

Research Article

Density Estimation in a Wolverine Population Using Spatial Capture–Recapture Models

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ABSTRACT Classical closed–population capture–recapture models do not accommodate the spatial information inherent in encounter history data obtained from camera–trapping studies. As a result, individual heterogeneity in encounter probability is induced, and it is not possible to estimate density objectively because trap arrays do not have a well–defined sample area. We applied newly–developed, capture–recapture models that accommodate the spatial attribute inherent in capture–recapture data to a population of wolverines (*Gulo gulo*) in Southeast Alaska in 2008. We used camera–trapping data collected from 37 cameras in a 2,140–km² area of forested and open habitats largely enclosed by ocean and glacial icefields. We detected 21 unique individuals 115 times. Wolverines exhibited a strong positive trap response, with an increased tendency to revisit previously visited traps. Under the trap–response model, we estimated wolverine density at 9.7 individuals/1,000 km² (95% Bayesian CI: 5.9–15.0). Our model provides a formal statistical framework for estimating density from wolverine camera–trapping studies that accounts for a behavioral response due to baited traps. Further, our model–based estimator does not have strict requirements about the spatial configuration of traps or length of trapping sessions, providing considerable operational flexibility in the development of field studies. © 2011 The Wildlife Society.

KEY WORDS Bayesian, capture–recapture, density, *Gulo gulo*, motion–detection cameras, spatial models, wolverine.

The wolverine (*Gulo gulo*) is an elusive species that occurs at low densities (Lofroth and Krebs 2007), maintains large home ranges (Persson et al. 2009), and at times undertakes long movements (Inman et al. 2004). For these reasons, estimating density for wolverines has been problematic and early attempts lacked measures of accuracy and precision (review by Lofroth and Krebs 2007). More recently, Golden et al. (2007) estimated wolverine density based on aerial track surveys in winter in open habitats. Mulders et al. (2007) and Fisher et al. (2009) used DNA from hairs collected at bait sites to estimate wolverine density. Lofroth and Krebs (2007) used capture–recapture estimates of density from live–trapped wolverines and were the first to publish density estimates using photographs of wolverines captured on motion–detection cameras. None of the methods above that used capture–recapture approaches considered the spatial context of the data.

Closed population models are widely used to estimate abundance or density of animal populations from fixed arrays of traps or other devices that obtain information on encounter history (Borchers et al. 2002). Direct interpretation of population density obtained from such models is difficult because the sampled area of trap arrays is not a well–defined

concept in that, although one may delineate a geographic area for the placement of traps, it is not usually possible to delineate the effective sampled area (i.e., that area from which captured individuals are drawn). The difficulty in determining the effective sampled area has long been recognized in the literature (e.g., Dice 1938, Stickel 1954, Wilson and Anderson 1985, Efford 2004). Authors have used different approaches to resolve the problem of defining the effective area, most often drawing polygons around trapping arrays, buffering, and adjusting estimates of population size obtained from closed population models (Karanth and Nichols 1998). The problem with this approach is that it is ad hoc. Rules for buffering (e.g., mean maximum distance moved) are arbitrary and not consistent among studies, and such approaches induce uncertainty into estimates of density that have not been accommodated formally into density estimation. Moreover, the spatial organization of traps within the resulting buffered area suggests heterogeneity in encounter probabilities among individuals, which this method does not formally accommodate.

Recent developments of spatial capture–recapture (SCR) models (Efford 2004, Borchers and Efford 2008, Royle and Young 2008) provide a formal method for inference from capture–recapture studies by allowing for density estimation. These models extend standard closed population models (e.g., Otis et al. 1978, Borchers et al. 2002, Lukacs and Burnham 2005) to include a spatially explicit model for distribution of individuals in space. These models are

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spatially explicit in that they are parameterized in terms of a spatially indexed, individual random effect. The trap-specific encounter probabilities are modeled as a function of distance between traps and individual activity centers. These models have proved useful for estimating density in several carnivore sampling problems including small cats (Gardner et al. 2010a), bears (*Ursus americanus*; Gardner et al. 2010b), and tigers (*Panthera tigris*; Royle et al. 2009a,b). Our objective was to develop a spatially explicit capture–recapture model for estimating density, using data from a camera-trapping study of wolverines in Southeast Alaska.

STUDY AREA

The study area comprised 2,140 km² of coastal tidelands, temperate rainforest, muskeg, alpine habitats, and glaciers

in the Tongass National Forest on the mainland of Southeast Alaska (Fig. 1) near Petersburg (56°48.67602'N, –132°57.07452'W). Elevation in the study area ranged from sea level to 2,164 m. Temperatures at sea level during the camera-trapping sessions ranged from –4°C to 7°C but were considerably colder at higher elevations, although rarely falling below –23°C. Precipitation (mainly as snow) was heavy during the study, exceeding 4-m snow depth at higher elevations. Sitka spruce (*Picea sitchensis*) or Western hemlock (*Tsuga heterophylla*) dominated the overstory on productive forest sites, but poorly drained sites supported mountain hemlock (*Tsuga mertensiana*) and Alaska-yellow cedar (*Chamaecyparis nootkatensis*). The forested habitat where we deployed cameras occurred within 50 km of the coast of Frederick Sound, which bordered the study area on the

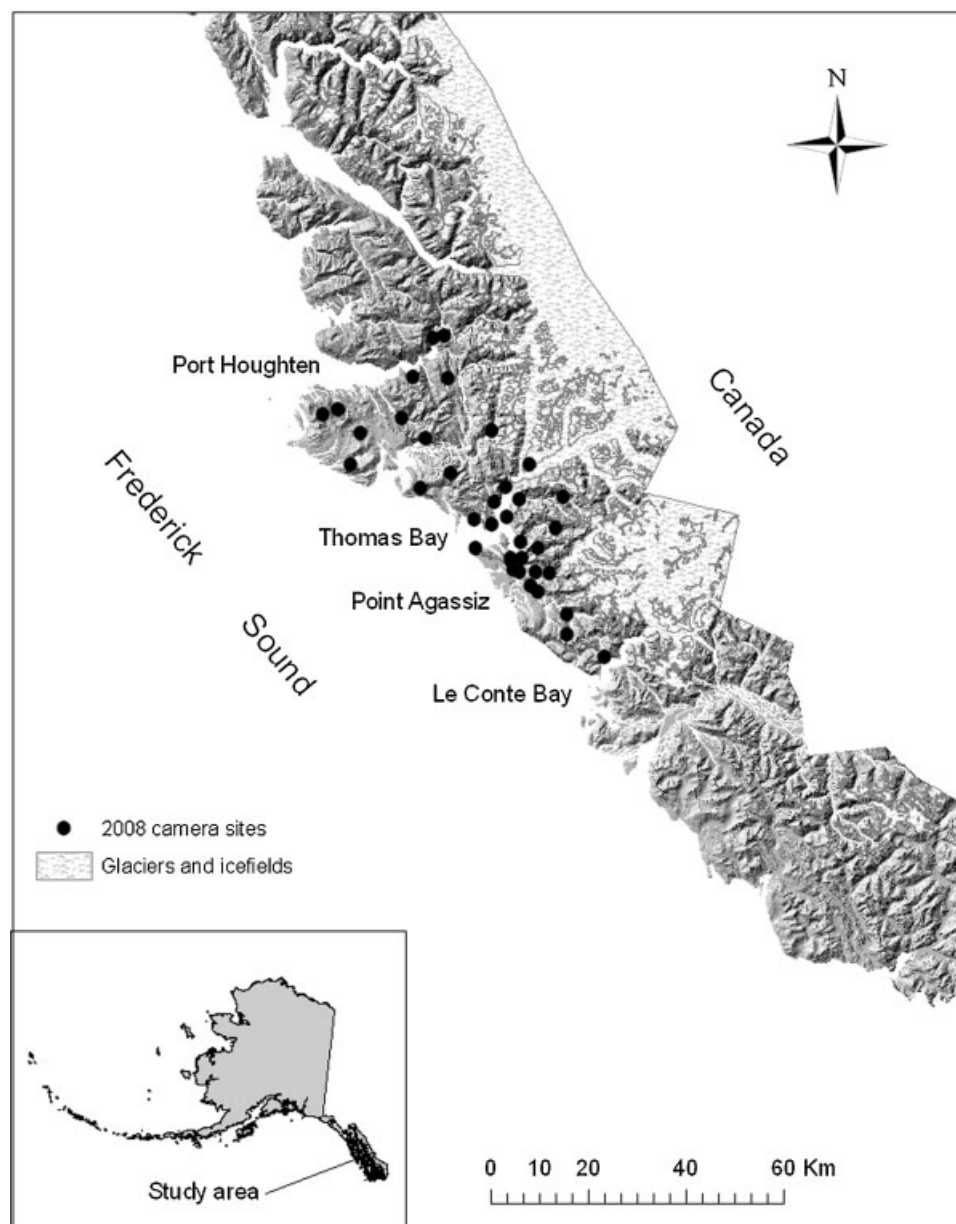


Figure 1. Study area on the mainland of Southeast Alaska near Petersburg showing location of camera and hair snag (C&H) stations (black dots) we used in 2008 for detecting wolverines. Stippled area indicates the extent of the Stikine Icefield to the Canadian border. The C&H array is largely surrounded by ocean and icefields except for a 20-km-wide forested area at the head of Port Houghton.

west. To the north the study area was bordered by Port Houghton, on the south by Le Conte Bay, and on the east by the Stikine Icefield. These geographic barriers limited movements of wolverines into the study area (Frances 2008). Prior to our study, fur trappers targeted wolverines along low-elevation forestry roads and along beaches but, in cooperation with our study, they refrained from setting traps for wolverines. Other than wolverines, the three species that triggered our camera traps most often, in order of frequency in photographs, were American marten (*Martes americana*), bald eagle (*Haliaeetus leucocephalus*), and black bear (*Ursus americanus*).

METHODS

Camera Trapping

Individual wolverines have a unique pattern of light-colored pelage on their ventral surface and this ventral pattern can be used to identify individuals from photographs, much as stripes and spots have been used to identify individual wild cats from photographs (Karanth and Nichols 1998, Soisalo and Cavalcanti 2006, Balme et al. 2009). Technique development with captive wolverines and radio-tagged wild wolverines demonstrated that this pattern remains the same over the lifetime of the individual (Magoun et al. 2011). To photograph the ventral pattern, we lured wolverines to camera traps using remnants of moose (*Alces alces*), deer (*Odocoileus hemionus*), and beaver (*Castor canadensis*) donated by hunters and trappers. We selected trap sites (Fig. 1) based on recommendations of local fur trappers, our knowledge of

suitable wolverine habitat, and logistical constraints of accessing mountainous terrain in our study area.

For camera sites accessed by helicopter, we fabricated run poles by mounting a 107-cm-long piece of 2×4 (38 mm \times 89 mm) dimensional lumber onto a 25-cm-long piece of 4×6 (89 mm \times 140 mm) dimensional lumber (Fig. 2; left panel). For camera sites accessed on the ground, we used either the same type of run pole or one fashioned from logs found on site. We suspended bait from a horizontal cable stretched between 2 trees 3–4 m apart. We attached a run pole to one of the trees at 1–2 m above ground or snow with the distal end of the run pole extending toward the other tree, on which we mounted a digital motion-detection camera (Trailwatcher[®], Monticello, GA). We suspended the bait 0.5–1.0 m above the end of the run pole. To access the bait, a wolverine would have to walk out to the end of the run pole, thereby triggering the camera while the animal was looking up at the bait exposing the ventral pattern (Fig. 2; right panel).

We set cameras to take photographs whenever there was motion in front of the camera. With the flash on all the time, cameras took photos approximately every 4 s when an animal was on the run pole. Each photograph file included the date and time the photograph was taken. We considered each 24-hr period a trapping session. We attempted to visit trap sites at least every 2 weeks to change batteries and flash cards and to rebait the sites, but this was not always possible due to weather and logistical constraints. If cameras were inoperable when we revisited the sites, we used the last day a photograph was taken to calculate the total number of days the camera was operational (i.e., number of trapping sessions).



Figure 2. Location of camera and hair snag (C&H) stations on the mainland of Southeast Alaska near Petersburg that we used for detecting wolverines in 2008. The left panel shows the configuration of the run pole, bait, and camera. The camera was approximately 3 m from the distal end of the run pole. We set the motion-detection camera to take photographs whenever an animal moved in front of the camera and with the flash on both day and night. The right panel shows a wolverine photographed at C&H station number 31 showing the ventral pattern we used to identify the wolverine in the photograph.

Statistical Methods

Data from a SCR study consist of the individual and trap-specific encounter histories $y_{i,j,k}$ for individual $i = 1, 2, \dots, n$; traps $j = 1, 2, \dots, J$; and sample periods $k = 1, 2, \dots, K$. In practice, sample periods are daily intervals and thus we obtain a conventional encounter history (i.e., a sequence of 0 s and 1 s) for each individual and trap. In our study, traps were operational for variable lengths of time. The temporal nature of encounter histories is important when time effects, such as date of the sample or behavioral response, are of interest (Gardner et al. 2010b). When explicit temporal effects are not relevant, we can summarize encounter histories by individual and trap-specific frequencies (i.e., $y_{i,j}$, the number of times that individual i was encountered by trap j out of K_j sample periods).

The key idea in SCR models is that they formally relate the encounters of individuals to where these individuals spend time over the trapping period. In particular, if we imagine that an individual occupies a defined area for a given period of time (i.e., a seasonal home range or use area) and its activities are centered in that area for that period, then it is natural to expect that the probability of an individual encountering a trap is a function of the distance between that individual's activity center and the trap. Efford (2004) introduced this concept, which was formalized in a likelihood framework by Borchers and Efford (2008). Royle and Young (2008) developed a Bayesian hierarchical formulation of a similar class of models. Here we assume that encounter probability is related to distance between each activity center and trap according to:

$$p_{i,j} = 1 - \exp \left[-\lambda_0 \times \exp \left(\frac{-d_{i,j}^2}{\sigma^2} \right) \right]$$

where $d_{i,j} = \|s_i - x_j\|$ is the distance between activity center of individual i , s_i , and location of trap j , x_j . This specific form of the detection function is justified as the probability of at least one encounter under a Poisson model where the encounter rate declines with distance according to a normal probability kernel with scale parameter σ (Royle et al. 2009b). To interpret this, suppose that it was feasible to deploy a very dense, regular grid of traps such that individuals are encountered frequently at many locations. Then, under the model, encounter frequencies would resemble a histogram approximation to a bivariate normal density around an individual's activity center. However, in practice we only observe individuals at a small fixed number of traps and thus such a pattern will typically not be evident. The parameter σ can be related formally to movement in that it corresponds to the standard deviation of locations under a bivariate normal model, if space is uniformly sampled (Royle and Young 2008).

We can express this model for detection probability as a linear model on the complementary log-log scale:

$$\text{cloglog}(p_{i,j}) = \log(\lambda_0) - b1 \times d_{i,j}^2$$

where $b1 = (1/\sigma^2)$. Thus, alternative detection functions arise by modifying either the choice of link function or

the linear predictor. For example, a linear distance term corresponds to an exponential detection function, which is not widely used in distance sampling applications because it does not have a shoulder at distance zero, and resulting estimates can be sensitive to rounding or sparse data (Buckland et al. 2001).

The encounter probability model indicates the structural similarity between SCR models and classical heterogeneity models (so-called Model M_h). Namely, distance is an additive random effect on a transformed scale, resulting in individual heterogeneity in encounter probability. Heterogeneity models can be extremely sensitive to choice of heterogeneity distribution, which can have severe consequences in the context of Model M_h (Link 2003). However, in our case the latent variable (distance) is partially observed because trap locations are fixed, so we might expect that SCR models are less sensitive than ordinary heterogeneity models considered by Link (2003).

Because we can formulate the model as a binary regression model in this fashion, useful extensions of the model are straightforward. For example, primarily a scavenger in winter, the wolverine tends to return repeatedly to a food source to remove food to caching sites (Banci 1994). As such, it is reasonable to assume that once a wolverine has found a baited camera site, the same wolverine is likely to visit the site repeatedly. Thus, we consider the possibility of a behavioral response (referred to as Model M_b in classical capture-recapture), which for our model involves adding one regression term to the model and defining a regression variable, say $x_{i,j,k} = 1$ if individual i was captured previous to sample session (day) k . In the context of SCR models, it is natural to define the behavioral response to be trap-specific (Royle et al. 2009b, Gardner et al. 2010b). That is, $x_{i,j,k} = 1$ if individual i has previously been captured in trap j . Thus, if an individual is captured in a specific trap, then the probability of subsequent encounter is increased or decreased only for that trap. We consider this a local behavioral response in contrast to what we could consider a global behavioral response as in the standard model (Model M_b) that is, a behavioral response that does not depend on where the individual was encountered. The latter type of response would be unrealistic in most spatial sampling situations. Because the covariate is time-dependent, we require a definition of the model in terms of individual Bernoulli trials, $y_{i,j,k}$, with probability of encounter $p_{i,j,k}$ with

$$\text{cloglog}(p_{i,j,k}) = \log(\lambda_0) - b1 \times d_{i,j}^2 + b2 \times x_{i,j,k}$$

Note that distance $d_{i,j}$ is a function of individual activity center s_i , which is an unobserved random effect. The model thus appears similar to so-called individual covariate models (e.g., Royle 2009). Because the individual activity centers are latent variables, we specify a probability distribution for them. The standard assumption is that s_i are uniformly distributed in space (Efford 2004, Borchers and Efford 2008, Royle and Young 2008). As such, we note that the model is essentially a standard, closed population model, but augmented with a spatial random effect that

describes the juxtaposition of individuals with the trap array.

With this additional model assumption for random effects, we can analyze the model using methods standard for analyzing generalized linear mixed models. In particular, models with random effects are conveniently analyzed by Bayesian methods using a technique known as data augmentation (Royle et al. 2007). Royle and Gardner (2011) and Gardner et al. (2010a,b) implement similar models in WinBUGS (Gilks et al. 1994) and provide the R and WinBUGS scripts to fit the models. In addition, a native R implementation developed from Royle et al. (2009a,b) provides a more efficient Markov chain Monte Carlo (MCMC) implementation in some cases. We used these R programs, which are now available in the freely available R package SPACECAP.

Bayesian analysis proceeds using a simulation-based method (i.e., MCMC; Link et al. 2002), which requires that we simulate realizations of the underlying point-process. To do this we must specify the region over which points are distributed (called the state-space of the point process), a geographic region that we denote by the set S . In general, we must specify the state-space regardless of whether one adopts a Bayesian or frequentist (e.g., Borchers and Efford 2008) approach to inference. In the latter case, we must integrate the random variables (activity centers) out of the conditional- s_i likelihood. When the state-space of the point process is precisely defined, it in turn defines the parameter N as the number of individual activity centers located within the prescribed state-space. We estimate the parameter N (see below). Density is a derived parameter $D = N/\text{area}(S)$, where N is the parameter of the model and $\text{area}(S)$ is the known area of the prescribed state-space. Although N is arbitrary in that it necessarily increases with the size of S , which we prescribe, the density of points $N/\text{area}(S)$ is invariant to S as long as S is sufficiently large, which we can verify by conducting a trial MCMC run.

That N is unknown is accommodated by imposing a discrete uniform prior on the integers $[0, M]$ where M is a large integer. If the posterior mass for N is concentrated away from M , then we can conclude that the posterior distributions are insensitive to M . As a technical matter, using the data augmentation formulation of the problem (Royle et al. 2007), the data set is augmented with $M - n$ all-zero encounter histories and we conduct the analysis on this augmented data set, which has a fixed number of M observations. The augmented data set induces a reparameterization of the model in which N is replaced as a formal parameter by a sequence of indicator variables z_i for $i = 1, 2, \dots, M$ indicating whether an individual is a member of the population (with probability ψ) or not (with probability $1 - \psi$). Formally, the z_i variables are binary latent variables having a Bernoulli distribution and we estimate N as a derived parameter, computed as the sum of the latent variables: $N = \sum z_i$. To obtain a posterior sample of N , we compute this sum at each iteration of the MCMC algorithm using the current values of each z_i . This construction of the model for the augmented data set induces the uniform prior

for N on the integers $[0, M]$ and also facilitates analysis of the model by MCMC (Royle et al. 2007).

In a Bayesian analysis, the size and configuration of the state-space requires careful consideration because the model is analyzed conditional on the underlying point process. That is, the point process is explicitly simulated, and thus we must describe the state-space precisely. There are two basic approaches to choosing the state-space. We might consider describing the geographic region containing the traps only where habitat is suitable. Alternatively, we can define a regular polygon (e.g., rectangle) containing the trap array without differentiating unsuitable habitat. Although defining the state-space to be a regular polygon has computational advantages (e.g., we can implement this more efficiently in WinBUGS and cannot for irregular polygons), a regular polygon induces an apparent problem of admitting into the state-space regions that are distinctly non-habitat (e.g., oceans, large lakes, ice fields). It is difficult to describe complex sets in mathematical terms that can be admitted to this spatial model. As an alternative, we can provide a representation of the state-space as a discrete set of points that will allow us to delete specific points or not depending on whether they represent habitat, which is primarily necessary to provide control over the geometry and morphology of what we consider to be suitable habitat. We analyzed the camera data using both approaches. In the first analysis, we defined the state-space to be a regular continuous polygon (a rectangle) but did not clip out non-habitat. To define the continuous state-space we overlaid the trap array (Fig. 1) on a rectangular region extending 40 km beyond the traps in each cardinal direction. In the second set of analyses, we used a discrete representation of the state-space but then deleted points that were not over land. For that approach we used two grid resolutions (2 km and 8 km) before clipping out unsuitable points to evaluate the relative influence of grid resolution on estimated density because coarser grids will be more efficient from a computational stand-point and so are preferable unless there is a strong influence on estimated density.

We chose priors customarily used to reflect little prior information. We used a uniform prior on $[0, 1]$ for the data augmentation parameter ψ (a probability), which implies a discrete uniform prior for N on the integers $[0, M]$ (Royle et al. 2007). For the regression parameters (intercept, coefficient on distance, and behavioral response), we used constant priors (default priors in the R library SPACECAP).

RESULTS

We operated 37 camera sites (Fig. 1) over a 165-day period during January–May 2008. Cameras were operational for variable periods (min. = 5 days, max. = 108 days, median = 45 days). Cameras captured 21 unique individuals 115 times. Individual encounter frequencies (Table 1) ranged from one capture (four individuals) to one individual captured 14 times, in three unique traps.

For the 2-km and 8-km discrete state-space models (Table 2), posterior summaries of model parameters and related quantities were similar. Densities were 8.6 individuals

Table 1. Individual frequencies of capture for wolverines captured in camera traps in Southeast Alaska in 2008. Rows index unique trap frequencies and columns represent total number of captures (e.g., we captured 4 individuals 1 time, necessarily in only 1 trap; we captured 3 individuals 3 times but in 2 different traps).

No. traps	No. captures									
	1	2	3	4	5	6	8	10	13	14
1	4	1	0	0	0	0	0	0	0	0
2	0	0	3	2	0	2	1	2	0	0
3	0	0	1	1	0	0	0	0	0	1
4	0	0	0	0	0	0	0	0	1	0
5	0	0	0	0	1	0	0	0	0	0
6	0	0	0	0	0	0	0	0	1	0

Table 2. Posterior summary statistics from the spatial capture–recapture models fitted to the 2008 wolverine camera-trapping data from Southeast Alaska. Models considered were: 1) a discrete approximation to the state-space using an 8-km grid, 2) a discrete state-space using a 2-km grid with no behavioral response, and 3) a behavioral response added to the second model; D is density per 1,000 km². λ_0 is the baseline encounter rate, $\sigma = 1/b1$, where $b1$ is the coefficient on distance-squared in the model for encounter probability, and N is the population size for the prescribed state-space.

Model	Parameter	Mean	SD	2.50%	50%	97.50%
Discrete 8-km	D	8.195	1.592	5.474	8.061	11.644
	λ_0	0.045	0.007	0.033	0.045	0.061
	σ	6.812	0.472	5.982	6.774	7.845
	$b1$	0.011	0.001	0.008	0.011	0.014
	N	82.343	16.001	55	81	117
Discrete 2-km	D	8.591	1.689	5.677	8.414	12.267
	λ_0	0.048	0.008	0.034	0.048	0.065
	σ	6.322	0.489	5.426	6.298	7.342
	$b1$	1.273	0.197	0.928	1.261	1.698
	N	84.737	16.66	56	83	121
Discrete 8-km and behavioral effect	D	9.6688	2.3255	5.872	9.355	15.028
	λ_0	0.0087	0.0022	0.005	0.008	0.0137
	σ	9.8356	1.335	7.484	9.743	12.747
	$b1$	0.0055	0.0015	0.003	0.005	0.0089
	$b2$	2.5988	0.2652	2.088	2.595	3.1326
N	97.152	23.367	59	94	151	

and 8.2 individuals per 1,000 km², respectively, consistent with that fact that the finer resolution grid accommodates higher levels of heterogeneity in detection probability (Link 2003). To improve computational efficiency, we used the 8-km discrete state-space to develop the behavioral response model (Table 2). Consistent with our expectations, there was a large positive effect of previous capture in a trap and an increase in estimated density under that model (posterior mean: 9.7 individuals/1,000 km²) compared to the model without the behavioral response.

DISCUSSION

The model based on the continuous state-space resulted in a much lower density estimate than that based on the discrete grid approximations to the state-space because most of the stated area of the continuous state-space lay over water. Thus the model distributed some individual activity centers over water, resulting in a corresponding decrease in apparent density compared with the discrete representation that allowed for water area to be removed. We noted little difference in estimated density and other model parameters between the 2-km and 8-km grids and thus we feel that, as an operational compromise, the coarser grid provided adequate estimates of density.

Integrating the trap identity information explicitly into the model allowed for consideration of more realistic models of the behavioral response. The intuitively appealing model we fitted to our data, in which the behavioral response operates on individual traps (what we referred to as a local behavioral response), has not been considered in the standard capture–recapture context. The model without a behavioral effect estimated a density of about 8.2 wolverines/1,000 km² with an estimated detection scale parameter (σ) of 6.8 km. In contrast, the estimated density was 9.7 wolverines/1,000 km² and $\sigma = 9.8$ km when we included the behavioral response. This strongly positive, trap-specific behavioral response indicated a tendency for individuals to revisit camera traps subsequent to their initial visit, a result that is unsurprising when traps are baited and successive captures are not independent. The apparent encounter probability was artificially high in the presence of a behavioral response and was properly adjusted downward when a behavioral response was added to the model, yielding a corresponding increase in estimated density.

By using SCR models for estimating wolverine density, we avoided several problems inherent in non-spatial models for species that are hard to detect and yield small sample sizes. Logistical constraints of operating in northern wilderness

environments in winter usually make it impossible to ensure that the number of trap sessions among camera sites is the same, but trapping sessions of equal length are not a requirement of the SCR models. For non-spatial models it is not at all obvious how to condense such variable trap-specific encounter histories into standard encounter histories that ignore trap identity, therefore, excess recaptures (i.e., wolverines captured multiple times at a unique site in a session) are discarded or pooled in some fashion, resulting in loss of information about the encounter process. An obvious problem with pooling data from a trap array into discrete periods to create non-spatial encounter histories is that it is not obvious how to do this when trap operation is staggered in time and deployed traps are operational for varying lengths of time. Pooling of data was not necessary in our SCR models because they are based on trap-level encounters of individuals.

The SCR models resolve two specific problems inherent in the application of non-spatial, closed population capture-recapture models. First, it is not necessary to use ad hoc methods to devise an effective sample area to which we applied the estimated N because, instead, we regard the location and number of individual activity centers (s) as unknown parameters (random effects) to estimate. Secondly, SCR models account for individual heterogeneity in encounter probability that is necessarily induced by juxtaposition of individuals with traps. In particular, the model assumes that encounter probability is a function of distance between traps and activity centers, and thus encounter probability decreases to zero as distance from the trap array increases.

As with all closed population models, the SCR models we used assume demographic closure (i.e., no permanent additions or removals from the population during the trapping period). The closure assumption in the SCR model is manifest in the static nature of the individual activity centers. Although each individual has its own activity center, the model assumes that activity centers are static over the trapping period. To the extent that non-closure is due to the presence of transients, such non-closure could perhaps be effectively modeled as an individual-specific encounter probability scale parameter, σ , accommodating apparent variability among individuals in home range size. We are currently devising methods for fitting such models. Extensions of the model that allow for mortality and recruitment have also recently been developed (Gardner et al. 2010a). In addition to accounting for explicit violation of the closure assumption due to population dynamics, such models can accommodate non-static activity centers, such as may be necessary in multi-year studies as individual home ranges shift due to resource variability, behavioral interactions, and other biological phenomena.

We also plan further extensions to this basic SCR model by adding covariates that could address other sources of heterogeneity in individual capture probabilities. For example, based on the smaller average size of home ranges for female wolverines (Persson et al. 2009), we expect that the sex of individuals influences average distances between activity centers and encountered traps for males and females. Sex of wolverines can be determined using camera-trapping

techniques (Magoun et al. 2011), as well as from DNA, and could easily be incorporated as an individual covariate in our models. Moreover, we suspect that camera traps visited by female wolverines, particularly lactating females in March and April, may indicate prime habitat where wolverines are concentrated across the landscape (A. Magoun, Alaska Department of Fish and Game, unpublished data). Therefore, we suggest a trap-specific covariate that considers visits by females. Finally, Copeland et al. (2010) showed that late spring snow cover may be correlated with suitable wolverine habitat, suggesting another covariate that could be incorporated into the SCR models for study areas that are heterogeneous for spring snow cover.

MANAGEMENT IMPLICATIONS

The SCR models we developed remove several mathematical and logistical problems that arise in estimating density of wolverines and other cryptic, low-density species. The SCR models can be applied to any capture-recapture technique that provides individual and trap-specific encounter histories. Besides incorporating spatial data and thereby avoiding ad hoc derivations of an effective area, the SCR models permit formal mathematical testing of assumptions regarding capture probabilities. Furthermore, the capability of the SCR models to incorporate variables that affect encounter probability provides managers the flexibility to modify camera-trapping techniques in ways that improve capture success (e.g., using multiple cameras at trapping stations or adjusting camera activation periods to accommodate species-specific activity). Finally, methods for estimating density of species are most useful when they accommodate the realities of working under rigorous and unpredictable field conditions on species that are difficult and expensive to study.

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