



Original Article

A Modification of Jacobson et al.'s (1997) Individual Branch-Antlered Male Method for Censusing White-Tailed Deer

MARK WECKEL,¹ Mianus River Gorge Preserve, 167 Mianus River Road, Bedford, NY 10506, USA; Division of Vertebrate Zoology, American Museum of Natural History, Central Park W at 79th Street, New York, NY 10024, USA; The Graduate Center, The City University of New York, 365 Fifth Avenue, New York, NY 10016, USA

ROBERT F. ROCKWELL, Division of Vertebrate Zoology, American Museum of Natural History, Central Park W at 79th Street, New York, NY 10024, USA

FRANK SECRET, John Jay High School, 60 N Salem Road, Cross River, NY 10518, USA; Wildlife Technician Program, Mianus River Gorge Preserve, Bedford, NY 10506, USA

ABSTRACT Jacobson et al.'s (1997) individual branch-antlered male (IBAM) method is a popular camera technique for estimating white-tailed deer (*Odocoileus virginianus*) abundance. Demographic ratios are estimated from raw photographic occurrences (RPO) of males, females, and fawns. Point abundance estimates of each group are estimated by using said ratios to extrapolate from a count of uniquely identifiable males. In 2009, using camera-trap data from the Mianus River Gorge Preserve (NY), we modified the IBAM technique to 1) generate measures of uncertainty for parameter estimates via bootstrapping camera stations, and 2) address the concern that RPO ratios may be biased if groups of animals differ in their probability of being photographed (e.g., trap success [TS]). For each sex–age group, we evaluated RPO as a function of TS using linear regression to generate photographic counts standardized by TS (standardized photographic occurrences [SPO]). We generated estimates of sex–age ratios and abundances using both RPO and SPO. To evaluate the accuracy of using SPO in conjunction with the IBAM method, we independently estimated the abundance of a marked group of female deer using a Poisson log normal (PNE) mark–resight estimator. Abundance estimates across sex–age classes were most similar between PNE and IBAM when SPO demographic ratios were used. Owing to the greater TS of females, using SPO discounted the relative abundance of females and, thus, lowered the female:male ratios and raised the fawn:female ratio. Uncertainty was broad across all approaches, yet accounting for TS reduced the confounding variability owing to differences in detection probability and generated more accurate parameter estimates. © 2011 The Wildlife Society.

KEY WORDS abundance, camera traps, census technique, detection, *Odocoileus virginianus*, sex ratios, trap success, white-tailed deer.

Population estimation techniques, such as aerial inventories, thermal infrared sensing, or spot-light surveys, provide useful metrics for monitoring white-tailed deer (*Odocoileus virginianus*) abundance (Fafarman and DeYoung 1986, Naugle et al. 1996), but may not be appropriate for the scale of smaller management areas characteristic of fragmented suburban and urban environments. Here, deer management can be highly localized (McDonald et al. 1998, Porter et al. 2004) and wildlife professionals need accurate abundance estimates specific to individual properties to plan harvest goals and track population trends. This is especially important where lethal means to reduce overpopulated suburban deer herds are subject to political pressure and public accountability.

Jacobson et al.'s (1997) individual branch-antlered male (IBAM) abundance estimator is a popular method suitable to this scale. The method uses camera-trap data to enumerate a minimum number of uniquely identifiable adult males and to estimate sex and age-class ratios (hereafter, demographic ratios). The abundance of all males, females, and fawns is calculated by way of extrapolation. However, there are 2 major drawbacks to the IBAM estimator that limit its broad application. First, the method does not provide error terms for parameter estimates (Curtis et al. 2009). Without a measure of precision, comparing abundance across time and place is limited. Second, the method estimates the relative abundance of males, females, and fawns using raw photographic occurrences (RPO), which assumes that the different groups have equal detection probabilities (McCoy 2010, O'Brien 2011). Failing to meet this assumption will bias abundance estimates in favor of those groups whose individuals are more frequently photographed.

Received: 22 December 2010; Accepted: 28 June 2011;
Published: 3 October 2011

¹E-mail: mweckel@mianus.org

In this paper, we propose modifications to Jacobson's IBAM method that generate measures of uncertainty for parameter estimates and that standardize photographic occurrences (SPO) by detection to minimize bias. By evaluating RPO as a function of detection, researchers can quantify differing detection rates among demographic groups and then standardize photographic captures, thus providing less-biased estimates of nonmale abundances. To evaluate the accuracy of the IBAM method using both RPO and SPO demographic ratios, we used McClintock et al.'s (2008) mark-resight estimator on a marked population of female deer to generate an independent deer-abundance estimate.

STUDY AREA

We conducted our camera survey at the Mianus River Gorge Preserve (MRGP; 309 ha or 764 acres), located in suburban Westchester (NY) and Fairfield (CT) counties, USA. The MRGP was established to protect an old-growth Eastern hemlock (*Tsuga canadensis*) forest and 70–100-yr-old mixed hardwood forest. Dominant overstory species included black birch (*Betula lenta*), yellow birch (*B. alleghaniensis*), black oak (*Quercus nigra*), red oak (*Q. rubra*), red maple (*Acer rubrum*), and sugar maple (*A. saccharum*). The MRGP lay along the Mianus Greenway and was surrounded by large estates, smaller suburban developments, and protected reservoir land. Since 2004, the deer population has been managed using controlled archery. Exact prehunt deer densities for the MRGP were unknown. However, in 2002, 2 independent aerial inventories were conducted adjacent to the preserve in unmanaged areas of Bedford, New York and Greenwich, Connecticut. Daniels et al. (2009) estimated the Bedford deer population to be 22 deer/km². More forested areas of Greenwich (which were contiguous with the MRGP via the Mianus Greenway) had densities of 23.6 deer/km² (Brash et al. 2004). From 2002 to 2008, 160 deer were harvested from the MRGP, with female deer comprising 72% of the total harvest.

METHODS

Deer Capture

We captured adult female deer (>1.5 yr old) between June and September of 2008 and 2009 using immobilizing drugs remotely delivered by cartridge-powered darts (Pneu-Dart, Williamsburg, PA). Deer were targeted for capture by driving roads bordering the MRGP. Darts contained a 1.0–1.5-mL solution of butorphanol (50 mg/mL), azaperone (100 mg/mL), and medetomidine (40 mg/mL) in a ratio of 6:2:3 (Wildlife Pharmaceuticals, Inc., Fort Collins, CO). Deer were revived by intramuscular injections of 3 mL antisedan (5 mg/mL), 1 mL naltrexone (50 mg/mL), and 1 mL tolazoline (200 mg/mL). In 2008, each deer received a uniquely color-coded ear tag embedded with a 14.7-g, 433-MHz active radiofrequency identification transponder (RF Code, Austin, TX). In 2009, transponders were embedded in radiocollars (Sirtrak, North Liberty, IA) rather than ear tags. Transponders actively broadcasted over an average range of 131 m at the MRGP (M. Weckel,

unpublished data), allowing authors to determine whether animals were alive and within the study area during the camera survey. Immobilization and tagging were carried out under Institutional Animal Care and Use Committee protocol 0715 approved by the City College of the City University of New York.

Camera Monitors

We conducted the camera survey from 16 August to 16 October 2009 at unbaited camera stations. We chose this 2-month period following fawning and prior to the NYS Region 3S hunting season because we assumed the population was closed, but also because antler growth was approaching full development. At each camera station, we deployed a Reconyx RC55 (Reconyx, Holmen, WI) camera affixed to a tree between 0.5 m and 0.75 m off the ground and 0.5–1.0 m off the trail. These cameras use an infrared flash and are passively triggered by heat and motion. Cameras were programmed to take 5 successive photos when triggered and had no delay between successive trigger events, allowing for near continuous photographic captures at the rate of 1 photograph/sec. For each event we recorded the age, sex, and number of deer seen.

We sampled the MRGP in 2 contiguous blocks of 12 cameras, each with each camera operational for an average of 29 days. (Twenty-three camera stations were included in the final analysis because one camera failed). Initial camera-station locations were randomly chosen, but they were slightly adjusted in the field so that well-used trails were sampled. Also, because mark-recapture procedures assume that no animal has a zero probability of being photographed, camera stations were separated by no more than 500 m. This configuration was based on the average summer home range (21.4 ha) of suburban female deer documented by Porter et al. (2004). We felt our camera stations were conservatively spaced because Porter et al.'s (2004) estimate was equal to or smaller than many other female suburban-deer home ranges (Kilpatrick and Spohr 2000, Etter et al. 2002, Grund et al. 2002, Storm et al. 2006).

Estimating RPO, SPO, and Demographic Ratios

Following Jacobson et al. (1997), we estimated 3 demographic ratios based on RPO: spike males:branch-antlered males (rP_s), females:all males (rP_d), and fawns:females (rP_f). For example, $rP_d = N_d/N_b$, where N_d = total number of antlerless adult deer occurrences in photographs and N_b = total number of male occurrences in photographs. We used 1,000 nonparametric bootstrapped resamples of camera-station data to generate 95% percentile intervals (PI) of the demographic ratios as a measure of parameter uncertainty (Efron and Tibshirani 1993). These 95% PI rely on variability among bootstrap samples and are distinct from confidence intervals for a Neyman-Pearson assessment of significance, which rely on data meeting assumptions of normality (Efron and Tibshirani 1993).

Jacobson et al.'s (1997) method assumed that the ratio of RPO to abundance is constant across demographic groups. Violations of this assumption would inflate or deflate the relative abundance of sex-age classes based on differences in

detection among males, females, and fawns (e.g., if F deer are more likely to be photographed, then their relative abundance would be biased high). We sought to compute SPO that corrected RPO for any potential inequalities in detection rates among the sex–age classes. To do so, we first estimated trap success (TS [the proportion of trap-nights with ≥ 1 deer photograph]) for each sex–age class at each camera station. For each sex–age class, we examined the relationships between RPO and TS using linear regression (Fig. 1). We forced a structural y-intercept of zero because the number of photographs must always be zero if TS equals zero. We estimated parameters using least-squares regression techniques and estimated SPO as the model beta, β . The model β , or slope, can be interpreted as the number of photographs per unit of TS; see Fig. 1). We used 1,000 nonparametric bootstraps of our camera stations to estimate uncertainty for SPO. We visually inspected standardized residual plots to check for any obvious departures from normality. We then used SPO estimates for each demographic group to generate standardized spike:branch-antlered male ratio (sP_s), female:male ratio (sP_d), and the standardized fawn:female ratio (sP_f). We again used nonparametric bootstrapping at this step, sampling from the distribution of SPO observed in each demographic group, to generate percentile intervals for demographic ratios.

Estimating Abundance Using IBAM and a Mark–Resight Estimator

We identified branch-antlered males based on antler size and configuration, as well as additional identifying characteristics such as relative body size and pelage patterns. This minimum number of unique branch-antlered males (B) was the starting point for calculating the number of spikes (M with unbranched antlers), spikes:all males, males:females, and females:fawns using both RPO and SPO ratios (e.g., where S = spike abundance; $S = B \times rP_s$ or $S = B \times sP_s$). We used 1,000 nonparametric bootstraps drawing from the observed frequency distribution of demographic ratios and abundances to estimate the abundance of successive age-classes. We refer to estimates generated by Jacobson et al.’s (1997) method either as IBAM + RPO or IBAM + SPO depending on whether raw or standardized photographs were used.

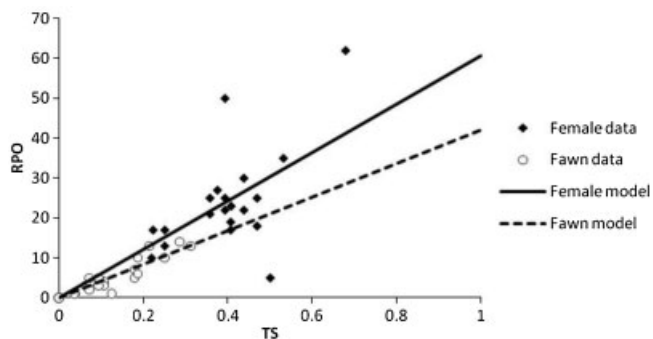


Figure 1. Linear functions relating raw photographic occurrences (RPO) to trap success (TS) for female and fawn white-tailed deer in Mianus River Gorge Preserve, Bedford, New York, USA, 2009.

We used the mark–resight Poisson log normal estimator (PNE; McClintock et al. 2008) in Program Mark (White and Burnham 1999) to analyze capture data of female deer. This estimator uses individual capture histories of marked animals and the number of photographs of unmarked animals to estimate total abundance. We used the mean female estimate generated by the PNE analysis as a starting point to extrapolate from females to all males, and from females to fawns using both RPO and SPO ratios. As with the above analysis, we estimated uncertainty in our parameter estimates in successive abundance calculations using nonparametric bootstrapping. We refer to estimates generated by McClintock et al.’s (2008) method either as PNE + RPO or PNE + SPO depending on whether raw or standardized photographs were used.

Generating estimates of males and females by extrapolating from females (PNE) and male estimates (IBAM), respectively, provided a cross-validation and allowed us to evaluate the relative accuracy of using RPO versus SPO. Ideally, an unbiased demographic ratio (either RPO or SPO) would yield agreement between estimated and extrapolated male and female abundances.

RESULTS

Estimating RPO, SPO, and Demographic Ratios

Camera stations were operated for 662 trap-nights. During this time we collected 130, 66, 480, and 112 RPO of branch-antlered males, spikes, females, and fawns, respectively. Across camera stations, female deer had a higher TS ($\bar{x} = 0.31$, SE = 0.02) than branch-antlered males ($\bar{x} = 0.14$, SE = 0.01), spikes ($\bar{x} = 0.08$, SE = 0.01), and fawns ($\bar{x} = 0.12$, SE = 0.01). Using camera data on TS to SPO via linear regression, we predicted the mean SPO for each sex–age class: spike males ($\beta = 27.86$, 95% PI = 19.64–33.98), branch-antlered males ($\beta = 42.65$, 95% PI = 33.58–54.04), all males ($\beta = 40.02$, 95% PI = 31.28–48.70), for females ($\beta = 60.57$, 95% PI = 49.16–72.99), and fawns ($\beta = 42.02$, 95% PI = 35.85–47.54).

Using SPO to estimate demographic ratios, the mean female:male ratio was 24% smaller as compared to RPO-derived ratio estimates (Fig. 2). The converse was true for the fawn:female ratio and spike:branch-antlered male ratios, which were 223% and 34.7% higher, respectively, when using SPO versus RPO. Nevertheless, owing to broader uncertainty, we found considerable overlap in demographic ratios computed from RPO and SPO for female:male and spike:branch-antlered male ratios (Table 1).

Estimating Abundance Using IBAM and a Mark–Resight Estimator

Using Jacobson’s criteria, we identified 19 distinct branch-antlered males. We found that 51.5% of photographs of branch-antlered males were of too poor quality to attempt individual identification. Average capture rate for these 19 branch-antlered males was 3.32 photos (SE = 0.48). Fourteen female deer were marked and remained alive within the study area during the entire camera survey. All 14 marked female deer were photographed, with a mean capture rate of

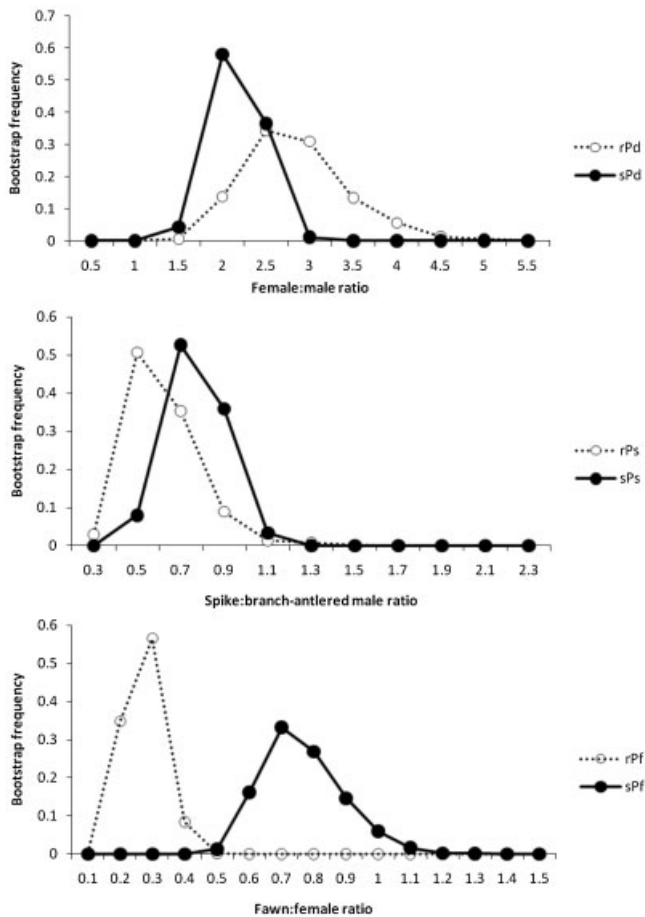


Figure 2. Frequency distribution for demographic ratios of white-tailed deer in Mianus River Gorge Preserve, Bedford, New York, USA, 2009, computed by nonparametric bootstrapping using both raw photographic occurrences (RPO, white circles) and standardized photographic occurrences (SPO, black circles). Demographic ratios based on RPO (r): spike males:branch-antlered males (rP_d), females:all males (rP_f), and fawns:females (rP_f). Demographic ratios based on SPO (s): spike males:branch-antlered males (sP_s), females:all males (sP_d), and fawns:females (sP_f).

7.86 photos (SE = 1.52). Twenty-two percent of marked female photographs could not be identified to an individual. Using the PNE mark-resight method of McClintock et al. (2008), we estimated the MRPG female herd at 49.5 females (95% PI = 38.7–63.4).

In comparing total male abundance estimates across all methods, there was similar agreement except for that generated using the PNE + RPO. Here, only 19 males were estimated, a likely underestimate considering that 19 IBAMs were identified from photographs. Regarding females, agreement between mean abundance estimates was closest for IBAM + SPO and PNE + SPO analyses (Table 2). Using SPO ratios, the IBAM-method female estimate was 22% higher than the mark-recapture female estimate, as compared to 43% higher when RPO was used. Regarding fawns, there was again most agreement between the IBAM + SPO and PNE + SPO estimates. Overall, mean total deer estimates were closest between the PNE + SPO and IBAM + SPO; nevertheless, there was considerable overlap among PI across methods, obscuring this difference.

Table 1. Comparing demographic ratios of white-tailed deer, computed using raw photographic occurrences (RPO) and standardized photographic occurrences (SPO), in Mianus River Gorge Preserve, Westchester County, New York, USA, 2009.

Sex-age ratio	Standardized or raw photographs	Symbol ^a	Mean	95% PI
Spike:branch-antlered M	RPO	rP_s	0.49	0.29–0.88
	SPO	sP_s	0.66	0.43–0.90
F:M	RPO	rP_d	2.52	1.67–3.91
	SPO	sP_d	1.92	1.50–2.40
Fawns:F	RPO	rP_f	0.22	0.14–0.34
	SPO	sP_f	0.71	0.52–0.95

^a Demographic ratios based on RPO (r): spike M:branch-antlered M (rP_s), F:all M (rP_d), and fawns:F (rP_f). Demographic ratios based on SPO (s): spike M:branch-antlered M (sP_s), F:all M (sP_d), and fawns:F (sP_f).

Table 2. Comparing abundance of male, female, and fawn white-tailed deer in Mianus River Gorge Preserve, Westchester County, New York, USA, 2009.

Sex-age group	Method	Mean	95% PI
M	IBAM + RPO ^a	28.30	24.74–35.57
	IBAM + SPO ^b	31.54	27.35–35.92
	PNE + RPO ^c	19.46	12.40–29.72
	PNE + SPO ^d	26.12	20.59–32.62
F	IBAM + RPO	70.86	45.54–113.69
	IBAM + SPO	60.43	44.78–77.38
	PNE + RPO	49.50 ^e	38.70–63.40
	PNE + SPO	49.50 ^e	38.70–63.40
Fawns	IBAM + RPO	15.56	8.67–29.05
	IBAM + SPO	41.79	28.00–61.76
	PNE + RPO	10.80	6.77–16.58
	PNE + SPO	35.04	25.33–46.42
Total deer	IBAM + RPO	106.96	79.09–147.06
	IBAM + SPO	134.89	111.82–162.31
	PNE + RPO	80.26	71.79–92.54
	PNE + SPO	110.52	99.34–123.89

^a IBAM + RPO—Abundance method using demographic ratios calculated from raw photographic occurrences (RPO) to extrapolate from a min. no. of individual branch-antlered M (IBAM) enumerated by Jacobson et al.'s (1997) criteria.

^b IBAM + SPO—Abundance method using demographic ratios calculated from standardized photographic occurrences (SPO) to extrapolate from a min. no. of branch-antlered M (IBAM) enumerated by Jacobson et al.'s (1997) criteria.

^c PNE + RPO—Abundance method using demographic ratios calculated from raw photographic occurrences (RPO) to extrapolate from the mean F estimate generated by McClintock et al.'s (2008) mark-resight Poisson log normal estimator (PNE).

^d PNE + SPO—Abundance method using demographic ratios calculated from standardized photographic occurrences (SPO) to extrapolate from the mean F estimate generated by McClintock et al.'s (2008) mark-resight Poisson log normal estimator (PNE).

^e PNE—Mean no. of F deer calculated using demographic ratios calculated from McClintock et al.'s (2008) mark-resight Poisson log normal estimator (PNE).

DISCUSSION

In our study, we used cross-validation to evaluate the relative accuracy of demographic ratios derived from RPO and SPO. We used a mark-resight analysis (PNE) to estimate the number of females, the IBAM method to estimate the number of branch-antlered males, and demographic ratios derived from photographs (RPO vs. SPO) to extrapolate the

abundances of other demographic groups. Only unbiased demographic ratios should converge on the same estimate of deer abundance, regardless of whether the starting point for extrapolation was branch-antlered males (IBAM) or marked females (PNE). In our study, we found estimates of total deer, females, males, and fawns were most similar between IBAM and PNE methods when SPO were used for extrapolation.

Jacobson et al.'s (1997) approach is a creative way of using natural markings of adult male deer to estimate a minimum number of branch-antlered males. If there are no biases due to different sex-age probabilities of being photographed, Jacobson's use of RPO would be suitable for extrapolating from branch-antlered males to females and fawns. However, we did document differences in TS with females being the most frequently photographed group, on average twice as often as males and fawns. Subsequently, using information on TS to generate SPO, the relative abundance of females was discounted, describing a deer herd with fewer females, more males, and more fawns.

At the MRGP and at nearby Westchester preserves, controlled hunts can be controversial and subject to political pressure to demonstrate declines in female abundance. A difference between 71 and 60 females generated by IBAM + RPO and IBAM + SPO, respectively, can mask whether or not herd reduction is occurring. Similarly, using RPO measures as an indication of recruitment would suggest a slower growing population and would strongly influence any attempt to model harvest scenarios. Based on RPO, the MRGP herd has an unlikely 5 females for every 1 fawn during our study's late-summer camera survey, compared to the SPO estimate of 1.4 females for every fawn. With the knowledge that mean fertility rates among suburban adult females are safely in excess of 1.0 (Witham and Jones 1992, Swihart et al. 1995) and suburban fawn survival at 6 months has been found to be >80% (Witham and Jones 1992, Swihart et al. 1995, Etter et al. 2002), the RPO fawn:female ratio of 0.22 is dubious. Using RPO to estimate demographic ratios may produce greater disparities in sex-age distributions where differences in TS are more extreme. For example, Curtis et al. (2009) documented a female:male ratio of 3.7 in comparison to 0.94 reported by Jacobson et al. (1997). Curtis et al. (2009) attributed this disparity to differing management strategies affecting the density of males and females; however, it can also be due to differences in male and female TS across study sites.

Several confounding variables, including sex-age-based differences in home range (Jacobson et al. 1997), baiting (McCoy 2010), social status (Séquin et al. 2003), and even the model of camera (Kelly and Holub 2008) can influence the rate and number of photographic captures. These factors ultimately bias relative abundance indices, making comparative use of camera data across groups (sex, age, or species) difficult to interpret. For example, our greater female TS may be an artifact of our camera density. We intentionally designed our camera array around a small female home range in order to maximize female captures and improve

our mark-resight estimates. Likewise, Jacobson et al. (1997) observed a higher rate of female capture as camera density increased, which they attributed to smaller female home ranges and an increased likelihood of photographing a female's core area. Although comparative studies of male and female movement are lacking for suburban areas, there is evidence that male home ranges are considerably larger than those of females (Gaughan and DeStefano 2005). In addition, MRGP hunters, as well as the authors, have noted that it is not uncommon to see the same marked female deer multiple times per week in the same location; while repeat visits by any branch-antlered male are less frequent (e.g., M. Weckel, personal observation). Consequently, knowing that our camera placement produced a positive bias in favor of female photographs and that female deer may have smaller home ranges, discounting female RPO by female TS facilitated a more conservative use of photographic data in estimating demographic ratios. This approach of using SPO can also extend the utility of camera traps as a multispecies monitoring tool and generate more accurate relative abundance indices of entire communities of species.

Accounting for TS may also renew the discussion surrounding the use of bait in conjunction with Jacobson et al.'s (1997) method. Several authors have warned against baiting due to differences in bait use by different sex-age classes (Koerth and Kroll 2000, Roberts et al. 2006, McCoy 2010). However, by standardizing photographs by differences in TS, one could potentially control for these differences. Bait could improve the initial enumeration of branch-antlered males by keeping animals within the frame and generating numerous photographs at many angles, ultimately facilitating identification. In our study, approximately half of branch-antlered photographs were eliminated from this analysis because they were of too poor quality to permit identification. These pictures were of males who walked perpendicularly to the camera, providing blurred photographs of only one flank. With that said, accounting for differences in the use of bait does not address the concern that baiting can shift deer ranges, thereby violating the assumption of geographic closure (Kilpatrick and Stober 2002, Curtis et al. 2009).

Standardizing photographs as a function of TS generated more accurate and biologically reasonable parameter estimates, yet is subject to meeting the assumptions of linear modeling. Although we did not observe any gross departures from linearity or homoscedasticity, parameter estimates of SPO are strongly influenced by the distribution and inherent variability in the data set. For example, we estimated the SPO of branch-antlered males (42.65) to be greater than that of all males (42.02). Clearly, the ratio of branch-antlered males to all males is not 1:1. Rather, this results from aggregating spike and branch-antlered males. Spikes generally produced fewer RPO at a lower TS, which served to depress the β in the all-male analysis. This provides a cautionary note that extreme RPO values (RPO larger or smaller than expected from the model), especially at low or high TS, can strongly influence parameter estimates. Extreme RPO

values may occur where cameras are placed in hotspots of activity (e.g., a scent station frequented daily by M bachelor groups, or a wildlife corridor funneling movement between fenced human developments). Cameras with low RPO at high TS can be expected if cameras are placed on or near bed sites of a solitary individual or small female social units. Here, camera stations may have frequent visitation (high TS), but photograph only 1 or 2 individuals. Using purely randomly generated camera stations may help in minimizing variability caused by the researcher's camera-site selection (Kays et al. 2009); however, doing so can only increase the chance of surveying sub-par habitat and underestimating the count of individually branch-antlered males, violating an assumption of Jacobson et al.'s (1997) IBAM method; this problem needs to be further addressed.

Whether one uses RPO or SPO with Jacobson et al.'s (1997) IBAM method, large uncertainty in parameter estimates can obscure detection of changes in deer abundance over time. Our exercise in bootstrapping camera traps demonstrated that the variability in RPO among camera stations alone can contribute to large uncertainty. As long as the study animal is not uniformly distributed in space, variability among camera traps will remain. Increasing sample size via additional camera stations may help decrease variability to the benefit of both the RPO and SPO approach; however, there is a limit to how densely cameras can be deployed before autocorrelation will become a concern (Koenig 1999, Silveira et al. 2003). Furthermore, large PI are compounded by the very nature of Jacobson et al.'s (1997) method, where uncertainty in each ratio estimate and uncertainty in each abundance estimate is compounded in calculating final total deer abundance. The basic technique relies on multiplication to extrapolate from the branch-antlered male abundance; therefore, wide PI will be hard to avoid.

MANAGEMENT IMPLICATIONS

Accurate estimation of deer herds, especially the abundance of females, is key to the long-term success of urban and suburban deer management programs. Jacobson's IBAM estimator offers a promising method by capitalizing on the natural markings of adult males to generate total deer abundance, including female abundance. However, as with any method that compares raw photographic captures across sex, age, space, time, or species, the use of camera data will be limited where the assumption of equal detection is not tested or supported (Cutler and Swann 1999, Séquin et al. 2003, Larrucea et al. 2007, O'Brien 2011). The method of standardizing RPO by TS acknowledges that TS is a complicated variable, contingent on a variety of factors that may be difficult to control. Our solution uses measurable differences in TS as a means of standardizing RPO delivering a more conservative interpretation of camera data. Ignoring differences in trap success may lead to inaccurate estimates. Furthermore, when using camera-based methods to census and monitor white-tailed deer, wildlife professionals need to consider the level of precision necessary for the question at hand and the magnitude of population change one needs to

discern. These concerns should be considered along with the benefits of using camera traps, which include the ability to simultaneously and noninvasively monitor activity period (Carthew and Slater 1991), spatial distribution (Atwood and Weeks 2002), sex and age structure (Jacobson et al. 1997), and to sample remote areas (Roberts et al. 2006) where vegetation cover (Anderson and Lindzey 1996) or prohibitive cost (Koerth et al. 1997) may preclude traditional methods such as aerial surveys.

ACKNOWLEDGMENTS

We extend our appreciation to R. Chrisite and C. Nagy of the MRGP for their aid in data analysis, as well as to the sportsman in the MRGP deer-management program for their assistance in interpreting camera images. Special thanks to S. McGuigan, A. Wincorn, and MRGP interns for their work in the capture and marking of deer. Funding was provided by the Conservation Fund of the Campfire Club of America and the MRGP. AE Charitable Foundation and the Dorr Foundation provided support for the Wildlife Technician Program.

LITERATURE CITED

- Anderson, C. R., Jr., and F. G. Lindzey. 1996. Moose sightability model developed from helicopter surveys. *Wildlife Society Bulletin* 24:247–259.
- Atwood, T. C., and H. P. Weeks, Jr. 2002. Sex- and age-specific patterns of mineral lick use by white-tailed deer (*Odocoileus virginianus*). *American Midland Naturalist* 148:289–296.
- Brash, A. R., E. V. P. Brower, L. Henrey, and D. Savageau. 2004. Report on managing Greenwich's deer population. Greenwich Conservation Commission Wildlife Issues Committee, Greenwich, Connecticut, USA.
- Carthew, S. M., and E. Slater. 1991. Monitoring animal activity with automated photography. *Journal of Wildlife Management* 55:689–692.
- Curtis, P. D., B. Boldgiv, P. M. Mattison, and J. R. Boulanger. 2009. Estimating deer abundance in suburban areas with infrared-triggered cameras. *Human-Wildlife Conflicts* 3:116–128.
- Cutler, T. L., and D. E. Swann. 1999. Using remote photography in wildlife ecology: a review. *Wildlife Society Bulletin* 27:571–581.
- Daniels, T. J., R. C. Falco, E. E. McHugh, J. Vellozi, T. Boccia, A. J. DeNicola, J. M. Pound, J. A. Miller, J. E. George, and D. Fish. 2009. Acaricidal treatment of white-tailed deer to control *Ixodes scapularis* (Acari: Ixodidae) in a New York Lyme disease-endemic community. *Vector-Borne and Zoonotic Diseases* 9:381–387.
- Efron, B., and R. J. Tibshirani. 1993. *An introduction to the bootstrap*. Chapman & Hall, New York, New York, USA.
- Etter, D. R., K. M. Hollis, T. R. Van Deelen, D. R. Ludwig, J. E. Chelsvig, C. L. Anchor, and R. E. Warner. 2002. Survival and movements and white-tailed deer in suburban Chicago, Illinois. *Journal of Wildlife Management* 66:500–510.
- Fafarman, K. R., and C. A. DeYoung. 1986. Evaluation of spotlight counts of deer in south Texas. *Wildlife Society Bulletin* 13:146–149.
- Gaughan, C. R., and S. DeStefano. 2005. Movement patterns of rural and suburban white-tailed deer in Massachusetts. *Urban Ecosystems* 8:191–202.
- Grund, M. D., J. B. McAninch, and E. P. Wiggers. 2002. Seasonal movements and habitat use of female white-tailed deer associated with an urban park. *Journal of Wildlife Management* 66:123–130.
- Jacobson, H. A., J. C. Kroll, R. W. Browning, B. H. Koerth, and M. H. Conway. 1997. Infrared-triggered cameras for censusing white-tailed deer. *Wildlife Society Bulletin* 25:547–556.
- Kays, R., B. Kranstauber, P. A. Jansen, C. Carbone, M. Rowcliffe, T. Foundtain, and S. Tilak. 2009. Camera traps as sensor networks for monitoring animal communities. The 34th IEEE Conference on Local Computer Networks, 20–23 October 2009, Zurich, Switzerland.

- Kelly, M. J., and E. L. Holub. 2008. Camera trapping of carnivores: trap success among camera types and across species, and habitat selection by species on Salt Pond Mountain, Giles County, Virginia. *Northeastern Naturalist* 15:249–262.
- Kilpatrick, H. J., and S. M. Spohr. 2000. Movements of female white-tailed deer in a suburban landscape: a management perspective. *Wildlife Society Bulletin* 4:1038–1045.
- Kilpatrick, H. J., and W. A. Stober. 2002. Effects of temporary bait sites on movements of suburban white-tailed deer. *Wildlife Society Bulletin* 30:760–766.
- Koenig, W. D. 1999. Spatial autocorrelation of ecological phenomena. *Trends in Ecology and Evolution* 14:22–26.
- Koerth, B. H., and J. C. Kroll. 2000. Bait type and timing for deer counts using cameras triggered by infrared monitors. *Wildlife Society Bulletin* 28:630–635.
- Koerth, B. H., C. D. McKown, and J. C. Kroll. 1997. Infrared-triggered camera versus helicopter counts of white-tailed deer. *Wildlife Society Bulletin* 25:557–562.
- Larrucea, E. S., P. F. Brussard, M. M. Jaeger, and R. H. Barrett. 2007. Cameras, coyotes, and the assumption of equal detectability. *Journal of Wildlife Management* 71:1682–1689.
- McClintock, B. T., G. C. White, M. F. Antolin, and D. W. Tripp. 2008. Estimating abundance using mark–resight when sampling is with replacement or the number of marked individuals is unknown. *Biometrics* 65:237–246.
- McCoy, J. C. 2010. Patterns of stress and suitability of camera surveys for white-tailed deer. Thesis, Auburn University, Auburn, Alabama, USA.
- McDonald, J. E., M. R. Ellingwood, and G. M. Vecellio. 1998. Case studies in controlled deer hunting. New Hampshire Fish and Game Department, Concord, USA.
- Naugle, D. E., J. A. Jenks, and B. J. Kernohan. 1996. Use of thermal infrared sensing to estimate the density of white-tailed deer. *Wildlife Society Bulletin* 24:37–43.
- O'Brien, T. G. 2011. Abundance, density, and relative abundance: a conceptual framework. Pages 71–96 in A. F. O'Connell, J. D. Nichols, and K. U. Karanth, editors. *Camera traps in animal ecology: methods and analyses*. Springer, Tokyo, Japan.
- Porter, W. F., B. H. Underwood, and J. L. Woodward. 2004. Movement behavior, dispersal, and the potential for localized management. *Journal of Wildlife Management* 68:247–256.
- Roberts, C. W., B. L. Pierce, A. W. Braden, R. R. Lopez, N. J. Silvy, P. A. Frank, and D. Ransom, Jr. 2006. Comparison of camera and road survey estimates for white-tailed deer. *Journal of Wildlife Management* 70:263–267.
- Séquin, E. S., M. M. Jaeger, P. F. Brussard, and R. H. Barrett. 2003. Wariness of coyotes to camera traps relative to social status and territory boundaries. *Canadian Journal of Zoology* 81:2015–2025.
- Silveira, L., A. T. A. Jacomo, and J. A. F. Diniz-Filho. 2003. Camera trap, line transect census and track surveys: a comparative evaluation. *Biological Conservation* 114:351–355.
- Storm, D. J., C. K. Nielsen, E. M. Schaubert, and A. Woolf. 2006. Space use and survival of white-tailed deer in an exurban landscape. *Journal of Wildlife Management* 71:170–176.
- Swihart, R. K., P. M. Piccone, A. J. DeNicola, and L. Cornicelli. 1995. Ecology of urban and suburban white-tailed deer. Pages 35–44 in J. McAninch, editor. *Urban deer: a manageable resource?* Proceedings of the Symposium of the 55th Midwest Fish and Wildlife Conference. North Central Section of The Wildlife Society, 12–14 December 1993, St. Louis, Missouri, USA.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46 (Supplement): 120–138.
- Witham, J. H., and J. M. Jones. 1992. Biology, ecology, and management of deer in the Chicago metropolitan area. Federal Aid in Wildlife Restoration, W-87-R. Illinois Department of Conservation, Springfield, USA.

Associate Editor: Rominger.