of individually identified males between the two study area units from our camera survey data which were divided by a major highway running between them. As noted, a habitat mask was applied to exclude the downtown city limits of Tullahoma adjacent to WMA Units 1 and 2 as well as the mask excluding Unit 2 as habitat for the Unit 1 analyses and vise versa. Had there been observable overlap between the two units, the habitat mask would not have been needed. Increasing the size of the state space would have resulted in a decrease in the density estimates because it would have accounted for individuals with home range centers near the boundaries of the state space that had a negligible probably of being detected. With the habitat mask applied, the state space used in the SECR analysis becomes very similar to the administrative boundaries already in place for the WMA Units 1 and 2 that were used for the estimated trap area in the traditional analysis. In this case, it was easy to estimate effective sample area for the traditional camera surveys with the boundaries that we knew limited deer movement. However, without SECR, it is difficult to designate an effective sample area for camera surveys where contiguous deer habitat occurs. Assumptions must be made concerning how far a deer may travel from range center. It is also important to consider that resources and camera failure rates will differ from property to property, and the effective sample area estimated using the SECR analysis can adjust to those differences whereas the traditional analysis cannot.

Unlike traditional use of camera surveys, our results suggest SECR modeling can be used with camera survey data to account for variation in capture probability because of the varying number and location of traps in each animal's home range (Efford et al. 2004, Efford et al. 2009). This confers a robustness that is lacking in traditional closed-population analyses of camera surveys. SECR modeling also showed that conventional sources of variation (i.e., time, response to capture, and individual heterogeneity) may affect either or both the detection probability and spatial scale parameter (Efford et al. 2004, Efford et al. 2009). Our two top models (Table 1) for both Units 1 and 2 suggested a strong behavioral response in the detection parameter. One of the top models had a behavioral effect on the spatial scale parameter; however, the strength of the behavioral response in the detection parameter was driving the importance of the model. The behavioral effect on spatial scale was considered an uninformative parameter (Arnold 2010).

Our study was designed to evaluate the effectiveness of using SECR approaches as an alternative to traditional camera survey analysis for estimating deer density. Therefore, our study does not have data to make any conclusions as to the behavioral bias or to what effect the behavior may have on density and capture rates. However, the strong behavioral response to the detection parameter in our models likely resulted from use of bait. Bait affects previous trapping experience which affects detection (Jacobson et al. 1997, Campbell et al. 2006). Any behavioral influence which affects detection can lead to biased results by violating the assumption of equal detectability.

Jacobson et al. (1997) indicated gender bias could be problematic for estimates of deer populations. Other studies indicated behavioral biases influence which animals are captured on camera (Jacobson et al. 1997, Cutler and Swann 1999, Larrucea et al. 2007). Behavioral responses to baiting violate the assumption of equal detectability (Cutler and Swann 1999, Kilpatrick and Stober 2002, Campbell et al. 2006, Roberts et al. 2006). Kilpatrick and Stober (2002) observed temporary bait sites caused a shift in activity, and Campbell et al. (2006) reported high variability among radio-collared female deer in response to baiting and shifts in activity centers during baiting periods. McCoy et al. (2011) reported sex ratio and recruitment estimates from randomly placed cameras differed from cameras at feed stations during all time periods evaluated. Donohue et al. (2013) evaluated deer density on social dominance and aggressive behavior at concentrated food sites. Mature bucks (>2 years) tended to dominate over all age and sex groups and as deer density increased, so did social pressures that limited access of subordinate age and sex groups to concentrated food sites. Failure to account for the effects of aggressive interactions and differential deer visitation on behavior during baited camera surveys could lead to biased density estimates (Donohue et al. 2013).

SECR modeling showed it can be used to improve the effectiveness of using cameras as a survey technique for white-tailed deer by providing managers with a measure of precision and a means of assessing related assumptions. A complete understanding of biases involved with camera surveys will enhance this tool as a density estimation technique for managing deer and other ungulates.

Management Implications

Spatially explicit capture-recapture models strengthen camera surveys by including spatial distribution of captured deer by incorporating capture heterogeneity and behavioral responses and by providing a measure of precision. We used model averaging to account for model uncertainty whereby top models received more weight when determining final density estimates. An estimate of precision gives more confidence to changes in population size when evaluating different harvest or other management strategies over time. Managers should be aware of potential biases in their data obtained from traditional camera surveys and how the bias might affect management decisions. Although there is a learning curve when using SECR methods, deer managers could collect data and work with other professionals who have the expertise in modeling.

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