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SHORT COMMUNICATION

Efficacy of N-mixture models for surveying and monitoring white-tailed deer populations

Allison C. Keever[1] · Conor P. McGowan[2] · Stephen S. Ditchkoff[3] · Peter K. Acker[3] · James B. Grand[2] · Chad H. Newbolt[3]

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Abstract Automated cameras have become increasingly common for monitoring wildlife populations and estimating abundance. Most analytical methods, however, fail to account for incomplete and variable detection probabilities, which biases abundance estimates. Methods which do account for detection have not been thoroughly tested, and those that have been tested were compared to other methods of abundance estimation. The goal of this study was to evaluate the accuracy and effectiveness of the N-mixture method, which explicitly incorporates detection probability, to monitor white-tailed deer (*Odocoileus virginianus*) by using camera surveys and a known, marked population to collect data and estimate abundance. Motion-triggered camera surveys were conducted at Auburn University's deer research facility in 2010. Abundance estimates were generated using N-mixture models and compared to the known number of marked deer in the population. We compared abundance estimates generated from a decreasing number of survey days used in analysis and by time periods (DAY, NIGHT, SUNRISE, SUNSET, CREPUSCULAR, ALL TIMES). Accurate abundance estimates were generated using 24 h of data and nighttime only data. Accuracy of abundance estimates increased with increasing number of survey days until day 5, and there was no improvement with additional data. This suggests that, for our system, 5-day camera surveys conducted at night were adequate for abundance estimation and population monitoring. Further, our study demonstrates that camera surveys and N-mixture models may be a highly effective method for estimation and monitoring of ungulate populations.

Keywords N-mixture models · White-tailed deer populations · *Odocoileus virginianus*

Communicated by: Dries Kuijper

✉ Allison C. Keever
ack0016@auburn.edu

[1] School of Forestry and Wildlife Sciences, Alabama Cooperative Fish and Wildlife Research Unit, Auburn University, Auburn, AL 36849, USA

[2] U.S. Geological Survey, Alabama Cooperative Fish and Wildlife Research Unit, Auburn University, Auburn, AL 36849, USA

[3] School of Forestry and Wildlife Sciences, Auburn University, Auburn, AL 36849, USA

Accurate estimates of population size and structure are essential for wildlife management decisions, particularly decisions regarding harvest. Ungulate populations that are harvested also require information about demographic composition due to differences between males and females (Connolly 1981; Ebert et al. 2012). Many methods to estimate population parameters, however, are limited in their applicability and feasibility. Survey methods used to estimate population parameters of white-tailed deer (*Odocoileus virginianus*), for example, have included spotlight counts (Fafarman and DeYoung 1986; McCullough 1982), pellet counts (Eberhardt and Van Etten 1956; Fuller 1991), aerial surveys (Potvin et al. 2002), and thermal imaging surveys (Gill et al. 1997). An assumption with many survey methods is that all animals have equal probability of detection (Krebs 1999) despite the fact that detection is often imperfect and variable between and among species, sites, and years (Pollock et al. 2002; Sollmann et al. 2013). Spotlight counts, for instance, are subject to variable detection rates (Collier et al. 2007; Collier et al. 2013) and bias associated with sampling along roads (Anderson 2001). Furthermore, many of these methods are labor intensive and limited to certain habitat types (Lancia et al. 1994). Dense vegetation has been shown to affect detection using thermal

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imaging surveys (Ditchkoff et al. 2005), spotlight counts (Collier et al. 2013), and pellet counts (Langdon 2001).

Automated cameras have been used to monitor wildlife in a variety of habitat types (Curtis et al. 2009; Jacobson et al. 1997; Koerth et al. 1997), and there are various options available for design and analysis of camera survey data. Burton et al. (2015) reviewed over 250 camera trap studies published from 2008 to 2013 and found that the majority estimated density of marked individuals. Mark-recapture or mark-resight models can be used to analyze camera data containing individuals that are marked or uniquely identifiable (Karanth and Nichols 1998); however, the process of capturing and marking animals often is expensive and time consuming and may not be possible in many situations. Although some methods exist for estimating abundance or density of unmarked populations, many camera trap studies on unmarked populations estimate relative abundance and assume equal detectability (Burton et al. 2015). Jacobson et al. (1997) developed a survey method for white-tailed deer which utilizes the unique features of branch-antlered males (antler configuration and mass, pelage, and body characteristics) to identify individual males, thereby eliminating the need to commit financial and time resources to capture and mark animals. Population estimates and demographic parameters are derived by this method using the number of individual branch-antlered males and ratios of the number of images of branch-antlered males to the number of images of spikes, females, and fawns. This method heavily relies on an assumption of equal detection between all age classes and sexes in order to produce reliable population estimates; however, these assumptions may be violated in practice, resulting in biased estimates (Koerth and Kroll 2000; McCoy et al. 2011; Weckel et al. 2011). Various methods, including Weckel et al. (2011), have attempted to correct the Jacobson et al. (1997) method to account for differences in detection between branch-antlered males, spikes, females, and fawns and bias resulting from baited camera sites and different visitation and feeding patterns of males, females, and fawns (Koerth and Kroll 2000; McCoy et al. 2011). However, the amendment proposed by Weckel et al. (2011) does not address variation in detection that exists due to environmental factors or temporal variation in visitation rates.

Variation in activity patterns throughout the day can result in temporal variation in detection probabilities. It is commonly accepted that detectability is not uniform and may differ between sexes, age classes, individuals, and location (Cutler and Swann 1999; McCoy et al. 2011); however, temporal variation is generally not considered. During the day, deer are generally less active (Beier and McCullough 1990) and may be detected less frequently during that time. Many species show temporal variation in activity patterns throughout the day such as grizzly bears (*Ursus arctos*; Munro et al. 2006), African ungulates (Owen-Smith and Goodall 2014), and elk (*Cervus elaphus*; Green and Bear 1990), for example. It would be prudent to know how detection varied during the day to better plan timing of camera surveys to increase detection rates of the species of interest.

An alternative to the Jacobson et al. (1997) method that can account for temporal variation is Royle's (2004) N-mixture model. Similar to the Jacobson et al. (1997) method, the N-mixture model does not require physically trapping and marking individuals, yet can account for local variation in detection probability. An additional advantage to this method is that individual identification is not required, which may reduce time and effort associated with surveys and facilitate large-scale monitoring (Lyons et al. 2012). Royle's (2004) N-mixture model incorporates detection probability into the abundance estimate using a mixture of binomial and Poisson distribution models from spatially and temporally replicated counts. Royle's (2004) N-mixture model is a hierarchical model that estimates two parameters, detection probability (p) and mean abundance (λ), with spatially and temporally varying covariates. This model assumes that the population is demographically closed, individuals are not counted at more than one site, and all individuals within the sampling unit have some probability of being detected (Royle 2004). N-mixture models have been applied to a multitude of avian species including red-legged partridge (*Alectoris rufa*; Jakob et al. 2014), black oystercatchers (*Haematopus bachmani*; Lyons et al. 2012), and wild turkeys (*Meleagris gallopavo*; Damm 2010). N-mixture models have also been used with mammals, such as white-tailed deer (Petroelje et al. 2014), yet these methods have not been thoroughly tested.

Our goal for this study was to test the accuracy and effectiveness of Royle's (2004) N-mixture model applied to camera surveys of white-tailed deer. We used game camera images from an enclosed population of white-tailed deer, containing a known number of marked individuals, to evaluate accuracy of abundance estimates from N-mixture models. In our study, the total number of tagged animals served as the known abundance against which estimated abundance from the statistical analysis could be compared. Our specific objectives were to (1) test estimation accuracy and (2) determine how survey effort affected accuracy of abundance estimation using Royle's (2004) N-mixture model. Further, by calculating the proportion of tagged animals observed at any given time of day, our study provided an opportunity to identify variations in daily activity patterns of white-tailed deer in our study area and evaluate how these variations influenced population estimates from N-mixture models. Rather than report estimated detection from the data, we report on the proportion of tagged animals observed at all survey locations at any given time step during the survey. Since true detection probability is unknown for the study population, we focused on the proportion observed metric so that we could make inferences about study design when practitioners apply this method on free-ranging wild ungulate populations.

Study area

Our study was conducted at Auburn University's deer research facility near Camp Hill, Lee County, Alabama. A 2.5-m high-tensile fence enclosed approximately 174 ha within the Piedmont Agricultural Experiment Station. A large creek bisected the property, and vegetation was dominated by hardwood bottomlands and uplands, old pastures, and planted pines. Supplemental feed was available at three feeding stations placed throughout the facility as well as several food plots during this study. The facility contained approximately 100 deer, which descended from the wild deer population within the fence at the time of construction in 2007. At the time of this study, our known number of marked deer was 75, consisting of 41 males and 34 females. The deer population was intensively monitored, with capturing and camera surveys occurring every year to track the population. Density of deer within the facility was estimated to be 57 deer/km^2, which was much greater than typical free-ranging deer populations in the Southeast. Keyser et al. (2005) found that deer density in the Southeast generally ranges from 1 to 32 deer/km^2 for free-ranging deer. No hunting occurred within the research facility.

Methods

Auburn University's deer research facility contained a population of white-tailed deer that had been extensively studied the previous 3 years. Researchers attempted to capture every individual each year and recorded antler and body size and tagged individuals [see Acker (2013) for specific capture and handling techniques]. Individuals were assigned a unique number, freeze branded, and tagged in both ears with cattle ear tags which made identification possible from multiple angles. Capture techniques followed American Society of Mammalogists' guidelines (Sikes et al. 2011) and were in accordance with Auburn University's Institutional Animal Care and Use Committee (2008–1241, 2010–1785). We used the known number of tagged males and females in the closed population as the basis for assessing N-mixture modeling estimation accuracy.

Camera surveys were conducted in 2010 from September 21 to 27 as part of another research initiative [see Acker (2013)]. Four sites were systematically established (i.e., the study site was divided into four grid cells with one camera per grid cell) for survey 1 with a camera density of approximately 1/44 ha. With free-ranging ungulate populations, establishing camera densities that are at least 1.5 times greater than mean home range size would probably be effective; however, in our case with marked animals, we could determine if an individual was detected at more than one survey site. Specific camera locations were sought beneath the forest canopy in areas where vegetation would not affect image quality and field of view. Sites were pre-baited 5 days prior to camera deployment with 22 kg of whole corn and were refreshed as needed. Infrared-triggered trail cameras (DigitalEye 7.2, PixController Inc., Export, PA) were set on a 5-min trigger-delay setting, meaning that no more than one photo could be taken in 5 min. Sensitivity, flash brightness, and ISO settings were all standardized. Cameras were set out for 7 days and were placed on steel mounting boards 1.5 m above ground level and aimed downward at a 15° angle (Holtfreter et al. 2008).

All images were processed by a single observer to maintain consistency throughout the study. Only images of marked deer with clearly readable ear tags were included in the count data because we wanted to estimate the marked population. We excluded unreadable tags or apparently unmarked animals because our objective was to estimate the abundance of marked animals so as to compare to the known total. Furthermore, freeze brands were inconsistently legible and were treated as unknowns since the deer could not be identified and were not included in the count. Even in an unmarked population, deer position within an image can make classification of sex or age unreliable and result in unknowns similarly to our study. We recorded tag number, time, date, and sex for marked deer in each picture. We constructed encounter histories as the number of marked individuals per 5-min time interval for each site. This interval was specified to standardize time of occasions for all sites, which allowed us to calculate time-specific detection probabilities. We chose the 5-min interval because images were separated by at least 5 min. For example, images taken at 06:02 were placed in the 06:00 time bin, and images taken at 06:03 were placed in the 06:05 time bin. Occasions for which there were no images or there were no identifiable marked deer were given a zero count.

We used an N-mixture modeling approach to estimate abundance from repeated count data from the camera trap data. N-mixture models assume population closure, individual IDs are ignored across occasions but not within occasions, individual detections are independent and all individuals have equal detection probabilities, individuals are not counted at more than one site, the count data are Poisson distributed variables, and individual detections are binomial random events (Royle and Dorazio 2008). Counts (n_{it}) from the sampling occasions $t = 1, 2, \ldots, T$ were assumed to be independent binomial random variables, and abundance (N_i) at each site $i = 1, 2, \ldots, R$ followed a Poisson distribution. The likelihood was

$$L(p, \lambda|\{n_{it}\}) = \prod_{i=1}^{R} \left\{ \sum_{N_i=max_t n_{it}}^{\infty} \left(\prod_{t=1}^{T} Bin(n_{it}|N_i, p) \right) f(N_i|\lambda) \right\}$$

where the estimated parameters were p, the individual detection probability, and λ, mean abundance. Explanatory variables could be included for both the detection process and the state (abundance) process. N-mixture models can produce biased estimates when detection probability is low or few sites are visited (Dénes et al. 2015; Dennis et al. 2015). For example, Dénes et al. (2015) found that estimates were biased high when detection probabilities were low and showed less precision than other methods tested. Within the high-fence enclosure, our data met the population closure, and though we used individual marks for counting animals, we counted all marked individuals at all sampling occasions and ignored marking data across occasions.

Detection probabilities generated from the N-mixture model (estimated detection) and used in the estimation process are not reported in this paper. Instead, we calculated the proportion of the tagged animals observed (P_{obs}) for a more direct, precise, and time-specific measure of animal availability for observation at each date and time as

$$P_{\text{obs},t} = \frac{n_{it}}{N}$$

where n_{it} is the number of marked individuals photographed in time t at location i and N is the total number of marked deer ($n = 75$). We chose to use this more direct, precise measure of availability, rather than focus on detection, as calculated here because it allowed us to calculate detailed, time-specific availability rates without the variability and uncertainty of the estimated detection from the N-mixture model. In other words, detection estimates are simply estimates of unknown parameters and the strength of our study is having a known tagged population to assess abundance estimates. When calculating P_{obs} for adult males and females that were marked, we divided by the number of each sex in the population at the time of the survey ($N_m = 41$ males, $N_f = 34$ females). Standard errors were calculated using all date and time-specific $P_{\text{obs},t}$ either during each time period or survey day. We compared P_{obs} between time periods for males and females using a Welch's two-sample t test with significance level set at $\alpha \leq 0.05$.

For analysis of abundance, we used the count of marked male and female deer with readable ear tags in each picture without respect to individual identity. We generated abundance estimates separately for males and females in MATLAB® (The MathWorks Inc., Natick, MA) using the maximum-likelihood N-mixture model (Royle 2004) with counts (photos) every 10 min. We standardized images to a 5-min interval because images could have been captured only 5 min apart. However, research has shown that deer typically spend >10 min feeding when bait is scattered on the ground (Kozicky 1997). To reduce computational time, we increased survey occasions to 10 min instead of using each image every 5 min. Using the 5-min occasions would have greatly increased computational time with no new information gleaned from the additional photos (Price Tack et al. 2016).

The N-mixture model (Royle 2004) estimates mean abundance (λ). With assumptions made about the area each site represents, total abundance of the sampled area can be calculated. Mean home range of adult male deer within a high-fence area of 260 ha was 58 ha, and ranged from 24 to 94 ha (Karns 2014). Deer partitioned the area into quadrants and only ventured outside that area a few times during peak rut (Karns 2014). Our study site was slightly smaller (174 ha), and home range size would likely be more constricted. We assumed that each of the four sites represented 43.5 ha (174 total ha/4 sites). As suggested by Royle (2004), we multiplied mean abundance (λ) by the number of sites (4) to get total abundance, which also represented the total marked population size within the facility.

We reduced camera survey effort for abundance analysis post hoc by using data only from certain time periods of the day and by eliminating number of survey days used to generate abundance estimates. In general, such a reduction limits the number of survey occasions in a data set and thereby reduces the time required for picture assessment and analysis, but could affect estimator precision. The time periods we evaluated were DAY (8-h time period from 2 h after sunrise to 2 h before sunset), NIGHT (16-h time period from 2 h prior to sunset to 2 h after sunrise), SUNRISE (4-h time period around sunrise), SUNSET (4-h time period around sunset), CREPUSCULAR (8-h time period including both SUNRISE and SUNSET time periods), and ALL TIMES (24 h). Accuracy of estimates was calculated as the relative deviation from the number of known, marked individuals, and was calculated as $\frac{N-N}{N}$, where N is the estimated abundance and N is the true population size. This is commonly referred to as the percent relative error, and can be either positive or negative depending on the direction of error.

Results

We observed 34 of 75 possible marked deer in the survey period. One deer was observed at more than one site. There was no clear trend in P_{obs} across survey days. However, mean P_{obs} of females ($\overline{P_{\text{obs},f}} = 0.00852 \pm 0.000791$) was greater ($p < 0.001$) than that of males ($\overline{P_{\text{obs},m}} = 0.00526 \pm 0.000631$). P_{obs} of females was greater than P_{obs} of males during the DAY, NIGHT, SUNSET, and CREPUSCULAR time periods also (Table 1). P_{obs} decreased following sunrise and increased and peaked following sunset (Fig. 1). We also found that detection during the DAY time period was less ($P < 0.001$) than all other time periods (Table 2).

We did not estimate abundance for the DAY time period because P_{obs} rates were too low. Abundance estimates for the ALL TIMES and NIGHT time periods provided the most accurate abundance estimates for the total population. Using

Table 1 Proportion of the population observed ($\overline{P_{obs}}$), estimated abundance ($\widehat{N}$), standard errors (SEs), and % accuracy of abundance estimates of male and female white-tailed deer by time period, DAY (2 h after sunrise to 2 h before sunset), NIGHT (2 h before sunset to 2 h after sunrise), SUNRISE (2 h before and after sunrise), SUNSET (2 h before and after sunset), CREPUSCULAR (2 h before and after both sunrise and sunset), and ALL TIMES (24 h) at Auburn University's deer research facility located near Camp Hill, Alabama, from September of 2010

	Male					Female				
	$\overline{P_{obs}}$	SE	$\widehat{N}$	SE	% accuracy	$\overline{P_{obs}}$	SE	$\widehat{N}$	SE	% accuracy
DAY	0.00068	0.00022	NA[a]	NA[a]	NA[a]	0.0038	0.00046	NA[a]	NA[a]	NA[a]
NIGHT	0.0076	0.00046	35.8	7.1	−12.7%	0.011	0.00055	34.7	7.1	2.1%
SUNRISE	0.0073	0.00090	12.8	8.4	−68.8%	0.011	0.0010	283.7	8.7	734.4%
SUNSET	0.0091	0.0010	102.9	27.8	150.9%	0.012	0.0013	32.4	8.6	−4.7%
CREPUSCULAR	0.0082	0.00096	23.4	7.7	−42.9%	0.012	0.0012	46.1	8.7	35.6%
ALL TIMES	0.0053	0.00032	38.0	6.9	−7.3%	0.0085	0.00040	35.9	7.1	5.5%

[a] These values were inestimable due to low detection probability

≥5 survey days resulted in abundance estimates closest to our true population size for the ALL TIMES and NIGHT time periods; however, there was no increase in accuracy with additional days surveyed beyond 5 days (Fig. 2).

Discussion

With the increasing use of automated cameras to survey wildlife populations, there have been a growing number of studies evaluating the accuracy of these survey methods. Previous studies have compared estimates with other forms of estimation to evaluate accuracy (Couturier et al. 2013; Curtis et al. 2009; Dénes et al. 2015; Doré et al. 2011; Jacobson et al. 1997; Kéry et al. 2005; McKinley et al. 2006; Weckel et al. 2011; Zylstra et al. 2010). In this study, we had the unique opportunity to compare our abundance estimates generated using Royle's (2004) N-mixture model with a known number of marked deer. Our findings suggest that repeated count data from camera surveys and N-mixture models can provide accurate abundance estimates for white-tailed deer. Abundance estimates from the NIGHT and ALL TIMES time periods were similar to our true population size with fairly small standard errors (coefficient of variation was consistently ~20% or less). We found that estimates of abundance were most accurate for the NIGHT and ALL TIMES time periods when surveying for a minimum of 5 days. Further, abundance of males and females were accurately estimated for the NIGHT and ALL TIMES time periods so male:female ratio estimates would be representative of the population. Because white-tailed deer are an important game species, accurate estimates of population parameters, including sex ratios and recruitment rates, are necessary for making management and harvest decisions. Due to the season in which we conducted our camera surveys, we could not estimate fawn abundance. In our study area, fawns are born in July and August (Gray et al. 2002) and would not be very mobile at the time of the survey, and hence would have very low visitation rates to camera sites (McCoy et al. 2011).

Although abundance estimates from the NIGHT and ALL TIMES time periods were accurate, estimates from the other time periods were biased high. Additionally, estimates were

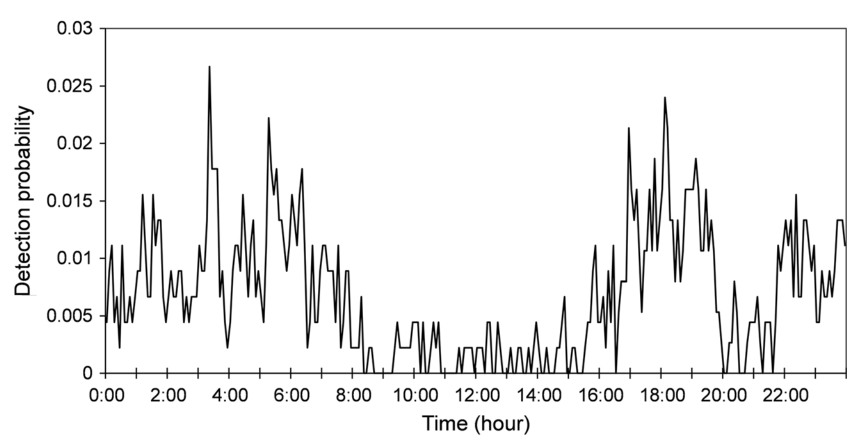

Fig. 1 Mean proportion of the population observed (P_{obs}) for a fenced population of white-tailed deer by time of day at Auburn University's deer research facility located near Camp Hill, Alabama from September of 2010

Table 2 Proportion of marked animals observed ($\overline{P_{obs}}$), cumulative proportion of marked animals observed, abundance estimates $\widehat{N}$ standard errors (SEs), and number of survey occasions (n) by time period, DAY (2 h after sunrise to 2 h before sunset), NIGHT (2 h before sunset to 2 h after sunrise), SUNRISE (2 h before and after sunrise), SUNSET (2 h before and after sunset), CREPUSCULAR (2 h before and after both sunrise and sunset), and ALL TIMES (24 h) of a fenced white-tailed deer population at Auburn University's deer research facility located near Camp Hill, Alabama, from September of 2010

Time period	Number	$\overline{P_{obs}}$	SE	Cumulative p	$\widehat{N}$	SE
DAY	288	0.0021	0.00024	0.451	NA[a]	NA[a]
NIGHT	551	0.0091	0.00035	0.994	70.5	14.1
SUNRISE	150	0.0089	0.00066	0.740	296.5	17.1
SUNSET	125	0.011	0.00084	0.742	135.3	36.5
CREPESCULAR	275	0.0099	0.00076	0.934	69.5	16.4
ALL TIMES	839	0.0067	0.00026	0.997	73.9	14.0

The true population size of marked deer was 75

[a] These values were inestimable due to low detection probability

biased high for the NIGHT and ALL TIMES time periods with less than five survey days. This is likely due to our low encounter rate (P_{obs}) combined with the effects of the number of survey occasions. The relatively low accuracy during the CREPUSCULAR period was particularly surprising given that P_{obs} peaked during these times and given knowledge of white-tailed deer daily activity patterns; however, the CREPUSCULAR time period simply did not result in sufficient sample size to generate good abundance estimates ($n = 275$; Table 2). This is supported by the fact that with less than 5 days of all-day and night time only data, abundance was overestimated, which we also attribute to low sample sizes. Dennis et al. (2015) found that the N-mixture model can produce biased estimates of abundance with low detection probabilities and a limited number of survey occasions. Similarly, Couturier et al. (2013) found that abundance estimates for tortoises were biased high with detection probabilities less than 0.5 and had lower precision than capture-recapture methods. We had more survey occasions than other studies; however, our detection probabilities were much lower. The ALL TIMES and NIGHT time periods had much greater cumulative detection probabilities than the other time periods which likely led to improved model estimates during these periods.

Surveying for a minimum of 5 days resulted in accurate abundance estimates for the ALL TIMES and NIGHT time periods in this study, suggesting that surveying for 5 days at night may be sufficient under similar conditions. Jacobson et al. (1997) required 10 days to observe >80% of marked deer in their study, suggesting that a greater survey period or greater camera density may be necessary to maximize the accuracy of their method compared to N-mixture models. N-mixture models (Royle 2004) are not hindered by individual identification, and surveys using these methods, consequently,

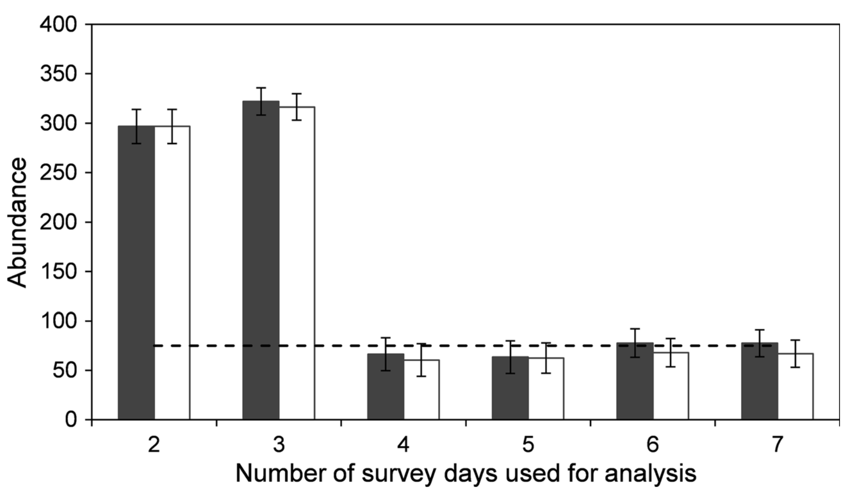

Fig. 2 Abundance estimates for a marked, known population of fenced white-tailed deer by number of survey days used for analysis using repeated point counts for two different time periods, night (2 h before sunset to 2 h after sunrise; *open bars*) and all times (24 h; *solid bars*) at Auburn University's deer research facility located near Camp Hill, Alabama, from September 2010. True abundance of the marked population is denoted by the *black dashed line*

may not require as many survey days. However, surveys lasting less than 5 days or only during SUNRISE, SUNSET, or CREPUSCULAR time periods may result in inaccurate abundance estimates. Surveys using time-lapse photography can generate tremendous amounts of data, especially if multiple cameras are employed at multiple sites with cameras taking photographs every few minutes. Consider that a study with ten cameras at five sites taking photographs every 15 min for 1 week would generate over 30,000 images to be reviewed. Price Tack et al. (2016) showed that labor costs to review photographs and record data from time-lapse camera trap studies can escalate quickly, so assessing the time of day to target monitoring based on higher activity levels or detection probability would decrease research costs and also improve model estimates.

Conducting our field assessment of the N-mixture modeling approach on a semi-captive herd presents some potential limitations for inference to free-ranging wild populations. There may be behavioral abnormalities present in the semi-captive population that affect detectability or population density. For example, there is a strong likelihood that the semi-captive deer are pre-conditioned to visit bait piles at camera stations, falsely inflating detection probabilities. But, these issues would likely affect the observation portion of the N-mixture hierarchical model, and those issues would only affect the resulting abundance estimate precision and time required to get an adequate sample size for estimating abundance. Free-ranging population studies might require longer survey periods to get sufficient sample sizes if their study population is not trained on bait sites. Or, those studies might require pre-bating at camera sites to begin attracting animals to the camera sites prior to data collection. For our high-fence, semi-captive population, we were able to comfortably assume population closure, especially for the tagged individuals since no new tags were added during our study. However, for most wild populations unless the sampling intervals are very short, which might restrict sample size and estimate precision, population closure may not be a valid assumption. In those instances, researchers can turn to other estimation techniques for similar data, such as the Dail-Madsen method (Dail and Madsen 2011) which is an extension of the N-mixture model that relaxes the closure assumption. We acknowledge that there are differences between our semi-captive population and free-ranging ungulates in terms of behavior, density, and demographics; however, we note that oftentimes analytical methods are devised and tested using ex situ approaches to first test and validate methodologies. For example, Nichols and Pollock (1983) used a semi-captive population of mice to study and test the assumptions of mark-recapture models, and more recently, a wide variety of simulation studies are used to assess the effectiveness of analytical methods (e.g., Pooler and Smith 2005; McGowan and Gardner 2013; Lyons et al. 2015). These ex situ assessments were not perfect reflections of the wild environment, but they have provided useful inferences about the utility of statistical methods and bolster the credibility of statistical methods.

Using N-mixture modeling to assess and monitor deer and other ungulate populations would represent a shift away from long accepted and mathematically simpler methods, e.g., the Jacobson method (Jacobson et al. 1997). However, an N-mixture-based approach can statistically address assumptions about detectability and other observation bias through the hierarchical modeling structure. In other words, though more complex, N-mixture modeling more directly accounts for and addresses sampling assumptions that the Jacobson and other count-based methods do not (McCoy et al. 2011). Many studies evaluating camera survey techniques have noted potential bias in different visitation rates among sexes and age classes, and suggest the need to account for this variability in detection (Jacobson et al. 1997; MacKenzie et al. 2002; McCoy et al. 2011; Pollock et al. 2002; Weckel et al. 2011). Jacobson et al. (1997) noted different photographic observation rates between males and females under a range of camera densities. They attributed this to differences in home range size between males and females but failed to account for this difference in the abundance estimates. We also found a difference between the sexes, where male detection probability was significantly less than female detection probability. This is contrary to Jacobson et al. (1997) who found that males were photographed more frequently, especially at low camera density (1/259 ha). The difference found by Jacobson et al. (1997) could have been due to their lowest camera density of 1/65 ha, whereas our camera density was 1/44 ha. Our results are similar to those of Weckel et al. (2011), who noted that females were photographed more frequently with a greater camera density (<1/25 ha). Home range size of female deer is approximately half that of males (Vanderhoof and Jacobson 1993; Walter et al. 2011); a lower camera density should result in fewer females counted at camera sites. Further, our study was conducted on a high-fence population with a high population density, which may exacerbate this effect (Marchinton and Hirth 1984).

We also observed a significant difference between P_{obs} during the day and all other time periods which could serve as another potential source of variability in observation that is often unaccounted for in camera surveys. We used P_{obs} as a surrogate and more precise measure of detection probability, but the inference with respect to detection probability is the same. It would be prudent to know how detection varied during the day to better plan timing of camera surveys to increase detection rates of the species of interest. Low detection probability can bias estimates using N-mixture models (Dénes et al. 2015; Dennis et al. 2015). Further, long-term studies may encounter changes in detection probabilities from year to year or season to season. For instance, white-tailed deer fawns and males are more likely to be detected in the spring than the fall (Keever 2014). Analyses based on indices or raw counts that do not account for temporal variation in detection may result in inaccurate conclusions about population change if a time trend in detection probability exists. Accounting for important sources of variation in detection can result in less biased, more accurate estimates of abundance and may affect management decisions.

It is important to note the fundamental differences in the underlying assumptions of the N-mixture models (Royle 2004) and those of methods which rely on individual identification, such as the Jacobson et al. (1997) method. The Jacobson et al. (1997) method assumes that individual branch-antlered males can be accurately identified, and that there is equal detectability among sexes and age classes. As noted above, the N-mixture model (Royle 2004) estimates mean abundance, assuming that all individuals within the sampling unit have some probability of being counted, and that individuals will not be counted at more than one site. If camera and sampling density are too great, then individuals may be counted at more than one site. Although estimates of the number of animals using each site are unbiased, estimates of the total population (extrapolated from the mean number of individuals visiting all sites) would be biased high. There were additional camera trap data available for this marked population from later in the fall when the rutting period begins and white-tailed deer typically exhibit increased mobility and maintain larger home ranges. We analyzed these data but found that 23 animals were observed and multiple camera sites and abundance estimates for the study area were greatly inflated. We excluded these data and analyses from our study because the animals' behavior was different when those data were collected and our camera density was not designed to account for that. However, this still emphasizes the importance of selecting an appropriate camera density and spatial arrangement for each study. Conversely, if camera and sampling density are too low, estimates of the number of animals that use a particular site and total abundance would be unbiased; however, estimates of the total population would be low, because some individuals would not be available to be counted.

Other studies have noted variation in abundance estimates due to camera density. Jacobson et al. (1997) and McKinley et al. (2006) found that the greatest camera density (<1/65 ha) they tested provided more accurate estimates than lower camera densities. This is because the Jacobson et al. (1997) method relies on individual identification, and increasing camera density should increase photographic recapture rates. For N-mixture models, however, a high camera density can result in individuals being observed at more than one site, which is in violation of one of the N-mixture model assumptions (Royle 2004). This could inflate abundance estimates. Therefore, when designing surveys applying N-mixture models, careful consideration should be given to ensure that all individuals have some probability of detection and that individuals are unlikely to be counted at more than one site. An alternative method, spatial capture-recapture (Royle et al. 2009), can be used to estimate animal densities, accounts for movements of individuals, and allows for complex models of detection; however, this approach requires the additional expenditures associated with marking individuals. The random encounter model (REM; Rowcliffe et al. 2008) estimates density of unmarked individuals by modeling encounter rates. This method requires auxiliary information of group size and movement speed to model encounter rates. If data are available for group size and movement speed, this could be a feasible option to estimate density of unmarked animals; however, it has not been widely tested.

We conclude that use of Royle's (2004) N-mixture model and count data collected from camera surveys can provide accurate population and demographic estimates for white-tailed deer if the survey design does not violate model assumptions and sample size is sufficient. We found that surveying for five nights returned highly accurate estimates of male and female deer abundance in our study area, so not only was total abundance accurate but also male:female ratios. Our results indicate that count data collected from camera surveys using N-mixture models has potential for use in monitoring ungulate populations.

Management implications

We suggest that N-mixture (Royle 2004) models could be widely adopted for surveying and monitoring free-ranging deer population with appropriate considerations for the behavioral differences between the semi-captive population studied here and wild populations. The models may in fact be useful in monitoring a variety of ungulate populations for informing harvest management decisions, with appropriate species-specific adjustments for space use and animal behavior. In our study, we used the trigger-delay setting; however, use of a time-lapse setting would eliminate variation in detection due to cameras (Damm et al. 2010) and also the potential for induced capture heterogeneity. Additionally, surveying only at night could reduce effort without reducing estimation precision; however, activity patterns of the targeted species should be taken into account. We found that for white-tailed deer, abundance estimates using only night time data provided comparable estimates to surveying for 24 h, which would result in a 50% decrease in the number of photographs using a time-lapse setting and could be sufficient for species with similar activity patterns to deer. Camera density should be low enough that multiple animals will be unlikely to be counted at more than one site. The camera density required to meet the assumption would be inversely related to the home range size of the targeted species. Male white-tailed deer have a greater home range size than females (Vanderhoof and Jacobson 1993; Walter et al. 2011) and would require a lower camera and sampling density than for females to meet the assumptions and accurately estimate abundance. Studies of free-ranging deer should evaluate the relationship between home range size and abundance estimates from N-mixture models.

Density can be calculated from mean abundance estimates generated from N-mixture models by determining what area the site represents (Jakob et al. 2014). If the sampling density is much larger or smaller than the home range size of the animal, the effective sampling area (ESA) must be adjusted to convert from mean site abundance to density. Otherwise, estimates of density would be biased. Another alternative for unmarked populations is to use the method developed by Chandler and Royle (2013), which places camera sites close together and determines density from the spatial structure of the count data. However, this method requires high sampling density and may not be feasible for large study areas.

Our study comparing known numbers of marked deer to abundance estimates from N-mixture models indicate that repeated counts of unmarked deer using time-lapse photography could be a highly effective and efficient way to survey ungulates. Although the code is available for Program R (R Core Team 2013; Fiske and Chandler 2011; Royle and Dorazio 2008) N-mixture models still require the knowledge of computer code and software. Further, hierarchical models are technically cumbersome, while the Jacobson et al. (1997) method is perceived to be a useful tool for managers because it does not require advanced quantitative analyses. However, the Jacobson et al. (1997) approach does not address sources of potentially significant estimation bias (spatial, temporal, gender, and age detection biases). We contend that although an analysis is more familiar and technically easier, potentially biased estimates that do not account for the complexities of detection variability could lead managers to incorrect inference and flawed decisions.

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