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Note

A Framework for Inference About Carnivore Density From Unstructured Spatial Sampling of Scat Using Detector Dogs

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ABSTRACT Wildlife management often hinges upon an accurate assessment of population density. Although undeniably useful, many of the traditional approaches to density estimation such as visual counts, livetrapping, or mark–recapture suffer from a suite of methodological and analytical weaknesses. Rare, secretive, or highly mobile species exacerbate these problems through the reality of small sample sizes and movement on and off study sites. In response to these difficulties, there is growing interest in the use of non-invasive survey techniques, which provide the opportunity to collect larger samples with minimal increases in effort, as well as the application of analytical frameworks that are not reliant on large sample size arguments. One promising survey technique, the use of scat detecting dogs, offers a greatly enhanced probability of detection while at the same time generating new difficulties with respect to non-standard survey routes, variable search intensity, and the lack of a fixed survey point for characterizing non-detection. In order to account for these issues, we modified an existing spatially explicit, capture–recapture model for camera trap data to account for variable search intensity and the lack of fixed, georeferenced trap locations. We applied this modified model to a fisher (*Martes pennanti*) dataset from the Sierra National Forest, California, and compared the results (12.3 fishers/100 km^2) to more traditional density estimates. We then evaluated model performance using simulations at 3 levels of population density. Simulation results indicated that estimates based on the posterior mode were relatively unbiased. We believe that this approach provides a flexible analytical framework for reconciling the inconsistencies between detector dog survey data and density estimation procedures. © 2011 The Wildlife Society.

KEY WORDS Bayesian, density, fisher, *Martes pennanti*, scat detector dogs, WinBUGS.

Estimates of population size and density are a fundamental component of wildlife management and conservation (Smallwood and Schonewald 1998, Solberg et al. 2006). Traditionally, these estimates are generated using a combination of visual and auditory detections, distance sampling, or capture–mark–recapture/resight (CMR) methods (Williams et al. 2002). Carnivores in particular present a suite of methodological and analytical challenges to traditional sampling techniques. Because they are secretive and often occur at low densities, sampling must be widespread yet often produces small sample sizes with high variability, for which many arguments in support of classical inference methods are invalid. Their sensitivity to habitat alteration and human presence varies by species and by individual, meaning that despite researchers following rigorous trapping protocols, capture success often is low and all individuals within a study area are not equally likely to be captured (Trolle and Kéry 2003, Kéry et al. 2010). They are often wide-ranging and move freely on and off a defined study site, creating a form of geographic non-closure resulting in potentially biased population estimates (Karanth and Nichols 1998, Kohn et al. 1999, White and Shenk 2001, Gardner et al. 2009). Carnivores are also generally territorial, meaning that within a defined study area all individuals are not equally exposed to traps. Those on the periphery have a reduced exposure, resulting in a heterogeneous probability of detection and, again, potentially biased estimates (Efford 2004). Unfortunately, taken together these characteristics mean that many classical approaches to density estimation are often the least useful when accurate estimates and conservation intervention are most needed, such as in studies of rare, secretive, or endangered carnivores (Kohn et al. 1999, Fisher et al. 2000, Kéry et al. 2010).

In response to the methodological challenges outlined above, a variety of survey techniques and modifications have been developed over the past 20 years (O'Connell et al. 2006, Long et al. 2008, Kéry et al. 2010). Techniques such as track plates, hair snares, and remote cameras have been carefully refined and applied to numerous species over a range of spatial scales in order to increase the spatial scale of sampling, reduce the effect of researcher

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presence, and increase the probability of detection (Zielinski et al. 1995, O'Connell et al. 2006, Long et al. 2008, Nichols et al. 2008). Simultaneous advances in the genetic identification of individuals has facilitated a rapid expansion in the use of non-invasive survey techniques to estimate not only occupancy but also abundance and density (Kohn et al. 1999, Lukacs and Burnham 2005, Schwartz et al. 2006, Royle et al. 2008, Schwartz and Monfort 2008). One promising survey technique, the use of scat detection dogs, has recently gained attention because of the dogs' effectiveness (Smith et al. 2005, Harrison 2006), high probability of detection (Reindl-Thompson et al. 2006, Long et al. 2008), and ability to quickly survey large areas (Wasser et al. 2004, Beckmann 2006). Furthermore, detector dogs are unique among non-invasive survey techniques in that they do not require bait, lure, or a fixed sampling station.

Typically, non-invasive datasets involving individual identification are analyzed using traditional CMR techniques that generate abundance estimates yet are not spatially explicit. That is, space is not an explicit component of standard capture–recapture models. To convert abundance to density, a post hoc estimate of effective trapping area is generated using available movement data that accounts for animals moving on or off the trapping array. This is typically accomplished by adding a buffer strip around the array equal to half the home range (if home range data is available) or half the mean maximum distance moved (MMDM; Karanth and Nichols 1998). Although this approach performed well in simulation studies (Wilson and Anderson 1985) and has been widely used, it has little theoretical justification (Williams et al. 2002) and recent comparisons between MMDM and Global Positioning System (GPS) telemetry data have cast doubt on its utility for wide-ranging carnivores (Soisalo and Cavalcanti 2006, Dillon and Kelly 2008). White and Shenk (2001) offer an alternative approach, correcting a population estimate based on the proportion of telemetry locations that fall within a defined study area; however, this method requires extensive telemetry data and is of limited utility to non-invasive survey data.

Recent advances in analytical techniques have reduced this reliance on auxiliary movement and location data as well as improved researchers' ability to estimate population parameters from sparse datasets. By incorporating spatial point process models into capture–recapture sampling frameworks using either maximum likelihood (MLE; Borchers and Efford 2008) or Bayesian (Royle and Dorazio 2008, Royle and Young 2008, Gardner et al. 2009) inference methods, new spatial capture–recapture models directly estimate density by combining the location data provided by trap or capture coordinates with individual encounter histories. These techniques have been successfully applied to several non-invasive datasets including camera resights of tigers (*Panthera tigris*; Royle et al. 2009*a*, *b*), hair snares of European wildcats (*Felis silvestris*; Kéry et al. 2010), the Pampas cat (*Felis colocolo*; Gardner et al. 2010*a*), and hair snares of black bears (*Ursus americanus*; Gardner et al. 2009, Gardner et al. 2010*b*). Although the methodology for sampling in these studies varies (i.e., camera traps, scent stations, and hair snares) the data structure produced by these different methods is identical because of the well-defined spatial structure of the sampling design. That is, each sampling device is located at a fixed point selected either randomly or systematically. In each case, an encounter history for each individual animal identified is produced indicating whether the individual is encountered ($y = 1$) or not ($y = 0$) at each point and during each sample period (e.g., nightly occasion of camera trapping).

Detector dog surveys are unique among non-invasive survey techniques in that sampling does not follow a spatially structured survey design based on fixed trap locations, transects, quadrats, or other spatial units. Despite researchers' best intentions regarding transects or survey grids, scent travels with air currents and dogs must be given some amount of leeway to track down the source. Although this greatly increases survey efficiency and subsequent sample size, it biases the sampling design resulting in violations of traditional CMR assumptions. Consequently, precise delineation of where sampling occurs is difficult. Coverage of an area can also vary greatly depending on climatic and topographic conditions, the individual dog used, and population density of the species being studied. Detector dog surveys therefore do not produce well-defined spatial encounter histories. Although characterizing locations associated with scat detection is simple, characterizing the locations of non-detection (e.g., analogous to when traps are not visited) is difficult. As such, opportunistic surveys for animal scat do not reconcile directly with studies based on camera trapping or hair snares, which involve fixed trap locations and for which spatial capture–recapture models have been devised.

As a solution to the methodological and analytical challenges presented by scat detection dog surveys, and to help capitalize on the dogs' high probability of detection with respect to rare or secretive species, we present an analytical framework under which density can be inferred from even a single comprehensive scat survey supported by genetic analysis to identify individuals. We extend the spatial capture–recapture models (e.g., Royle et al. 2009*b*) to account for both the unstructured nature of scat detection dog surveys and variable survey effort. We applied the method to a dataset of fisher (*Martes pennant*) scat locations collected via detector dog surveys in the Sierra National Forest, California. We then performed a series of simulation analyses to investigate the influence of both small sample sizes and the influence of analytical scale.

METHODS

Data Structure and Model

Following the development in Gardner et al. (2010*b*) and Royle et al. (2011) we begin by describing a conventional sampling design based on a fixed array of cameras or hair snares. Then we describe how this concept can be applied to sampling designs that do not involve fixed sampling locations, such as detector dog surveys.

In a fixed array, the coordinates of each sampling device or trap are denoted by $x(j)$ for trap j. Let $s(i)$ denote the home

range center for individual i, which is a hypothetical construct representing the centroid of an individual's activity during the period of sampling (Royle et al. 2011). A useful class of spatial capture–recapture models assumes that whether or not individual i is encountered in trap j is a Bernoulli outcome with probability that depends on the distance between the home range center $s(i)$ and the trap location $x(j)$, or $d(i,j) = ||s(i) - x(j)||$. Simply put, the further a trap is located from the center of an individual's home range, the less likely that the individual will be captured in that trap. Therefore, $y(i,j) = 1$ if individual i is encountered in trap j and $y(i,j) = 0$ if it is not. Let $\Pr(y(i,j) = 1) = p(i,j)$ and we develop models for $p(i,j)$ that accommodate the spatial context of the sampling problem. The assumption that the encounter hazard rate of individuals in traps is bivariate normal centered on an individual's activity center leads to a complementary log–log link (instead of the logit link) for modeling the relationship between $p(i,j)$ and distance from trap to activity center (see Royle et al. 2009*b*). In this case

$$c \log\log(p[i,j]) = a0 + a1 \times d_{ij}^2$$

where $a0$ and $a1$ are parameters to be estimated and $c \log\log(u) = \log(-\log(1 - u))$ corresponds to the complementary log–log link relating $p(i,j)$ to the square of distance, $d(i,j)$, which is a deterministic function of the unknown home range center $s(i)$.

In spatial capture–recapture models, $s(i)$ are unobserved random effects or latent variables. Thus, the spatial capture–recapture model can be described as a version of the widely used individual covariate models (Pollock 2002, Royle 2008). Analysis of such models is straightforward and no special considerations arise in the context of spatial capture–recapture. As with the analysis of classical random effects model, we require a distribution for the latent variables $s(i)$. For the present purposes, we suppose that they are uniformly distributed over some region that contains the sample area, a region which we will denote by S.

Under this model, the home range centers of all individuals in the population are regarded as a realization of a point process, having state-space S (i.e., possible values of each $s(i)$). Associating a non-random spatial attribute with each individual is the main distinction between traditional and spatially explicit capture–recapture models. This element of the model allows estimation of density over S, or the conversion of abundance values to density estimates without post hoc analysis, and accounts for the non-geographic closure of many sampling designs. Specifically, the density over some well-defined region is the number of individual activity centers that occur in that region.

Sampling based on detector dogs does not provide a precise characterization of space analogous to a fixed array of traps as in camera or hair-snare sampling. We provide such an array by gridding the survey area, and regarding each grid cell as a distinct sample unit. Grid cells must be large enough to be biologically meaningful, yet small enough to capture heterogeneity in presence–absence across the landscape. Ideally, we can then view this problem as a standard spatial sampling problem and draw a statistical sample of grid cells. We might think about sampling each grid cell and subjecting it to a uniform search intensity by, for example, carrying out a systematic transect survey of the grid cell or using random sub-samples. Alternatively, as described below, sampling might be completely unstructured or even opportunistic. For such cases we advocate the same approach, assuming that the sampled areas or search paths are known, resulting in characterizations of grid cells as surveyed or not surveyed. Survey routes must be independent of population density. For example, if investigators targeted areas where individuals were known to live (e.g., because of other survey activities) or sampling was concentrated in areas of high quality habitat, we would expect a positive bias under the model described here. Therefore with an unstructured survey technique such as detector dogs, where the survey route is influenced by detection location (e.g., the survey restarts after each detection, see below), grid cells should be large enough that a detection in one does not strongly influence the likelihood of detection in an adjacent cell. We associate detection or non-detection of individuals with the center point of the grid cell, essentially treating each grid cell as a trap, and apply the model described previously. The center point of the cell must be used rather than the actual sample coordinates in order to account for non-detection.

Using detector dogs, spatial sampling is necessarily unstructured. Although choosing random starting points and directions is possible, sampling by scat detector dogs requires a certain amount of freedom for dogs to follow scent trails. Despite the resulting unstructured sample, characteristic of detector dog surveys, the method is efficient and yields greater encounter rates. During sampling, search paths are logged using GPS receivers such that we can not only associate each detected scat with a grid cell but also provide an indication of which grid cells were sampled but did not produce a scat, that is, this provides the $y = 0$ observations which are critical to inference under any capture–recapture model. We therefore obtain formal encounter histories $y(i,j)$ for individual i and grid-cell j, where $y(i,j) = 1$ if individual i was encountered in grid-cell j, and $y(i,j) = 0$ otherwise. Then, the spatial capture–recapture model can be applied directly.

In contrast to standard fixed-point traps, sampling with detector dogs causes variance in the sampling intensity of grid cells because of the irregular search path of dogs through grid-cells. To accommodate this, we used the georeferenced survey path to generate an estimate of survey effort. For example, the length of the sample path through each grid cell or possibly the time spent within a cell, or some combination of the 2, can be used to quantify search intensity. Thus, each grid-cell "trap" has as a covariate associated with it, the survey effort that was expended within it. To accommodate this in the model, we modeled it as a linear effect on the linear predictor for detection probability

$$c \log\log(p[i,j]) = a0 + a1 \times d_{ij}^2 + a2 \times \log(\text{effort}[j])$$

This parameterization implies that effort is a multiplicative effect on encounter rate, which seems reasonable in the context of spatial sampling.

We carried out a Bayesian analysis of the model in the freely available software package WinBUGS (Lunn et al. 2000), which is facilitated by the use of the R library R2WinBUGS. See Royle et al. (2009*a*) for a general Bayesian formulation of model-based inference for individual covariate models. Implementation in WinBUGS renders the models widely accessible because one must only describe the distributional assumptions underlying the model. Bayesian analysis of spatial capture–recapture models has been used in a number of other applications including Royle and Young (2008), Kéry et al. (2010), and Gardner et al. (2010*a*).

Case Study

In June and October 2007, 2 scat detector dog teams composed of dogs and handlers from the University of Washington's Center for Conservation Biology (UWCBC) and field biologists from the United States Department of Agriculture (USDA) Forest Service Pacific Southwest Research Station surveyed a 21,100-ha study area in the Sierra National Forest for fishers. Fishers' secretive nature, large territories, and natural rarity make them difficult to monitor and as a result, accurate demographic estimates have been difficult to generate (Spencer et al. 2008). Furthermore, fishers are currently absent from much of their historic range in California, the native Southern Sierra population has been effectively isolated, and their conservation is believed to be in conflict with regional fuel management objectives (Zielinski et al. 1995, Spencer et al. 2008). Therefore, an immediate need exists for improved monitoring and population estimation techniques.

The survey area was divided into 15 approximately 1,400-ha hexagons which is roughly the size of a female fisher's home range, and each hexagon was surveyed 3 times by alternating teams in each month-long sampling period. Unlike traditional CMR techniques, the 3 surveys constituted a single sampling period and not 3 sequential survey sessions. Three surveys were conducted within a single sampling period to minimize the effect of weather, temperature, and variable dog skill (survey replication). Surveys began in the early morning hours and lasted 5–7 hours, capitalizing on morning moisture and air movement. Scat detector dogs are trained to detect the scent of a particular species' scat and track the scent to its source. Because detector dogs are trained and rewarded for finding the scat of the target species, and not the actual animal, they pose no direct threat to rare or endangered animals. Once a scat is located, the dog is rewarded with play and a ball or favorite toy for several minutes, then the scat is collected, the scat position is recorded, and the survey is continued. Teams carried GPS receivers that logged the team's location at 90-second intervals, generating a track log of the survey route. Because of the large number of mesocarnivores in the region and the risk of misidentification, collected scats were sent to the UWCBC genetic lab for species confirmation. Confirmed fisher samples were then forwarded to the USDA Forest Service Rocky Mountain Research Station's Wildlife Genetics Lab for individual identification. Because of the high likelihood of genotyping errors influencing the identification of new individuals, researchers used a combination of multi-tube analysis and program DROPOUT (McKelvey and Schwartz 2005) to verify unique individuals.

Post hoc, we imposed a square, 1-km^2 grid over the survey area resulting in 650 1-km^2 cells (Fig. 1). We generated grids post hoc in order to insure that grid boundaries did not influence survey routes and to provide analytical flexibility. We assigned each cell a survey effort based on the sum of the length of all track logs that crossed that cell. Essentially, we considered each cell to represent a trap, and generated encounter histories for each individual fisher based on whether or not a scat from that individual was located within a particular grid cell. This resulted in a matrix of encounters with each row representing an individual fisher and columns representing either a detection or non-detection within that grid cell. We analyzed the resulting spatially explicit encounter history using WinBUGS and the model described above. We ran the model for 10,000 iterations, with the first 2,000 being discarded as a burn-in period.

Simulation

To better understand the potential biases associated with both the non-random deposition of scat and variable density, we conducted 2 sets of simulations. First, we repeated the above analysis across a range of grid cell sizes to determine the influence of sample autocorrelation and grid cell size on density estimates. In order to bracket our original analysis, we both increased and decreased cell size in 400-m increments, resulting in cell sizes of 600 m, 1,000 m, 1,400 m, and 1,800 m. We ran 3 Markov chains for 10,000 iterations each and discarded the first 2,000 iterations as burn-in, resulting in 30,000 posterior samples per cell size. We conducted these simulations over a larger extent, totaling 1,296 km^2. We limited the number of simulations performed because of the extensive computational time required; each new cell size simulation required between 3 days and 9 days to run.

Second, we used the density estimates generated by the case study analysis as a starting point and created 3 simulated populations at low, estimated, and moderate densities (e.g., 9.2 fishers/100 km^2, 12.3 fishers/100 km^2, and 16.9 fishers/100 km^2). These values equated to 60, 80, and 110 activity centers within the prescribed state-space (S) of the model. For each population level (N), we ran 100 Monte Carlo iterations and fit the model in WinBUGS. We then computed the mean, median, and mode as well as how often the 95% posterior interval contained the true value of N.

RESULTS

Case Study

Detector dog teams collected 241 scats. Fifty-seven failed to amplify, and 102 of the remaining 184 were genetically confirmed as fisher. Of the 102 confirmed fisher samples, 25 were successfully identified to the individual level based on a panel of 22 microsatellite loci (Jordan et al. 2007),

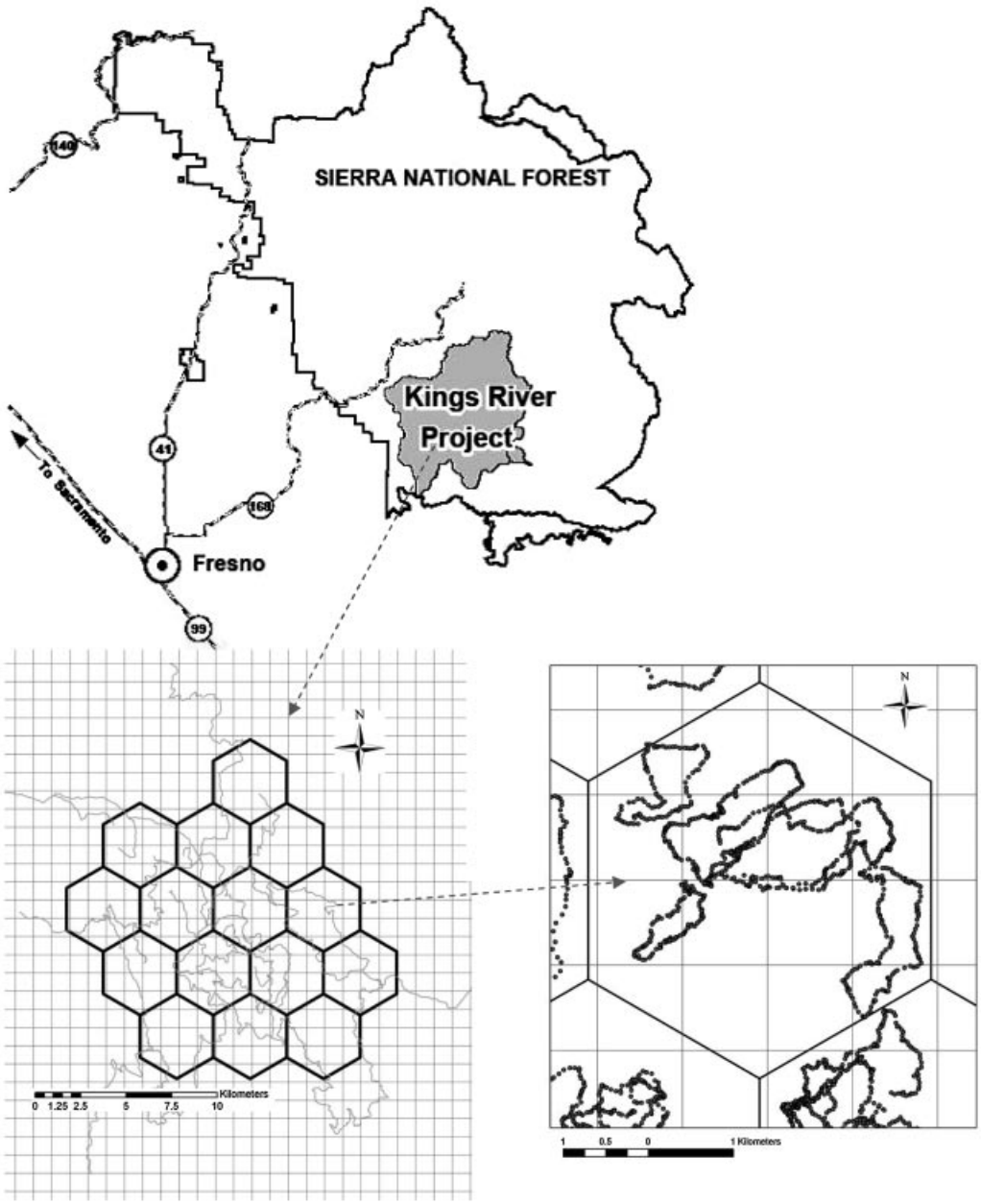

Figure 1. Study design of the U.S. Forest Service Kings River Fisher research project in the Sierra National Forest, California, showing the primary hexagonal detector dog sampling units as well as the post hoc analysis grid. Enhanced view of a single sampling hexagon shows the six associated survey tracklogs and the variable sampling intensity.

resulting in the identification of 15 individual animals. The resulting population size estimate, 80 ± 33 (SD) fishers (Table 1, Fig. 2), applied to the prescribed state-space of the model (650 km^2) over which activity centers were simulated by the Markov chain Monte Carlo algorithm. The resulting density estimate (posterior mean), 12.31 fishers/100 km^2 with an associated 95% confidence interval of 6.5–28.0 fishers/100 km^2, is likely biased as a point estimate because of the skew of the posterior distribution (Fig. 2; see below). We recommend using a point-estimate based on the mode (10.4 fishers/100 km^2) because of its unbiased performance in the simulations as well as reports from similar analyses (Kéry et al. 2010, Gardner et al. 2010*a*).

Table 1. Posterior summary statistics of model parameters based on 3 Markov chains of 40,000 iterations each (120,000 posterior samples total) predicting fisher abundance and density. *N* is the population size of individuals on the prescribed (fixed) state-space and *D* is the corresponding density estimate. We present lower (2.5%) and upper (97.5%) confidence intervals around each estimate.

Node	Mean	SD	2.5%	97.5%	Median	Mode
N	80.43	33.01	39.00	168.00	73.00	63.00
D (fishers/100 km^2)	12.37		6.00	25.85	11.23	9.69
*a*0 (log(lam0))	−2.75	1.15	−5.16	−0.64	−2.67	−2.73
*a*1 (1/sigma)	21.42	9.89	5.94	44.17	20.13	17.80
*a*2 (effort effect)	0.37	0.21	0.03	0.82	0.35	0.31

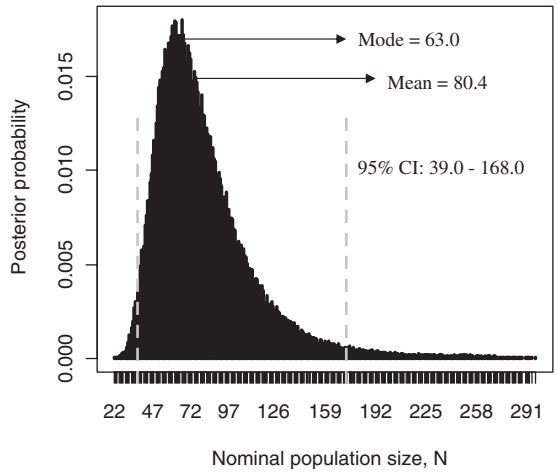

Figure 2. Posterior distribution of the number of fisher activity centers (population size) estimated to be located within the Kings River Project area of the Sierra National Forest, California, based on 120,000 Markov Chain Monte Carlo iterations.

Simulation

Across a range of grid cell sizes, density estimates based on mean values ranged from 12.3 fishers/100 km^2 to 14.2 fishers/100 km^2 (Fig. 3). Estimates based on mode values were slightly less, ranging from 10.0 fishers/100 km^2 to 11.9 fishers/100 km^2. In the second set of simulations and for all 3 simulated densities, the mean and median were slightly positively biased because of the skew of the posterior distribution (Table 2, Fig. 2). Despite this, the true value of N was contained within the 95% confidence intervals in 94%, 93%, and 93% of all runs (Table 2). Comparatively, the posterior mode appeared relatively unbiased.

DISCUSSION

Scat surveys, whether conducted by human or canine surveyors, are inherently unstructured. "Captures" can occur at any point in sampled space rather than at predetermined fixed points, such as trap or camera locations. Standard CMR designs generally rely on repeated sampling of trapping arrays or webs to estimate encounter probability and hence density. Conversely, scat encounter surveys do not have a clear sense of temporal replication, as scat deposition and decomposition

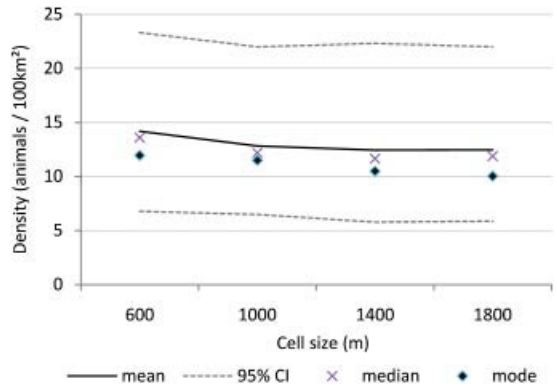

Figure 3. Posterior summary statistics (mean, 95% CI, median, mode) representing the influence of cell size selection on fisher density estimates in the Sierra National Forest, California.

Table 2. Simulation results based on 100 Monte Carlo iterations for each of 3 predetermined fisher population densities. For each case, data-generating parameter values were equal to those estimated from our case study (Table 1).

	Posterior results			
Simulated density	**Mean**	**Coverage**	**Median**	**Mode**
9.2 fishers/100 km^2	9.91	0.94	9.63	9.13
12.3 fishers/100 km^2	12.92	0.93	12.65	12.21
16.9 fishers/100 km^2	17.66	0.93	17.43	16.99

rate interacts with the sampling process to complicate the definition and interpretation of repeated sampling. Because of these problems, although scat is a ubiquitous sign of animal presence and it is often used to characterize relative abundance, it is rarely used to estimate density.

The fisher density estimate we generated compared well with previous estimates from the same area. Jordan (2007) estimated fisher population density at 13.4 (95% CI: 7.6–24.2), 9.5 (95% CI: 5.6–17), and 10.0 fishers (95% CI: 6.7–14.4)/100 km^2 during 2002, 2003, and 2004, respectively, based on extensive remote camera surveys and Program NOREMARK (White 1996). In North America, fisher densities range from 5 fishers/100 km^2 to 38 fishers/100 km^2 (Powell 1993), and 2 studies in Northern California using camera recapture methods estimated 12–17 fishers/100 km^2 (M. Higley, Hoopa Tribal Forestry, personal communication) and 8–17 fishers/100 km^2 (J. Thompson, Western EcoSystems Technology, Inc., personal communication). Although the above estimates were based on multiple years of extensive and expensive capture–recapture effort, our estimate was derived from 2 30-day detector dog surveys, supported by genetic identification and involving only 15 animals captured 25 times. Additional precision can be expected with the inclusion of additional sampling periods.

Although additional testing is necessary, our approach appears insensitive to several potential sources of bias. Small sample sizes are a typical occurrence in studies of carnivores and we carried out a simulation study to evaluate the frequentist performance of the estimator. Our simulation results indicate that although the posterior mean was slightly positively biased, as would be expected given the fact that the posterior distribution is highly skewed (Fig. 2), the posterior mode appeared relatively unbiased (Table 2). This is similar to the results reported by Kéry et al. (2010), who based similar simulations on a small population of European wildcats sampled using hair snares.

Despite the fact that our results did not vary substantially across a range of cell sizes, they indicated that estimates decreased as grid cell size increases (Fig. 3). This is consistent with the effects of unmodeled heterogeneity that also occurs in classical Model Mh (Dorazio and Royle 2003). In particular, the effect is analogous to increasing complexity of finite-mixture models of heterogeneity (Pledger 2000). Failure to account for individual heterogeneity leads to a negative bias in the Model M0 estimator of N, which matches the pattern we observed (Fig. 3; we note that Model M0 can be viewed as a limiting case where the whole study region is a single grid

cell). Thus, grid cell size should not be too large or else the model is understating the heterogeneity in the data because of the spatial organization of individuals and traps. In practice, grid cell size must be based on a combination of the ecology and movement capacity of the target species, local topography or other landscape features, and logistics. Cell sizes should be large enough to minimize the spatial autocorrelation associated with clusters of scats, yet small enough to adequately model the heterogeneity due to spatial organization of individuals and traps. We selected a 1-km^2 grid based on fishers' high capacity for movement, the ability of dog teams to survey the rugged Sierra terrain, as well as the rough spacing between fisher scats. In the Brazillian cerrado, Vynne et al. (2010) selected 6.25-km^2 cells for a similar study because of the movement capacity of the target species, maned wolf (*Chrysocyon brachyurus*), jaguar (*Panthera onca*), puma (*Puma concolor*), giant armadillo (*Priodontes maximus*), and giant anteater (*Myrmecophaga tridactyla*). Further work comparing density estimates generated by detector dogs with those generated by more traditional methods such as telemetry or camera traps, will help define this balance. In addition, because grid cells are assigned post hoc, we recommend that researchers experiment with several cell sizes to see where thresholds occur for their species and system.

Two aspects of scat detector dog surveys warrant further discussion. First, defining grid cells a priori and systematically surveying each cell would generate more structured, well-distributed survey data. However, the need for survey replication (multiple visits in 1 survey session) would require the either grid cells to be large or a smaller overall area to be surveyed. Instead, we agree with McDonald (2004) that to be most effective, a method-analysis combination should facilitate inference about cells not surveyed. Second, scats are ephemeral indicators of animal presence. Both the scats and the DNA contained within degrade over time, and the rate of decay is highly variable because of environmental conditions, animal diet, etc. In any analysis based on scat samples, this leads to confusion about what time frame the data represents and a form of non-closure, where a sample may represent an individual who has since died or left the study area. In reality, this concern is minimized because of the rapid degradation of scat-based DNA in the environment; even though dogs often find older scats, these samples rarely amplify to the individual level. Therefore, researchers might reduce this concern and limit the overall cost by only analyzing fresh scats based on odor, appearance, etc. However, to be consistent with a detector dog's training, all samples of the target species should be collected and the dog rewarded regardless of the final use or disposition of the sample. Failure to reward the dog for locating a target sample, regardless of sample age, risks confusion and should be minimized.

We transformed the encounter data into simple binary encounters for each grid cell. However, in some cases, multiple (sometimes many) encounters of an individual occur in the same grid cell. The model could accommodate this by modifying the Bernoulli observation model to a model that is valid for frequency data, such as a Poisson or negative binomial model. However, the use of frequency data would require that we select among potential models for encounter frequency, and at least for fishers in the Sierra Nevada mountains we feel that there are good reasons to avoid this. Specifically, the process of local scat deposition is related to complex behavioral considerations and scat locations are not necessarily independent. Like most survey data, scat locations are often spatially autocorrelated; when dogs find one they more likely to find another nearby: in a den or core use area, at a territory boundary, or at a latrine site they may find many. For these reasons, we feel that the additional within-grid-cell cluster of encounters provides relatively little information about density. Instead, we treated each cluster as a single observation to reduce the influence of spatial autocorrelation, which justifies the reduction of data to simple binary encounters at the relatively coarse resolution of grid cells.

From a statistical perspective, a rare species is one for which the probability of detection is low, regardless of whether that is because of low density, secretive behavior, or clustered distribution (McDonald 2004). Therefore increasing the probability of detection associated with any survey method is always desirable in order to increase the precision and reliability of estimates. However, increasing the probability of detection, by definition, often involves violating the assumption of a randomized survey design. This may involve some form of stratified, systematic, or adaptive sampling (Morrison et al. 2001, McDonald 2004) or it may involve the use of a priori knowledge about a species.

The use of dogs to locate scats from a target species has greatly increased the efficiency and effectiveness of many research programs because of their high probability of detection (Long et al. 2008), yet at the same time it magnifies the difficulties presented by spatially unstructured surveys. By imposing spatial structure on the survey area after a survey has been completed, viewing fine-scale polygons as traps in a classical sense, and including a covariate related to survey effort conducted in each polygon, we were able to exploit newly developed, Bayesian spatial capture–recapture models (Borchers and Efford 2008, Royle and Young 2008, Royle et al. 2009*b*, Gardner et al. 2010*a*) to formalize modeling and inference from scat-survey data collected using generalized survey protocols. The framework that we present facilitates estimating population density using this effective yet unstructured survey technique.

Surveys of carnivores or rare or endangered species commonly result in small datasets and low estimated densities with poor precision. For example, a recent paper on the fossa (*Cryptoprocta ferox*), an endangered carnivore in Madagascar, estimated an adult density of 0.18 adults/km^2 based on 20 animals captured over 3 years (Hawkins and Racey 2005). Sepulveda et al. (2007) estimated a density of 0.25 endangered southern river otters (*Lontra provocax*) per river kilometer based on 12 individuals captured over 3 years. Furthermore, many applications of CMR methods to endangered carnivore populations result in population estimates of less than 10 individuals (Jackson et al. 2006,

Trolle and Kéry 2003). These datasets, and the resulting inferences, are often criticized as being poor and unreliable despite the fact that they represent the best estimates available and that the species involved are in dire need of conservation intercession. Because conventional likelihood-based inference is typically only justifiable asymptotically, studies of rare and/or secretive carnivores necessarily violate one of Le Cam's Basic Principles, that of "If you need to use asymptotic arguments, do not forget to let your number of observations tend to infinity" (Le Cam 1990). Conversely, Bayesian inference is not predicated on asymptotic arguments—the posterior distribution is valid for whatever the observed sample size, given the specific set of models prescribed (Gazey and Staley 1986, Royle et al. 2009*b*).

MANAGEMENT IMPLICATIONS

The pairing of detector dog surveys with a spatial capture–recapture modeling framework offers several advantages over more traditional approaches to density estimation. First, many non-invasive techniques that use fixed survey stations can be coupled with conventional non-spatial CMR analyses. However, these often suffer from the biases associated with ignoring the spatial organization of individuals and traps, such as inability to define sample area and heterogeneity induced by variable exposure to encounter (Borchers and Efford 2008, Royle and Young 2008). In addition, although fixed-station, non-invasive survey techniques such as hair snares or remote cameras have increased the probability of detection for many species, detector dogs offer significantly greater rates of detection (Long 2006). And although many traditional CMR and occupancy models require multiple sampling sessions (McKenzie et al. 2006), density estimates can be generated from spatial capture–recapture models using a single sampling event of accumulated encounters with no loss in precision (Petit and Valiere 2005). Despite the increased cost associated with genetic analysis, non-invasive surveys are often cheaper because of the need for fewer sampling sessions (Solberg et al. 2006). Combining unstructured detector dog survey data with spatially explicit, Bayesian capture–recapture models offers researchers an opportunity to maximize the availability and utility of location data for rare, secretive, or otherwise challenging species.

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