



Tools and Technology Article

Estimating Black Bear Density Using DNA Data From Hair Snares

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ABSTRACT DNA-based mark–recapture has become a methodological cornerstone of research focused on bear species. The objective of such studies is often to estimate population size; however, doing so is frequently complicated by movement of individual bears. Movement affects the probability of detection and the assumption of closure of the population required in most models. To mitigate the bias caused by movement of individuals, population size and density estimates are often adjusted using ad hoc methods, including buffering the minimum polygon of the trapping array. We used a hierarchical, spatial capture–recapture model that contains explicit components for the spatial–point process that governs the distribution of individuals and their exposure to (via movement), and detection by, traps. We modeled detection probability as a function of each individual’s distance to the trap and an indicator variable for previous capture to account for possible behavioral responses. We applied our model to a 2006 hair–snare study of a black bear (*Ursus americanus*) population in northern New York, USA. Based on the microsatellite marker analysis of collected hair samples, 47 individuals were identified. We estimated mean density at 0.20 bears/km². A positive estimate of the indicator variable suggests that bears are attracted to baited sites; therefore, including a trap-dependence covariate is important when using bait to attract individuals. Bayesian analysis of the model was implemented in *WinBUGS*, and we provide the model specification. The model can be applied to any spatially organized trapping array (hair snares, camera traps, mist nests, etc.) to estimate density and can also account for heterogeneity and covariate information at the trap or individual level.

KEY WORDS abundance, Bayesian analysis, black bears, hair–snare trapping, hierarchical model, Markov chain Monte Carlo (MCMC), spatial capture–recapture.

Many bear species worldwide are threatened with extinction. In 2009, 6 of the 8 bear species were on the International Union for Conservation of Nature (IUCN) Red List. At the same time, other bear populations are increasing and expanding their ranges potentially creating human–wildlife conflicts. One of the first steps in making informed bear conservation and management decisions is obtaining reliable population and density estimates (Mowat and Strobeck 2000, IUCN 2007). There are a number of techniques for sampling and tracking bear species, including ear tags, colored bands, neck collars, and radiotransmitters. Arguably, the most common method now used for estimating bear population size is the application of mark–recapture techniques to data from systematically collected hair samples (Mowat and Strobeck 2000, Poole et al. 2001, Boersen et al. 2003, Belant et al. 2005, Kendall et al. 2008). Enough DNA is contained in the roots of mammalian hair for the identification of species, sex, and individuality. This is advantageous in studying bears because they are easily attracted to hair traps using bait or scent lures; therefore, samples can be collected more economically than with traditional capture–recapture methods (Woods et al. 1999).

The traps are often constructed with barbed wire and bait or an attractant and are simple to design and inexpensive (Woods et al. 1999). Accordingly, the number of studies using hair–snare traps for DNA-based mark–recapture methods has grown in recent years, contributing to the evolution of the techniques of Woods et al. (1999; see Garshelis 2006 for a detailed review). Hair–snare studies

have been conducted on grizzly bear populations in British Columbia, Canada (Mowat and Strobeck 2000, Poole et al. 2001, Romain-Bondi et al. 2004) and Glacier National Park, USA (Boulanger et al. 2008, Kendall et al. 2008, Kendall et al. 2009); on brown bears in France (Taberlet et al. 1997) and Italy (Lorenzini et al. 2004); and on black bears in the Canadian Rocky Mountains (Mowat et al. 2005), Louisiana, USA (Boersen et al. 2003, Triant et al. 2004), and Wisconsin, USA (Belant et al. 2005).

After microsatellite genotyping of hair samples from a trap array, researchers can create individual encounter histories for each bear that was captured at least once. Historically, researchers have taken such data and applied capture–recapture methods for estimating the size of a closed population (Mowat and Strobeck 2000, Boulanger et al. 2004, Romain-Bondi et al. 2004, Boulanger et al. 2006, Kendall et al. 2009). However, there are a number of practical problems with this approach. One issue is that bears move into and out of study areas, thus violating the assumption of geographic closure (Boulanger et al. 2001, Boulanger et al. 2004). Consequently, this causes ambiguity and difficulty in defining a precise sample area.

Bears have large home ranges; therefore, movement of individuals in the vicinity of trap locations can influence estimates of detection probability and abundance (Efford 2004, Borchers and Efford 2008, Efford et al. 2008, Gardner et al. 2009, Royle et al. 2009). Conceptually, movement of individuals can be viewed as a form of temporary emigration, and its effect is to lead to positive bias in estimators of abundance (N ; Kendall et al. 1997, Kendall 1999, Boulanger et al. 2004). To address this

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problem, various adjustments to the nominal sample area (i.e., the area within which traps were located) have been suggested, such as buffering the trapping array (Dice 1938, Karanth and Nichols 1998, Bales et al. 2005) to obtain an estimate of the effective trap area or using independent data from telemetry studies (White and Shenk 2001). Even in studies with collared individuals, small sample sizes can still cause problems and techniques, such as buffering the trap array by half the mean maximum distance (Wilson and Anderson 1985), can severely underestimate movement (Ríos-Uzeda and Gómez 2007).

In addition to ordinary encounter histories, data from hair-snare arrays provide auxiliary information in the form of spatial locations for each individual. The recent development of unified capture–recapture models provide a rigorous and integrated way of using individual capture histories and trap coordinates to directly estimate density without ad hoc determination of an effective trapping area (Efford 2004; Borchers and Efford 2008; Royle and Young 2008; Gardner et al. 2009; Royle et al. 2009b). The encounter history contains information about detection probability, whereas the spatial coordinates of the trap at which an individual was captured provides information about the distribution of individuals in space (i.e., territories or home ranges). This information can be used to estimate absolute density in the presence of variable trap exposure and heterogeneous detection.

We apply a spatially explicit, capture–recapture model to data obtained from a black bear study in New York, USA, collected from an array of hair-snare traps. Our model describes trap-specific encounter frequencies as a function of a latent variable (a random effect) interpreted as an individual’s activity or home range center (Efford 2004, Royle and Young 2008). The model can be formulated as a Generalized Linear Mixed model (Royle et al. 2009a, Royle and Gardner 2010), where the random effect is a function of the individual activity center. We then specify a distribution for the latent activity centers and apply standard inference methods for the analysis of the resulting hierarchical model. We provide a Bayesian analysis of the model using Markov chain Monte Carlo (MCMC) methods in *WinBUGS* (Gilks et al. 1994) using data augmentation (Royle et al. 2007).

We assume a model in which individuals may be captured at most one time per trap during each occasion, but in an arbitrary number of traps. This is typical of hair-snare studies in which separate visits by individuals to the same trap cannot be discerned. In a previous analysis, Gardner et al. (2009) used a multinomial observation model, which assumes that each individual can be captured in only a single trap during any sampling occasion; we compare the results obtained under the 2 models here. We also extend the Gardner et al. (2009) model by including the sex of individuals in the detection function and an indicator of previous detection covariates to account for a behavioral response after the bear is first captured. We used baited traps, which may cause bears to be more likely to visit traps and thus their detection rate may change after the first capture. In contrast, in studies that use only an attractant,

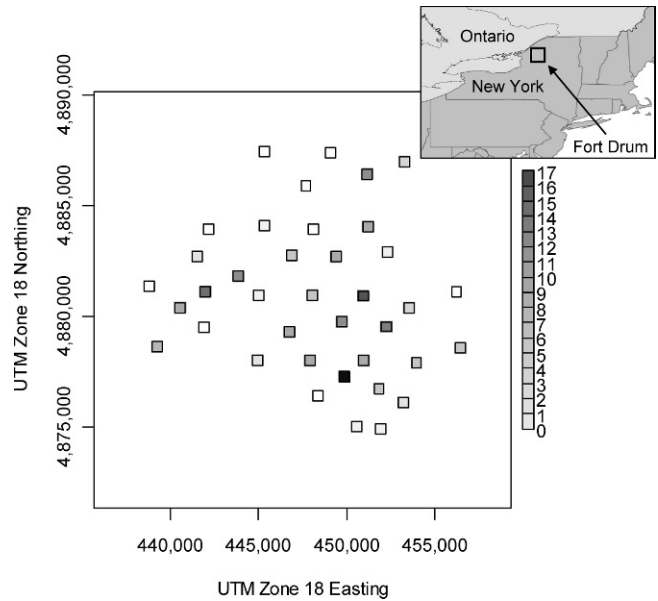


Figure 1. Study region and trap locations ($n = 38$) shaded according to the number of encounters that occurred at each trap; the darker the trap location, the greater the number of encounters. Data were collected in summer of 2006 on black bears on Fort Drum, New York, USA, as shown on the inset map. Coordinates are in Universal Transverse Mercator (UTM) Zone 18.

bears may learn that the attractant does not result in a food reward, which may lead to bears not bothering to visit sites, which would also directly affect their detection rate after the first capture.

STUDY AREA

The data we used were collected from a black bear population at the Fort Drum Military Installation, located in northern New York, USA (Fig. 1). Fort Drum is part of the northern black bear range in New York State (New York State Department of Environmental Conservation Bureau of Wildlife–Black Bear Management Team 2007).

METHODS

Data Collection

To collect hair samples, we established and baited 38 barbed-wire traps (Fig. 1). Each trap was checked weekly for 8 weeks during June–July 2006. Traps were located approximately 3 km from one another and were baited again weekly (for details, see Wegan 2008). Based on the Universal Transverse Mercator (UTM) coordinates for each trap, the area of the minimum convex polygon for the trapping array was 157.1 km². For modeling, we rescaled the UTM coordinates to kilometers by division of 1,000. We packaged hair samples into envelopes and labeled them for DNA testing, which was conducted by Wildlife Genetics International (Nelson, BC, Canada) using microsatellite genotyping. Each usable hair sample was analyzed at 6 microsatellite loci—G10L, G1D, G10P, G10M, G10J, and MU59. Heterozygosity of the 6 markers used was 0.80, which indicates a low probability of improperly matching 2 samples from individuals with differing genotypes (Paetkau

2003). Genotyping errors were reduced in the laboratory by using a multiphase procedure that included setting minimum selection standards for each hair sample, eliminating samples that failed to produce 3 of the 6 loci, examining the data set for matching genotypes displaying patterns typically produced by genotyping errors, and reanalyzing those with suspected amplification problems (D. Paetkau, Wildlife Genetics International, personal communication). Genotyping error should always be considered when doing individual-based analyses (e.g., mark-recapture modeling), and precautions should be taken to reduce the error.

Model Formulation

We suppose that sampling occurred at J traps, having coordinates $\{x_j = (x_{1j}, x_{2j}); j = 1, 2, \dots, J\}$. The observations generated from hair-snare studies were the encounter histories y_{ijk} , for individual $i = 1, 2, \dots, n$, trap $j = 1, 2, \dots, J$, and sample interval (occasion) $k = 1, 2, \dots, K$. We suppose that an individual could be captured at most one time in a trap during any particular interval but may have been captured in any number of traps. This is typical in hair-snare studies because separate visits by the same individual to a single trap cannot be uniquely identified during the sampling interval. Thus, $y_{ijk} = 1$, if an individual was encountered in trap j during sampling occasion k , and $y_{ijk} = 0$ otherwise.

A key feature of our model is that trap-specific encounter probabilities [$\Pr(y_{ijk} = 1) = \pi_{ij}$], which we describe below, depend on the distance between a trap and an individual's activity center (Efford 2004, Borchers and Efford 2008), a geographic coordinate, denoted by s_i . We cannot observe the location of these activity centers, and so they are regarded as latent variables (or, equivalently, random effects) and are treated similarly to classical individual covariate models (e.g., Royle 2009).

Let $s_i = (s_{1i}, s_{2i})$ denote the activity center for individual $i = 1, 2, \dots, N$, where N is the population size of individuals exposed to sampling by the hair-snare array. We assumed the population of N activity centers, $s_i; i = 1, 2, \dots, N$, were distributed uniformly throughout some region, S , and did not change throughout the study. We denote this as

$$s_i \sim \text{Uniform}(S).$$

This uniformity assumption is the basis of all current spatial capture-recapture models that view individual activity centers as the realization of a spatial point process (e.g., Efford 2004, Borchers and Efford 2008, Royle and Young 2008) having state-space S . The region S throughout which individual activity centers are distributed will be prescribed for any particular configuration of traps (e.g., by specifying the coordinates for a polygon that contains the entire trapping array). Although the population size parameter N is sensitive to the size and extent of S , the density of points is invariant to S as long as S is sufficiently large and detection probability is decreasing in distance as described below.

We defined the trap-specific encounter probabilities conditional on s_i and the trap locations according to

$$\Pr(y_{ijk} = 1) = 1 - \exp(-\lambda_0 g_{ij})$$

where $g_{ij} \equiv g(s_i, x_j)$ is some function of the distance between individual activity center s_i and trap x_j . This formulation of the encounter probabilities can be motivated as the probability of ≥ 1 encounter under a model where individual encounter frequencies (unobservable with hair-snares) are Poisson (Royle et al. 2009a, Royle and Gardner 2010). The parameter λ_0 is a baseline encounter rate, which is the expected number of captures in a trap given that an individual's activity center is located precisely at that trap.

To include a behavioral response covariate (i.e., an indicator of previous detection) and the sex of the individuals, we describe λ_0 as a function of covariates such that

$$\log(\lambda_{0,ik}) = \lambda_0 + aIND_{ik} + \beta Sex_i$$

where IND is a binary $n \times k$ matrix with $IND_{ik} = 1$, if individual i was captured previously to sample occasion k , and zero otherwise. Sex is a binary vector indicating whether an individual is male or female, and λ_0 remained the baseline encounter rate for individuals not previously captured in the study. An interesting element of this model is that Sex is an individual covariate that was missing for the unobserved individuals, and thus, was estimated within the model (see Royle 2009). We then described the trap-specific encounter probabilities as a function of $\lambda_{0,ik}$, such that

$$\Pr(y_{ijk} = 1) = 1 - \exp(-\lambda_{0,ik} g_{ij}).$$

We defined g_{ij} according to

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

where σ^2 controls the effect of distance between an individual's activity center and trap location on encounter probabilities, and $d_{ij} = \|s_i - x_j\|$ is the Euclidean distance between the activity center of individual i and trap j . To incorporate a potential difference between males and females, we indexed σ^2 by sex of the individual and estimated σ^2 for males and females. This function is similar to a half-normal detection function widely used in distance sampling (Buckland et al. 2001) and other spatial capture-recapture applications (Efford 2004, Borchers and Efford 2008).

Model Extensions

Moving trap locations (sites) after each sampling occasion is advantageous for many reasons, including capturing and recapturing more bears (Boulanger et al. 2006). Similarly, rotating traps is a standard design used in camera trapping (Karanth and Nichols 2002, Royle et al. 2009a). For studies in which traps were moved after each sampling period, we constrain the encounter probability to be zero for periods during which the trap was inoperative. Let m_{jk} be a binary indicator of whether trap j was operational during occasion k . Then, the encounter probability is

$$\Pr(y_{ijk} = 1) = 1 - \exp(-\lambda_{0,ik} m_{jk} g_{ij})$$

where $m_{jk} = 1$ if trap j was operational during trapping

occasion k , and $m_{jk} = 0$ otherwise. Thus, whenever a trap was not operational, $\Pr(y_{ijk} = 1) = 0$, as it should be.

For studies where the trap locations were moved, we considered each possible trap location as a trap in the analysis. For example, if one physical trap was relocated 10 times during a study, that trap would appear as 10 traps in the analysis (i.e., once for each relocation). Following the model setup, we considered the trap to be operational at the location where it was set up, and we considered it to be turned off (i.e., inoperational) at the other 9 locations for that time period.

Based on the model formulation, adding covariates into the observation model is straightforward, similar to how the indicator of previous detection covariate was incorporated into the model. Covariates can be specific to traps, individuals, or time (i.e., sampling occasion). For example, if some traps were baited and others were not, we might expect a difference in the detection between trap types, thus we could add this into the observation model by including a term for baited traps as

$$\lambda_{0j} = \alpha_0 + \alpha_1 \text{baited}_j$$

where baited_j indicates whether trap j was baited or not. The model is flexible enough that we can account for variation from trap-dependence to individual heterogeneity, the latter of which can be dealt with by introducing an additional individual latent effect.

Bayesian Analysis and Implementation

The model was described conditional on the individual activity centers, $\mathbf{s}_i = (s_{1i}, s_{2i})$, which were unobserved and, thus, unknown; hence, their coordinates can be viewed as random effects, and the model could be analyzed by integrated likelihood, as in classical random effects models (see Borchers and Efford 2008 and Efford et al. 2008). We adopted a Bayesian analysis of the model based on MCMC sampling from the posterior distribution.

In addition the population size, N , of activity centers for the state-space S is also unknown. To deal with this, we used a technique known as data augmentation, which yields a tractable Bayesian implementation of capture–recapture models with an unknown N and is also easily implemented in *WinBUGS* (Royle et al. 2007). This technique has been used recently in a number of spatial–capture–recapture articles (Gardner et al. 2009; Royle 2009; Royle et al. 2009a, b). In data augmentation, we set a uniform $[0, M]$ prior number on N , which can be shown to justify adding a large number ($M - n$) of encounter histories consisting of all zeroes (i.e., augmentation) to the data set and then analyzing the augmented data as simple zero-inflated logistic regression type model with a zero-inflation parameter $1 - \psi$ (Royle et al. 2007). The model is a formal reparameterization, in which the parameter N is replaced by the parameter ψ . Data augmentation can be motivated by the similarity between closed population models and models of site occupancy (MacKenzie et al. 2002) as noted in Royle et al. (2007). To carry out the analysis, we must set M to be a sufficiently large upper bound for N . In practice, this

means setting M to be much larger than the expected population size for the region, but not too large, because a larger M incurs a greater computational cost. We deduced whether or not M was sufficiently large by inspecting the posterior distribution of N , which should be concentrated away from the boundary $N = M$. In our application, we added 103 all-zero histories, and thus, $M = 150$.

We chose conventional uninformative prior distributions for all parameters to reflect our desire for inference that was based on the observed data alone rather than any existing prior knowledge. We reported σ in kilometers based on the scaled coordinate system, and we chose a uniform distribution on $[0, 15]$. For λ_0 , α , and β , we used a uniform distribution on $[-10, 10]$. We fit the model in *WinBUGS* (Gilks et al. 1994; see Appendix for the model specification). To compute the posterior summaries for the parameters, we ran the MCMC algorithm for 25,000 iterations, discarded the first 10,000, and computed the results from the remaining 15,000 iterations. We checked for convergence by evaluating the \hat{R} statistic, such that all parameters were < 1.1 (Gelman and Hill 2006).

RESULTS

The results of the DNA tests indicated that 47 individual bears visited the traps 151 times during the 8-week survey. We provide posterior summaries for each model parameter (Table 1). During the 8-week study, encounters at each trap varied from 0 to 17 (Fig. 1). A number of exterior traps appeared to have fewer captures than those in the interior of the study area. The posterior mean estimated number of activity centers (N) for the area of S was 113.6. We estimated density (D) as the number of bears/km² at 0.20 with a 95% posterior interval of (0.15, 0.26). Despite the uniformity assumption imposed on the prior distribution for the activity centers, the posterior densities of activity centers for captured and uncaptured individuals (Fig. 2) indicate spatial heterogeneity in bear density.

We used the discrete, uniform prior number for N , with an upper bound of $M = 150$, which was about 100 larger than the observed number of individuals (47). We deduced that $M = 150$ was a sufficiently large upper bound for the uniform prior number on N because the posterior distribution of N was concentrated well below the value assigned to M . For λ_0 , the posterior mean estimate was -2.27 , and for β , the posterior mean estimate was -0.29 . However, β was not statistically different from zero, indicating that there was no difference in the detection of males versus females. For α , the posterior mean estimate was 1.04. We converted that into the detection probability for an individual whose activity center was located precisely at a trapping location (i.e., $g_{ij} = 1$), using the formula $\Pr(y_{ijk} = 1) = 1 - \exp(-\lambda_{0,ik})$, which equals 0.10 for individuals not previously captured and 0.25 after an individual's first capture. Thus, after a bear was captured, we were more likely to detect that bear again. The estimated posterior means for σ were 3.24 and 2.15 for males and females, respectively. The parameter σ is related to the shape of the curve defining the weights, g . We translated our estimated σ into a 95% home range

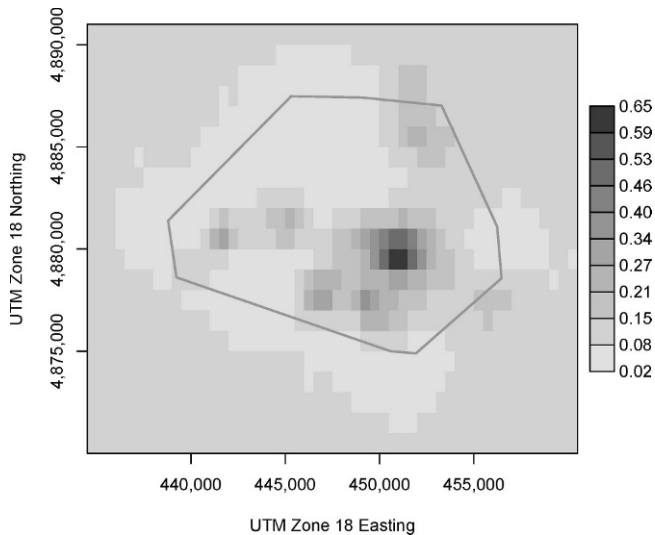


Figure 2. Map of the posterior density of activity centers, specifically, $E[N(b)|data]$, where $N(b)$ is the estimated number of activity centers located in pixel b . The grey polygon is the convex hull around the trap array, and the map is displayed in Universal Transverse Mercator (UTM) Zone 18 North coordinates. These results are based on a study of black bears conducted in northern New York, USA, during the summer of 2006.

radius by assuming a bivariate, normal model for movement. We estimated mean home range radii of 5.61 km and 3.71 km for males and females, respectively.

Gardner et al. (2009) provided estimates of N under a classical closed-population model with homogeneous detection probabilities (termed model M_0 ; Otis et al. 1978) and with heterogeneous detection probabilities using a logit-normal model (model M_h ; Coull and Agresti 1999, Pledger 2000, Dorazio and Royle 2003), which are 2 standard models used in hair-snare studies. The estimates of N were 49.2 under the model M_0 and 104.1 under the logit-normal model M_h . N , as estimated under these 2 models, has a different definition than the spatially explicit models (i.e., N in our model applies to an explicit spatial region that is fixed and known), and thus, direct comparisons are not useful. It is more constructive to compare the estimated density. By buffering the minimum convex hull of the trap array by the radius of the mean female home range size to estimate the effective trapping area (Bales et al. 2005), we translated these estimates of N into a density using the more ad hoc method of many earlier studies. The mean female home range radius was estimated for our study region as 2.19 km (Wegan 2008), and the effective trapping area with this technique was 255.30 km². Hence, the estimated densities are 0.19 and 0.41 bears/km² for models M_0 and M_h , respectively.

DISCUSSION

A fundamental objective of many population studies, including this one, is estimation of the size or density of a population. Applying mark-recapture techniques to DNA-based, individual detection data derived from hair samples is one of the most common methods currently used for estimation of population size for bear species, and the

Table 1. Posterior summaries of model parameters for a black bear study in northern New York, USA, where 47 unique individuals were observed during 8 sample occasions in the summer of 2006. We define N as the number of estimated activity centers in the region S , and calculate density (D) as the number of bears/km²; α is the parameter associated with the behavioral-response covariate, β is the parameter associated with female detectability, and $\exp(\lambda_0)$ is the baseline detectability for an individual who has not been previously captured and whose activity center is located precisely at a trap. We define σ as the shape parameter related to the distance function, separated by males and females, and ψ as the inclusion parameter for the augmented data set.

Parameter	\bar{x}	SD	2.5%	Median	97.5%
D	0.20	0.03	0.15	0.20	0.26
σ_F	2.15	0.19	1.80	2.13	2.55
σ_M	3.24	0.28	2.74	3.21	3.77
λ_0	-2.27	0.29	-2.84	-2.26	-1.69
α	1.04	0.24	0.58	1.04	1.50
β	-0.29	0.28	-0.83	-0.29	0.26
ψ	0.75	0.11	0.55	0.75	0.96
N	113.62	15.30	86.00	113.00	144.00

technique is likely to increase in the future. A number of spatial capture-recapture models and methods have been developed since the initial conceptual formulation described by Efford (2004). Royle and Young (2008) describe a hierarchical model that includes a spatial model for the distribution of individual activity centers and an explicit model governing the movement of individuals about their activity center. They apply their model to surveys of lizards that involve repeated sampling of an areal sample unit, so locations of individuals are recorded in continuous space, subject to the truncation of space induced by the sample unit. Borchers and Efford (2008) formalize inference under a model that is relevant to certain types of trap arrays (i.e., multicatch systems, such as arrays of mist-nets). Their analysis is based on integrated likelihood, under which, the conditional-on- s likelihood is integrated over the random effects distribution for s . As we have done here, they also adopt a uniformity assumption on s .

Gardner et al. (2009) and Royle et al. (2009a) consider a Bayesian framework for inference under a hierarchical formulation of that model. In particular, Gardner et al. (2009) applied a multinomial observation model to the bear data considered in this article and estimated a density of 0.16 bears/km². One deficiency of that analysis is that the multinomial model is a technical misspecification for the type of data generally collected in hair-snare traps. The model assumes that an individual can only be captured in one trap in a given sample occasion; however, because hair-snare traps do not physically trap the individual, multiple traps can be visited during any sampling occasion. In making the assumption that individuals could only be captured in one trap per sample occasion, Gardner et al. (2009) were unable to make use of all of the data collected on each individual, which resulted in a smaller estimate of N . In the data set, one individual was captured at 5 different traps within one sample occasion, and overall, 12 individuals were captured multiple times during at least one sample occasion. The Gardner et al. (2009) model also did not include the behavioral response covariate, which affected the detection

probabilities, and thus, the estimated N and the model did not include sex, which appears to greatly influence home range size.

Under our model, we estimated density to be 0.20 bears/km², whereas we estimated density to be $D_0 = 0.19$ bears/km² under model M_0 and $D_b = 0.41$ bears/km² under model M_h . The density estimates from model M_0 are similar to our current estimates, but the model M_h is greater than that determined from our spatial capture–recapture model. Interestingly, we estimated $N_b = 104.10$ under model M_h , which was much closer to the estimated $N = 113.00$ under our spatially explicit model. This discrepancy is the result of the difference in the definition of N and the estimation of the effective trapping area under traditional approaches. A flaw with the traditional approaches, and hence with this comparison, is that there is no formal, objective basis for converting estimates of N under traditional closed-population models to density. The choice of buffers is completely subjective and lacking a formal method for estimation or assessing adequacy, and the models themselves (e.g., model M_h) are purely phenomenological. In contrast, space in our model is fixed and known, and the underlying mechanism that induces heterogeneity (i.e., spatial location of individuals relative to traps) is directly related to the biological context of the problem.

Our analysis indicated that bears are more likely to be detected after having been previously detected. This is probably a result of the traps being baited and individuals then seeking out the bait. The detection probability of individuals that were never seen during our study is smaller than in Gardner et al. (2009). In particular, the smaller detection probability for uncaptured individuals then resulted in a higher estimate of bears in the study region. Because we found a strong behavioral response for bears after their first capture, it is possible that the activity patterns of individuals that have been captured may be altered because of the incentive for food. It is not entirely clear whether this change in activity patterns (i.e., behavior) influences only detectability or whether it also affects the activity center. One possible extension to the model is to allow activity centers to change in a Markovian fashion, which can be done with sufficient data or in multiyear studies.

Additionally, based on the formulation of the model, which allows for individual heterogeneity in the detection probability, we could easily include other covariates that we might expect to influence either the detection probability or the scaling parameter, σ . We expected individual capture rates would likely vary by age or sex classes for bear species (Woods et al. 1999, Noyce et al. 2001). We found detection probability was not statistically different between males and females; however, there was significant difference in σ , which showed that male bears effectively have a larger home range. The extension of our model to include sex as a covariate in both the detection probability and σ is a clear example of the ease of implementation using our approach.

Our hierarchical model can also accommodate moving traps (Royle et al. 2009a, b) and inclusion of other

covariates. Boulanger et al. (2006) suggest that moving trap locations after each sampling occasion is advantageous for increasing the number of captures and recaptures. This is becoming a more common practice in hair-snare studies (Kendall et al. 2008, Kendall et al. 2009) and camera trapping studies (Karanth and Nichols 2002, Karanth et al. 2004). It is not fully clear how moving the trap locations would influence the current nonspatially explicit techniques because the trap array polygon is altered at each sampling occasion when traps are moved. However, in a formal model-based framework, such as ours with the simple extension for including traps that are relocated, we can account for the variations in trap array geometry.

Our model, as well as many of the spatially explicit, capture–recapture models, relies on the assumption of a “circular” detection function, which may be interpreted as implying a circular-shaped home range for individuals (Borchers and Efford 2008, Efford et al. 2008, Royle and Young 2008, Gardner et al. 2009), although this has not been established. Although circular home ranges are not realistic (Smith 1983, Samuel and Garton 1985), that does not imply that a circular detection function is inadequate or even unrealistic. However, it is necessary to provide explicit assumptions about activity centers and individual detection probability for the population of all individuals (encountered or not) so that inference can be made about the entire population. Although the simplistic assumptions that underlie our model may not necessarily be realistic, our model provides an improvement over models that ignore space and movement, and the hierarchical formulation of our model allows us to easily change the functional form of the assumption and potentially evaluate it formally, given sufficient data.

MANAGEMENT IMPLICATIONS

With many bear species in threatened and endangered status, it is ever more important to develop the tools and statistical methods to properly analyze the collected data. Management issues range from decisions about population viability and habitat preservation to harvest regulations (Garshelis and Noyce 2006). For most of these issues, one of the first steps in making informed conservation and management strategies is determining reliable population and density estimates. The model we presented makes use of the spatial information that is inherently collected in studies that use trapping arrays. We use this spatial information to estimate movement and detection of individuals in a way that provides more accurate estimates of population size and density. It is important to explicitly include information, such as the sex of the individual or baited traps, in the model because detectability directly affects estimates of population size. In the realm of conservation and management related to populations, accurate estimates of density in conjunction with the uncertainty associated with those estimates, is crucial.

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LITERATURE CITED

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Appendix. The *WinBUGS* model specification for the spatial capture–recapture model with the behavioral response (trap happiness or trap shyness) to capture, and *Sex* as covariate in detection and σ . Although this model was developed for a black bear study that occurred in northern New York, USA, during the summer of 2006, the specification is not specific to that study.

```

model {

sigma[1]~dunif(0, 15)    #prior specification for sigma for females
sigma[2]~dunif(0, 15)    #prior specification for sigma for males
loglam0~dunif(-10,10)   #prior specification for log(lambda)
alpha~dunif(-10,10)     #prior specification for alpha
beta~dunif(-10,10)     #prior specification for alpha
psi~dunif(0, 1)        #prior specification for psi
tau~dunif(0,1)         #prior specification for tau

for (i in 1:M){
  z[i]~dbern(psi)
  SEX[i]~dbern(tau)
  SEX2[i] <- SEX[i] + 1
  SX[i]~dunif(xlower, xupper) #sets the prior on the X and Y- coordinates as uniform
  SY[i]~dunif(ylower, yupper) #over the given range

  for(j in 1:ntraps) {
    D2[i,j] <- pow(SX[i]-trapmat[j,1], 2) + pow(SY[i]-trapmat[j,2],2)
    #D2 is the distance between an activity center at (SX,SY)
    # and the trap j (trapmat is a matrix of x,y coordinates for
    # each trap)

    for(k in 1:K){
      log(lam0[i,j,k])<- loglam0 + alpha*IND[i,k] + beta*SEX[i]
      # calculate lam[i,j,k] with the behavioral response covariate (IND) and
      # with a difference based on SEX of the individual
      LamG[i,j,k] <- lam0[i,j,k]*exp(-D2[i,j]/sigma[SEX2[i]])
      # use the distance function with sigma specified by SEX of the individual
      # and the detection probability to calculate the trap specific encounter
      # probabilities
      pmean[i,j,k]<-1-(exp(-LamG[i,j,k]))
      tmp[i,j,k]<-pmean[i,j,k]*z[i]
      y[i,j,k]~dbin(tmp[i,j,k],1)
    }
  }
}

N<-sum(z[1:M])          #calculate the abundance
D<-N/((xupper-xlower)*(yupper-ylower)) #calculate the density
}

```

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