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Research Article

Estimating Abundance of Mountain Lions From Unstructured Spatial Sampling

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ABSTRACT Mountain lions (*Puma concolor*) are often difficult to monitor because of their low capture probabilities, extensive movements, and large territories. Methods for estimating the abundance of this species are needed to assess population status, determine harvest levels, evaluate the impacts of management actions on populations, and derive conservation and management strategies. Traditional mark–recapture methods do not explicitly account for differences in individual capture probabilities due to the spatial distribution of individuals in relation to survey effort (or trap locations). However, recent advances in the analysis of capture–recapture data have produced methods estimating abundance and density of animals from spatially explicit capture–recapture data that account for heterogeneity in capture probabilities due to the spatial organization of individuals and traps. We adapt recently developed spatial capture–recapture models to estimate density and abundance of mountain lions in western Montana. Volunteers and state agency personnel collected mountain lion DNA samples in portions of the Blackfoot drainage (7,908 km^2) in west-central Montana using 2 methods: snow back-tracking mountain lion tracks to collect hair samples and biopsy darting treed mountain lions to obtain tissue samples. Overall, we recorded 72 individual capture events, including captures both with and without tissue sample collection and hair samples resulting in the identification of 50 individual mountain lions (30 females, 19 males, and 1 unknown sex individual). We estimated lion densities from 8 models containing effects of distance, sex, and survey effort on detection probability. Our population density estimates ranged from a minimum of 3.7 mountain lions/100 km^2 (95% CI 2.3–5.7) under the distance only model (including only an effect of distance on detection probability) to 6.7 (95% CI 3.1–11.0) under the full model (including effects of distance, sex, survey effort, and distance × sex on detection probability). These numbers translate to a total estimate of 293 mountain lions (95% CI 182–451) to 529 (95% CI 245–870) within the Blackfoot drainage. Results from the distance model are similar to previous estimates of 3.6 mountain lions/100 km^2 for the study area; however, results from all other models indicated greater numbers of mountain lions. Our results indicate that unstructured spatial sampling combined with spatial capture–recapture analysis can be an effective method for estimating large carnivore densities. Published 2012. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS Bayesian analysis, cougars, genetic sampling, Montana, *Puma concolor*, snow tracking, spatial capture–recapture, spatial models.

The management of mountain lions (*Puma concolor*) and other large carnivores is complex. Wildlife managers must consider the interests of livestock producers, the general public, hunters, and the conservation community (Treves and Karanth 2003, Shaw and Negri 2005). In the northern Rocky Mountains, human persecution and reductions in prey availability contributed to a dramatic decline in mountain lion abundance during the latter 19th century and early 20th century (Logan and Sweanor 2001). Population levels then rebounded and in 1971, the state of Montana classified mountain lions as a game species and began to manage them through a general harvest season (Montana Fish, Wildlife and Parks 1996). Statewide, annual mortality estimates from hunting, vehicle collisions, animal damage control, and natural causes increased from 68 in 1981 to 617 in 1994 indicating likely increases in mountain lion abundance during this time (Riley and Malecki 2001).

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Additional supporting information may be found in the online version of this article.

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In the late 1990s, concerns about the stability of the mountain lion population were raised and hunters in Montana urged Montana Fish, Wildlife and Parks to reduce quotas (Robinson and DeSimone 2010). Simultaneously, encroachment of human development into mountain lion habitat resulted in increased rates of human–mountain lion encounters (Riley and Decker 2000), and increased public concern regarding mountain lion population numbers. Additionally, a recent decline in ungulate populations in Idaho has been partially attributed to increasing predator abundance, including mountain lions (White et al. 2010).

Cost-effective methods for estimating abundance of large carnivores including mountain lions are needed for conservation and management (Cougar Management Guidelines Working Group 2005, Balme et al. 2009, Marucco et al. 2011). Population estimates of harvested populations allow wildlife managers to evaluate hypotheses regarding the impacts of different harvest season structures on populations (Cooley et al. 2009, Rice et al. 2010, Robichaud and Boyce 2010), and adjust season quotas to ensure harvest levels are sustainable. Large carnivores with extensive home ranges and low probabilities of capture represent unique challenges to wildlife managers charged with maintaining harvestable populations (Choate et al. 2006, Robichaud and Boyce 2010). Public perception and auxiliary data such as harvest data, age structure of the harvested population, and game damage complaints are often used as population indices because of the difficulty in quantifying population sizes of these species (Minnis 1998). Recently, survey methods such as DNA sampling with hair snares, rub trees, snowtracking, or other techniques, have been used to estimate abundances of large carnivores including grizzly bears (*Ursus arctos*; Kendall et al. 2008), wolves (*Canis lupus*; Marucco et al. 2009, Stenglein et al. 2010), mountain lions (Sawaya et al. 2011), and tigers (*Panthera tigris*; Mondol et al. 2009).

In 1997, a large-scale mountain lion project was implemented by Montana, Fish, Wildlife and Parks to determine cost-effective measures of monitoring lion populations and reduce uncertainty in mountain lion abundance estimates. The methods evaluated included using DNA sampling for estimating population size, intensive mark–recapturing, and minimum number known alive techniques that include backdating older mountain lions caught in the area (Hornocker et al. 2009).

Robinson and DeSimone (2010) used snowtracking for the collection of genetic samples to estimate the density of mountain lions in the Blackfoot River watershed in western Montana. In this effort, adult mountain lion densities were estimated through intensive capture efforts during winters (Nov to Mar) 1997–2007 in a 915-km^2 portion (Garnet study area) of the 7,908-km^2 Blackfoot watershed. Minimum population estimates for the Garnet study area ranged from 37 mountain lions (4.0 mountain lions/100 km^2) in 1997 to a low of 20 (2.2 mountain lions/100 km^2) in 1999 before rebounding to 33 (3.6 mountain lions/100 km^2) in 2006. To obtain a total population size for the first year of the study (1997), the density of mountain lions in the Garnet study area was extrapolated across the entire watershed (7,908 km^2) for an estimate of 310 mountain lions. The methods used by Robinson and DeSimone (2010) were time-consuming, costly, and relied on a number of assumptions. For example, the backdating of individuals for inclusion in estimates of the mountain lion population in previous years assumes that older-age mountain lions were present in the study area but undetected. Several years are required to saturate the population with collars, and the method assumes that field personnel can identify the point in time when every mountain lion had been collared. Though these methods provide a wealth of information on dispersal, morphometrics, health, and age, minimum number known alive methods do not account for undetected individuals, or provide formal uncertainty estimates.

Mark–recapture models (Seber 1973) allow for the estimation of animal abundance corrected for imperfect detection and characterize the uncertainty associated with the estimate. Model-based estimates in general provide a framework for testing alternative hypotheses regarding the processes that generate the observed data, as well as measures of the statistical significance of the effects in the model (Jolly 1982). Traditional methods for analyzing mark–recapture data, however, do not account for spatial variations in sampling or arrangements of individuals on the landscape, both of which may affect individual probabilities of detection. Additionally, large carnivores such as mountain lions that travel extensively may venture beyond study area boundaries and lead to violations in the assumption of closure necessary to obtain unbiased estimates of population size (Choate et al. 2006). Corrections for temporary emigration (Nichols and Kendall 1995, Kendall et al. 1997, Kendall 1999) or movements across study areas have included buffering with strips equal to one-half the average territory size (Dice 1938, Karanth and Nichols 1998, Bales et al. 2005), or using additional information from previous studies to estimate amounts of movement expected of individuals (White and Shenk 2001, Parmenter et al. 2003, Lukacs and Burnham 2005). Recent developments of spatial capture–recapture models provide explicit estimates of density using individual trapping histories and the spatial organization of captures to estimate trap-specific probabilities of encounter, and the spatial distribution of individuals within the study area (Efford 2004; Borchers and Efford 2008; Royle and Young 2008; Gardner et al. 2009, 2010; Royle et al. 2011*a*). In these models, trap-specific probabilities are modeled as a function of the distance of individual's activity center to a trap, and each individual activity center is regarded as a random effect. Unlike minimum number known alive techniques, these methods incorporate imperfect detection probability as well as the spatial locations of the captures to generate density estimates.

Spatial capture–recapture models have been developed for arrays of traps or encounter devices in which encounter of individuals can occur at prescribed locations in space. This includes camera traps (Royle et al. 2009), hair snares or scent lure stations (Gardner et al. 2009, 2010) or networks of mist net stations (Borchers and Efford 2008). Previously described models for search-encounter sampling (i.e., not based on fixed arrays of traps) assumed a constant survey effort across the surveyed location (Royle and Young 2008) or assumed that sampling occurred along a pre-determined survey path (structured search-encounter data; Royle et al. 2011*b*). Thompson et al. (2012) recently expanded these methods to work with scat dog derived data where sampling occurs along a path or transect that is not established a priori but, rather, develops in response to observer search activity. We apply these methods to unstructured search-encounter data for mountain lions, where, similar to Thompson et al. (2012), paths are not established a priori. In our study, the intensity of effort is determined adaptively in response to the surveyor's previous success at detecting a mountain lion in the area. Lastly, we include goodness-of-fit methods for these types of analysis.

STUDY AREA

We used capture–recapture data collected in the Blackfoot River (7,908 km^2) watershed and in a portion of Lewis and Clark County in Powell, Granite, and Missoula counties in west-central Montana (Fig. 1). Terrain was characterized by gentle to moderate slopes dissected by steep limestone canyon areas along drainages with elevations ranging from 1,160 m to 2,156 m (Robinson and DeSimone 2010). Mean annual precipitation fell mainly as snow and ranged from 19 cm to 33 cm of water equivalent (Western Regional Climate Center, Ovando, MT). Habitat varied with elevation from high elevation mixed lodgepole pine (*Pinus contorta*)-subalpine fir (*Abies lasiocarpa*) stands, to more mesic Douglas-fir (*Pseudotsuga menziesii*)-western larch (*Larix occidentalis*) stands at mid-elevations, and Douglas fir, ponderosa pine (*Pinus ponderosa*), and aspen (*Populus tremuloides*) at low elevations (Robinson and DeSimone 2010). Prey species present in the area included elk (*Cervus elaphus*), white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), and moose (*Alces alces*). Large predators besides mountain lions included black bear (*Ursus americanus*), grizzly bear, and wolf (Robinson and DeSimone 2010).

METHODS

Field Methods

From late November 2005 through February 2006, trackers spent 77 days systematically searching for mountain lion tracks and treeing mountain lions with the use of trained hounds. They collected tissue from treed animals using biopsy darts fired from a CO_2-powered rifle (Beausoleil et al. 2005). Additionally, crews on foot followed tracks of mountain lions backwards (hereafter back-tracking) collecting hair samples, which consisted of hair fragments, single intact hairs, or clumps of hair, from logs or other natural features along the tracks. Field crews systematically surveyed for mountain lion tracks on Forest Service and Plum Creek Timber Company roads within the study area using snowmobiles. If they located a fresh track, the houndsman would release his hounds and tree the mountain lion. Trackers back-tracked old and fresh mountain lion tracks on foot. All crews used hand-held Global Positioning System (GPS) units to record the length and location of their survey efforts. We conducted a genetic analysis of tissue and hair samples to

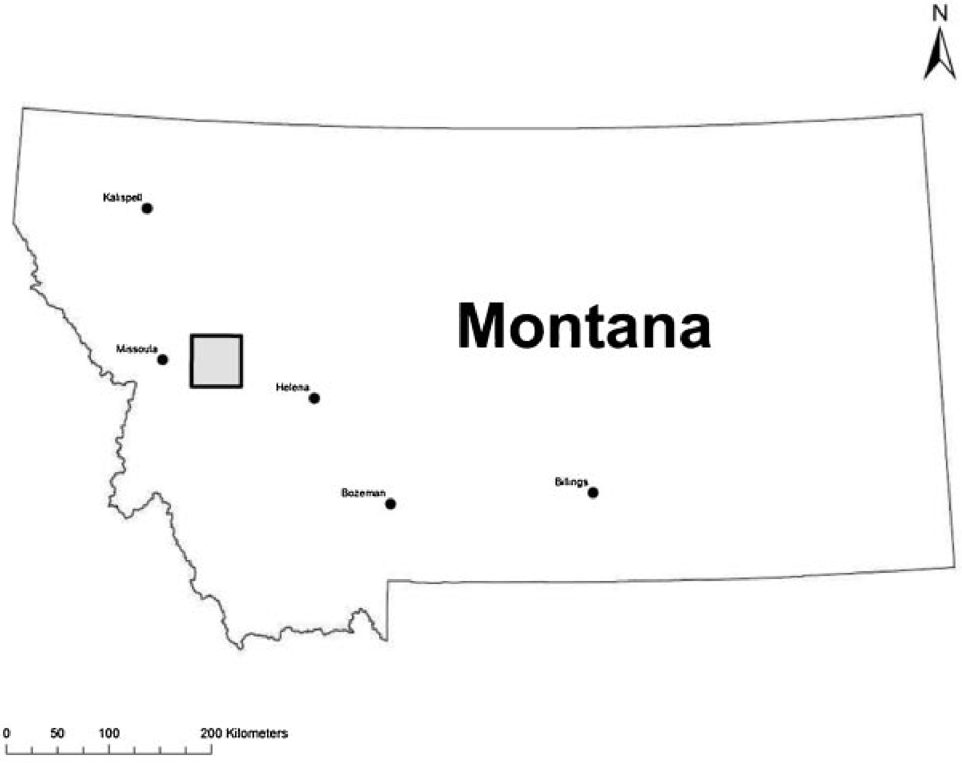

Figure 1. Map of study area (gray square) surveyed for mountain lions in the Blackfoot Mountains of Montana from November 2005 to February 2006.

identify individuals. Regardless of the circumstances under which we sampled the mountain lion, we treated individuals as independent in the model (i.e., female and dependent young entered the model as separate individuals; see the Discussion Section for more on this issue).

Genetic Analysis

We performed genetic analyses of tissue and hair samples at the United States Forest Service Rocky Mountain Research Station (Missoula, MT, USA). We successfully genotyped tissue samples using 12 variable microsatellite loci (details concerning amplification protocols and the genetic characteristics of these loci can be found in Biek et al. 2006). We amplified all hair samples 3 times using the protocols outlined in Biek et al. (2006) to eliminate most genotyping errors associated with identifying unique individuals. When we detected inconsistencies between amplifications, we ran samples an additional 3 times. Lastly, we used 2 computer algorithms implemented in program DROPOUT (McKelvey and Schwartz 2004, 2005) to ensure that the genotypes produced did not inflate the estimate of mountain lions in this study.

Model Formulation

Spatial capture–recapture models (Borchers and Efford 2008, Royle and Young 2008, Gardner et al. 2009) extend ordinary (non-spatial) capture–recapture models to accommodate individual locations. This is accomplished by introducing an individual-level random effect corresponding to the coordinates of the center of activity of individuals in the population during the study period. The area surveyed by the trackers represents potential capture locations, which do not necessarily correspond to the area where the animal is most active. Some animals may primarily reside outside of the surveyed area and therefore have low probabilities of capture. An assumption of these models is that an individual's capture probability is greater at locations that are closer to a core area used most frequently by the animal (i.e., activity center). Collectively the activity centers are regarded as a realization of a point process, and spatial capture–recapture models estimate the number of such points in any well-defined spatial region in proximity to the sampled region. The number of activity centers in any spatial region is the population size of individuals in that region.

A key element of the data structure in our study, which is not addressed in most standard spatial capture–recapture models, is that individual encounters do not arise from discrete trap locations, such as camera traps, hair snares, or mist nets used in conventional capture–recapture studies. Instead, observers searched areas where mountain lion tracks were detected either by the individual observer or by others (state, Bureau of Land Management, Forest Service employees, etc.). To resolve this, following Thompson et al. (2012), we gridded the study area into a coarse grid of 5-km × 5-km cells and used these grid cells as conceptual traps, producing encounter histories (see below) based on whether individuals were encountered or not in each grid cell. If the grid cell was searched, then an individual could be encountered in that trap, otherwise, if a grid cell was not searched, no encounters were possible.

We assigned each capture to the center point of the grid cell within which the capture took place. We assembled individual encounter histories (y_{ijk}) for individual i, trap j, and sampling occasion k; where the value of $y_{ijk} = 0$ if the individual was not encountered in the grid cell on sampling occasion k and $y_{ijk} = 1$ if the individual was captured in the trapping area during that sampling occasion (Gardner et al. 2010). For our study, however, we combined both hair samples and biopsy samples because hair samples did not allow us to determine the date when mountain lions traversed the sampling grid where the hair was found. As a result, we were unable to clearly define distinct temporal sampling occasions. Therefore, we collapsed the data matrix of sampling occasions to reflect 1 sample period. We generated individual encounter histories (y_{ij}) for individual i and trap j. These values equaled 0 if we never captured the mountain lion (either treed or collected hair from the individual) in the grid cell, and 1 if we detected the mountain lion at least once in the grid cell over the study period. As a result, information about detection probability comes from repeated detections of the same individual in different traps, rather than detections from visits to the same trap over a period of time. We only included coordinates of capture locations, locations where we collected DNA or hair samples (i.e., grids that observers tracked mountain lions through but did not obtain a DNA sample were not recorded as a capture location).

A problem in our study is that search intensity was likely intensified in relation to local mountain lion density. This differs from the scat dog transects analyzed in Thompson et al. (2012), which were distributed uniformly and scat dog routes deviated from these predetermined transects based on detected scats. Here, after encounter of sign (such as a track), observers would expend additional search effort to obtain hair or tissue samples from that individual. Most grid cells contained at least some effort (i.e., at least 1 GPS point was recorded with the grid cell; see Fig. 2), and we believe this phenomenon primarily affected encounter probabilities at the level of the grid cell. In other words, each grid cell had a relatively small base encounter probability simply for being sampled by some search route length >0 m, and subsequent increases in search effort led to increases in effective encounter probability.

Thus, we used search intensity (sampling effort) as a covariate on encounter probability to adjust the baseline probability of capture. Therefore, grid-specific encounter probabilities included 3 parameters we expected to influence the detection probability (P) of an individual mountain lion at a particular grid cell: Euclidian distance from activity center, survey effort, and sex of mountain lion. In this formulation, an activity center corresponds to the center of an animal's movement over the course of the study period. We followed Gardner et al. (2010) by describing the trap-specific encounter probabilities as a function of distance as

$$P_{ij} = \Pr(y_{ij} = 1) = 1 - \exp(-\lambda_{0i} g_{ij})$$

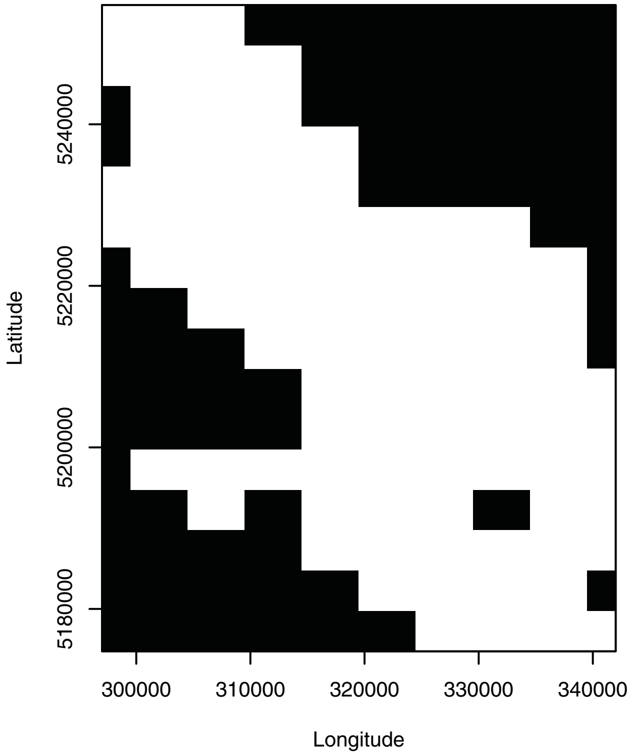

Figure 2. Schematic of area surveyed for mountain lions in the Blackfoot Mountains of Montana from November 2005 to February 2006. Each grid cell is 5 km^2. White cells indicate that the cell was surveyed (i.e., observers recorded at least 1 location in the cell), black cells were not surveyed.

where

$$\log(\lambda_{0ij}) = \lambda_0 + \beta_1 \times \log(\text{EFFORT}_j) + \beta_2 \times \text{SEX}_i$$

and λ_{0ij} is the expected number of captures in a trapping area given the individual's activity center. This encounter rate model implies a constant baseline (at the average search effort) encounter rate (λ_0) for each grid cell searched. The effects of the covariates sex and effort are included in the detection function, where effort is the distance in kilometers covered by trackers in the grid cell. The sex of unknown animals, including unobserved animals and observed animals of unknown sex, are estimated from the sex ratio of males to females in the population (ψ_{sex}), corrected for sex-specific detection probabilities, *P*. This is accomplished by regarding SEX$_i$ as a latent variable in the model and updating its unknown values as part of the Markov chain Monte Carlo algorithm (MCMC). For our models, we define sex = 1 as a male and sex = 0 for as a female; therefore ψ_{sex} is an estimate of the proportion of the population that is male.

The effect of distance on detection probability is modeled as $g_{ij} = \exp(-d_{ij}^2/\sigma^2)$ (sensu Buckland et al. 2001, Efford 2004, Borchers and Efford 2008) where d_{ij}^2 is the Euclidian distance between an individual's activity center and trap *j*, and σ is a scaling parameter (Gardner et al. 2010). This formulation corresponds to the half-normal assumption or a circular bivariate normal home range (Jennrich and Turner 1969). We ran several models where σ was estimated separately for males and females.

To estimate the number of activity centers in the survey area, we assigned a prior uniform distribution to the individual activity centers $s_i \sim \text{Uniform(S)}$ (Efford 2004, Borchers and Efford 2008, Royle and Young 2008, Gardner et al. 2009); where S is the state-space of the point process and s_i designates individual potential activity centers (1, 2, 3,... up to the number of activity centers in the state space). We estimated the number of mountain lions in the Blackfoot drainage by multiplying the estimated density of mountain lions by the 7,908 km^2 (the area of the Blackfoot). Code for running the spatial-capture recapture models described here along with the data used in this manuscript are available (Appendices A and B, available online at www.onlinelibrary.wiley.com).

Bayesian Analysis by MCMC

We conducted a Bayesian analysis of the models using data augmentation (Royle and Dorazio 2008, Royle and Young 2008), a process in which the data set is augmented with a large number of undetected individuals, each having an all zero encounter history. We inspected the posterior to ensure that estimates were not being constrained by the augmented number of animals (i.e., posterior distributions were not truncated by the upper limit of the number of augmented animals) to determine the size of the augmented data set (*M*). An individual in the superpopulation *M* is a member of population *N* if the indicator $z_i = 1$ and $z_i = 0$ otherwise. Furthermore, $z_i \sim \text{Bernoulli}(\psi)$, where ψ is the probability that an individual in *M* is a member of the population *N* (Royle and Young 2008). Introducing the latent variables z_i with a uniform(0,1) prior on the data augmentation parameter ψ ensures that the induced prior distribution on population size *N* is uniform, a natural uninformative prior for population size.

We fit models using MCMC methods implemented in the R programming environment (R Development Core 2011; Appendices A and B, available online at www.onlinelibrary.wiley.com). Models were run for 30,000 iterations with 10,000 iterations as burn-in. Starting values for model parameters were as follows: $\sigma = 1$, $\log(\lambda_0) = 0$, all β's were started at 0, $\psi = 0.5$, $\psi_{\text{sex}} =$ the probability of a mountain lion being a male in the sampled population (in our case 0.38), and sex for the mountain lions with unknown sex was estimated as Bern (ψ_{sex}). We report 95% credible intervals calculated from the posterior distribution, with 2.5% of the values above and below the interval. Priors for λ and β were improper uniform ($-\infty$, ∞), and we used uniform(0,1) priors for ψ_{sex} and ψ. We used the R package, boa (Smith 2007), and ran the Gelman–Rubin statistic (Gelman and Rubin 1992) to assess convergence.

Model Selection, Evaluation, and Goodness-of-Fit

We selected a priori variables (lion sex and survey effort) that we thought would be associated with mountain lion detection rates. However, no published literature currently exists on factors affecting mountain lion detection rates in a mark–recapture survey. Given that these models are newly developed, our candidate model set included a suite of models that represented an exploratory approach with all possible combinations. We ran 8 models including the null model with an effect of distance-only on detection probability. The other 7 models represented various combinations of sex and effort effects on detection probability (including sex specific estimates of σ).

We assessed goodness-of-fit of the model using a standard Bayesian *P*-value approach (Gelman and Rubin 1992). Following Royle et al. (2011*a*), we tested the goodness-of-fit of the encounter process separately from goodness-of-fit of the underlying spatial point process. For the encounter process, we computed a discrepancy measure for the encounter frequencies of each individual at each trap location, and compared posterior samples of this discrepancy measure to an analogous one based on encounter frequencies of new realizations of the data set generated from the posterior distribution. We used the Freeman–Tukey statistic (Freeman and Tukey 1950) as the basis for the Bayesian *P*-value calculations:

$$D = \sum_{i-1}^{N} \left(\sqrt{n_i} - \sqrt{e_i}\right)^2$$

where n_i is the (observed or simulated) encounter frequency conditional on s_i (the activity center) and e_i is the expected value under the model. The Bayesian *P*-value is the proportion of times $D(\text{obs}) > D(\text{posterior})$.

We evaluated the assumption that activity centers are independently distributed uniformly over the state space (similar to complete spatial randomness, CSR; Cressie et al. 2009) using a similar Bayesian *P*-value approach but based on the statistic $I = (G - 1) \times s^2/\bar{n}$, where $\bar{n}$, and s are the mean and variance of the number of activity cells per grid cells, and G is the total number of grid cells. We compare I calculated using posterior realizations of the point process to the value of I obtained by simulations under complete spatial randomness (see Royle et al. 2011*a* for additional details).

Sensitivity to Model Assumptions

Similar to Thompson et al. (2012), we evaluated the sensitivity of estimates to buffer size by running our original models with 5-km, and 10-km buffers, in addition to the 15-km buffers we report in this manuscript. We buffered our survey area by 15 km, 10 km, and 5 km and therefore our state-space encompassed 8,800 km^2, 7,000 km^2, and 5,400 km^2, respectively. Additionally, we evaluated sensitivity to choice of the grid size within the state space, by running models with 2 × 2 km, 4 × 4 km, and 8 × 8 km grid sizes, in our largest state space.

To investigate the effects of dependence in mountain lion movements, we ran 1 simulation where we grouped any mountain lions captured and biopsied in the same grid cell on the same day. We re-ran the model with family groups instead of individual mountain lions and estimated the density of group activity centers. Then we multiplied density of activity centers by the area of the Blackfoot Drainage and the mean family group size to estimate the total number of mountain lions.

To investigate the effects of the half-normal detection function on our estimates of mountain lion abundance we ran simulations where we adjusted the exponent of the detection probability function (θ) where $\theta = 2$ for the half-normal detection model. We ran an additional model where $\theta = 1$ (exponential). Lastly, we investigated the effects of potential sampling bias due to non-random searching of space on estimates of population size. We simulated populations of different sizes where search effort was proportional to the unknown number of activity centers in a grid-cell, and used effort as a covariate on encounter probability. In other words, we assumed a search pattern that resulted in areas with more animals being searched more thoroughly. We compared true population size to population size estimated by spatial-capture recapture models in which we used effort as a covariate on encounter probability, in order to assess potential bias in estimating population size by not using the correct covariate (number of activity centers, which is unknown) in the spatial-capture recapture model.

RESULTS

We recorded 72 individual capture events, including captures both with and without tissue sample collection and hair samples, resulting in the identification of 50 individual mountain lions (30 females, 19 males, and 1 unknown sex individual). We collected 52 tissue samples, which represented 38 individual mountain lions. In addition, field personnel back-tracked 73 lion tracks and collected 204 hair samples. We analyzed 165 samples of which 23% of back tracks and 13% of hair samples resulted in DNA of sufficient quality to allow for individual and sex identification. Nine of the mountain lions identified from hairs collected on back-tracks were individuals not detected from the treed mountain lion group and 4 were recaptures. In addition, 3 mountain lions were captured, identified by ear tags, and released without a tissue sample. Houndsmen and back-tracking crews covered a total of 15,852 km and captured up to 5 different mountain lions in a grid cell over the course of the sampling period. Field crews captured 1 mountain lion 4 times, 3 mountain lions 3 times, and 10 mountain lions twice. They captured the majority of mountain lions (36) only once.

Density estimates of mountain lion adults, including females with dependent young, and sub-adults ranged from a minimum of 3.7 mountain lions/100 km^2 (95% CI 3.6–5.7) from our base model (including only an effect of distance on detection probability) to 6.7 mountain lions/100 km^2 (95% CI 3.1–11.0) from our full model (including effects of distance, sex, survey effort, and distance × sex on detection probability). The posterior distributions of density overlapped considerably among the different models fitted (Table 1).

For model selection, we evaluated 95% credible intervals for individual parameters across models. As expected, the probability of detecting a mountain lion increased with the amount of effort expended in a grid cell (i.e., only positive

Table 1. Estimates of total numbers and density of the population of mountain lions in the Blackfoot Drainage, a 7,908-km^2 portion of west-central Montana. Estimates are from spatial capture–recapture models containing the covariates sex, distance, and survey effort on detection probability. We also report goodness-of-fit (GOF) results; point process *P*-value tests the hypothesis that the spatial locations of individuals violate the uniformity assumption (*P*-values between 0.05–0.95 indicate an adequate fit). Goodness-of-fit *P*-value tests the overall adequacy of the model fit to the observed encounter frequency (*P*-values between 0.05 and 0.95 indicate an adequate fit).

	Estimate for Blackfoot	Mean density	Median density	95% CI	Point process *P*-value	GOF *P*-value
Distance	301	3.7 ± 0.9 SD	3.6	2.4–5.7	0.56	0.30
Full	529	6.7 ± 3.1 SD	5.6	3.1–11.0	0.52	0.58
Sex + distance × sex	395	5.0 ± 1.9 SD	3.5	2.5–4.0	0.62	0.40
Distance + sex	344	4.0 ± 1.7 SD	4.0	2.5–10.3	0.61	0.38
Distance × sex	364	4.6 ± 1.3 SD	4.4	2.4–7.8	0.64	0.32
Effort + distance	316	4.0 ± 1.0 SD	3.9	2.5–6.4	0.52	0.47
Effort + sex + distance	435	5.5 ± 1.5 SD	5.3	3.3–9.0	0.53	0.63
Effort + distance × sex	427	5.4 ± 1.6 SD	4.5	3.0–9.0	0.52	0.56

values were included in the 95% credible intervals for the effort parameter; Table 2). Parameter estimates from all models indicated that the effect of a mountain lion's sex on the baseline encounter probability was negligible (i.e., credible intervals overlapped zero for 3 out of 4 models; Table 2). Model parameter estimates indicated that σ was larger for males than for females (Table 2). Larger values for σ indicated a slower decline in the detection function at greater distances from activity centers. Lastly, mean estimates of the proportion of male mountain lions in the population (ψ_{sex}) were relatively similar across all 8 models ranging from 0.26 to 0.39. Goodness-of-fit tests indicated that we could not reject the null hypothesis of complete spatial randomness and that the fit of all encounter models were adequate (i.e., *P*-values were between 0.05 and 0.95). Convergence diagnostics reported $\hat{R}$ values <1.2 for all σ, λ, and β parameters.

Sensitivity Analysis

Field crews captured 8 mountain lions in 4 pairs (i.e., in the same grid cell during the same sampling period); therefore, we estimated mean group size as 1.1. A null model collapsing

Table 2. Parameter estimates ± 1 standard deviation from spatial capture recapture models of mountain lion abundance in the Blackfoot Drainage of western Montana. The 95% CI rows indicate the lower and upper Bayesian credible intervals. The $\sigma_{parameters}$ estimate a scaling factor on the distance effect in the detection function (this parameter can be estimated separately by sex), ψ_{sex} is the probability a mountain lion in the population is male, the $\beta_{parameters}$ denote the effect of survey effort (km traveled), and lion sex on the detection probability.

Model	Female σ	Male σ	β_{effort}	β_{sex}	ψ_{sex}
Distance					
Mean	1.31 ± 0.21	1.31 ± 0.38	0.00	0.00	0.38 ± 0.08
Median	1.30	1.30	0.00	0.00	0.38
95% CI	0.99, 1.82	0.99, 1.82	0.00	0.00	0.24, 0.56
Distance + effort					
Mean	1.38 ± 0.26	1.38 ± 0.26	1.18 ± 0.15	0.00	0.39 ± 0.08
Median	1.34	1.34	1.18	0.00	0.39
95% CI	1.07, 1.80	1.07, 1.80	0.92, 1.49	0.00	0.25, 0.56
Distance + sex					
Mean	1.25 ± 0.18	1.25 ± 0.18	0.00	0.40 ± 0.49	0.32 ± 0.11
Median	1.22	1.22	0.00	0.33	0.12
95% CI	0.97, 1.66	0.97, 1.66	0.00	−0.39, 1.60	0.12, 0.54
Distance + effort + sex					
Mean	1.35 ± 0.20	1.35 ± 0.20	1.19 ± 0.16	0.45 ± 0.55	0.37 ± 0.09
Median	1.32	1.32	1.22	0.35	0.36
95% CI	1.02, 1.80	1.02, 1.80	0.88, 1.51	−0.42, 1.83	0.21, 0.57
Distance + distance × sex					
Mean	1.11 ± 0.21	1.48 ± 0.30	0.00	0.00	0.31 ± 0.10
Median	1.09	1.42	0.00	0.00	0.31
95% CI	0.80, 1.57	1.04, 2.26	0.00	0.00	0.12, 0.52
Distance + effort + distance × sex					
Mean	1.14 ± 0.21	1.47 ± 0.31	1.22 ± 0.13	0.00	0.30 ± 0.10
Median	1.11	1.47	1.27	0.00	0.29
95% CI	0.82, 1.64	1.05, 2.27	0.66, 1.53	0.00	0.12, 0.54
Distance + sex + distance × sex					
Mean	1.04 ± 0.19	1.49 ± 0.34	0.00	−0.12 ± 0.72	0.31 ± 0.09
Median	0.86	1.19	0.00	−0.78	0.30
95% CI	0.48, 0.80	1.27, 2.44	0.00	−1.59, −0.45	0.16, 0.52
Distance + effort + sex + distance × sex					
Mean	1.18 ± 0.26	1.61 ± 0.39	1.23 ± 0.19	0.23 ± 0.86	0.26 ± 0.12
Median	1.14	1.53	1.25	0.26	0.26
95% CI	0.77, 1.81	1.05, 2.61	0.86, 1.57	−1.36, 1.72	0.06, 0.52

Table 3. Results of simulations comparing mountain lion density estimates for models with a) different buffer sizes around the surveyed area (i.e., different state space sizes), and b) different grid sizes within the state space. Point process *P*-value tests the hypothesis that the spatial locations of individuals violate the uniformity assumption (*P*-values between 0.05 and 0.95, indicate an adequate fit). Goodness-of-fit (GOF) *P*-value tests the overall adequacy of the model fit to the observed encounter frequency (*P*-values between 0.05–0.95, indicate an adequate fit).

	Buffer size		
Grid size = 4 by 4	**5 km**	**10 km**	**15 km**
a)			
Mean abundance	208	263	334
Mean density	3.5 (±0.9 SD)	3.7 (±0.9 SD)	3.8 (±0.9 SD)
Median density	3.3	3.6	3.7
95% credible interval	2.2–5.6	2.4–5.7	2.4–5.9
Point process *P*-value	0.62	0.58	0.56
GOF *P*-value	0.30	0.31	0.30

	Grid size		
Buffer size = 15 km	**2 by 2**	**4 by 4**	**8 by 8**
b)			
Mean number	332	334	324
Mean density	3.8 (±0.9 SD)	3.8 (±0.9 SD)	3.7 (±0.8) SD
Median density	3.6	3.7	3.7
95% credible interval	2.3–5.7	2.4–5.9	2.3–5.8
Point process *P*-value	0.59	0.56	0.64
GOF *P*-value	0.30	0.30	0.30

8 individuals into 4 pairs for a total of 46 mountain lions versus 50 individual lions estimated 3.2 lion groups per 100 km^2 or 3.5 individual lions per 100 km^2 (95% CI 1.9–5.1). Our simulations to assess the effects of buffer size and grid size on model results indicated no effect on density estimates (Table 3). Adjusting the exponent of the distance metric, θ, in our models resulted in no change to our abundance estimates (Fig. 3a); however, baseline encounter rates, λ_0, and estimates of σ changed in response to changes in θ (Fig. 3b and c). Our assessment of the effects of sampling bias induced by knowledge of mountain lion presence indicated that population size estimates from spatial-capture recapture models display moderate negative bias (1–3%) when search effort is used as a covariate on encounter probability (Appendix C, available online at www.onlinelibrary.wiley.com).

DISCUSSION

Estimates from our base model were similar to Robinson and DeSimone's (2010) estimate of 3.6 mountain lions/100 km^2 for the Garnet Mountains, an area located within the Blackfoot Drainage. Estimates of mountain lion densities from other studies also correspond to the range of values we estimated from our models. For example, Robinson et al. (2008) reported mountain lion densities of 5.03 mountain lions/100 km^2 for a game management unit in Washington, Ross and Jalkotzy (1992) report estimated densities of 2.7–3.3 mountain lions/100 km^2 to 4.5–4.7 mountain lions/100 km^2 for a hunted population in Alberta, and Logan et al. (1986) reported 3.4 mountain lions/100 km^2 and 4.5 mountain lions/100 km^2 during two winters on study sites in Wyoming. Choate et al. (2006) compared several

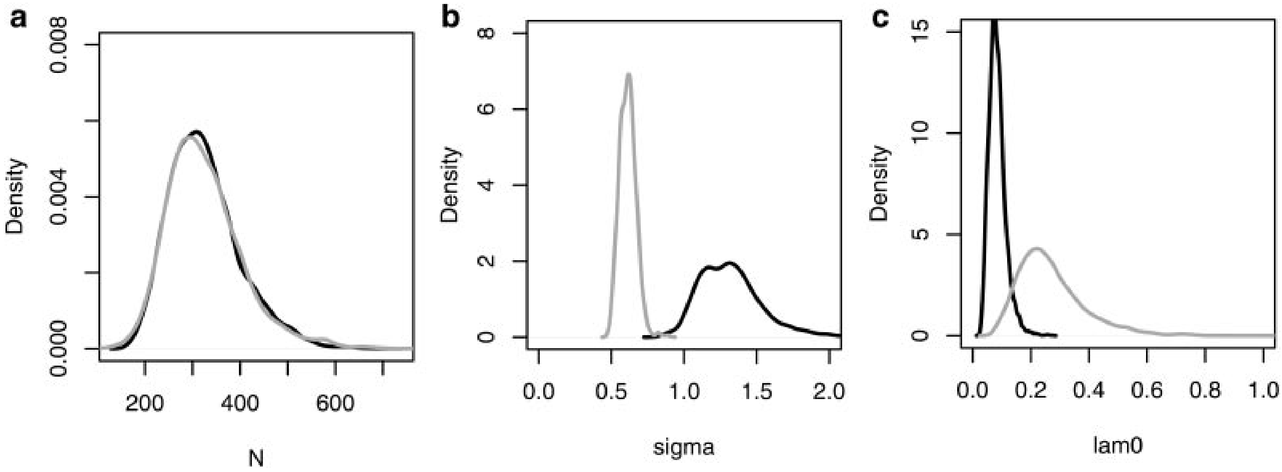

Figure 3. Simulation results for estimates for different values of the decay function in the detection probability (θ). We present posterior densities of (a) *N*(abundance), (b) sigma (σ, scaling factor for the detection function), and (c) lam0 (λ_0, intercept term for the detection function) for the half-normal (black line), and the exponential (gray line).

different indices and methods for estimating mountain lion abundance and concluded that costly and intensive mark–recapture efforts were the only method that produced reliable estimates of lion abundance. Estimates from the mark–recapture study conducted in Utah were 3.2 adult and sub-adult lions/100 km^2 in 1997 and 1.2 mountain lions/100 km^2 in 2001 for a hunted population and 2.8 mountain lions/100 km^2 for a nearby non-hunted population (Choate et al. 2006).

In winter, mountain lion populations often concentrate around congregations of prey populations (Seidensticker et al. 1973). Additionally, female mountain lions and their offspring typically remain together for 1 year, and the mean dispersal age in the Garnet mountain lion study was 15 months (Robinson and DeSimone 2010); therefore, movements of females and their offspring may not be independent. In our study, females traveling with dependent young, overlapping male and female mountain lion ranges (Hornocker 1969, Seidensticker et al. 1973), and winter concentrations of prey, may have resulted in higher densities of mountain lions than what is typical for areas where prey do not congregate in the winter. We attempted to correct for non-independence of movements in our study by grouping animals together that were captured in the same grid during the same time period. The estimates from this model were slightly less than our estimates from models that assumed lion movements were independent. However, our estimates of group sizes were likely underestimates (we assume that we did not capture all female and young combinations). We suggest that, particularly in cases where family groups are larger, some effort should be expended in identifying individuals with movement patterns that are dependent in some way on other individuals.

As with many models of large carnivores, our study produced a sparse data set with few individuals and even fewer recaptures. This necessitated the use of relatively simple models with few parameters. For example, we used a simple 2-parameter encounter model, which implies that space usage by individuals is approximated by a bivariate normal (Jennrich and Turner 1969) distribution. We regarded activity centers not as equivalent to individual home ranges but rather as the centroid of space used by an individual during the specific time period of the study (i.e., over which samples accumulated). Therefore, the model implies a bivariate normal approximation to this area of space usage. Our model also assumes that activity centers are distributed uniformly in space. Although both these assumptions represent simplifications of actual patterns of space use, our goodness-of-fit evaluation based on Bayesian P-values suggest these assumptions provide adequate descriptions of our data.

We adapted a spatial capture–recapture model for opportunistic search-encounter data based on unstructured spatial sampling (Thompson et al. 2012). In our application, observers track mountain lions until a sample of DNA can be obtained. As a result of this non-independence, the encounter model of Royle et al. (2011*b*) based on cumulative hazard to the search path is not reasonable. Instead, we developed spatial encounter histories for a coarse (5-km grid) based on whether each grid cell had any non-zero amount of search effort. We then used search effort (length of search path) as a covariate in the model. The Royle et al. (2011*b*) model accommodated individual locations as the outcome of some movement model. In the present case, locations of individuals correspond (typically) to points along the search path because of the non-independence of the sampling and thus the second stage of the model in Royle et al. (2011*b*) is not meaningful in the context of opportunistic search-encounter data.

When detection is uncertain and probabilities of detection are not taken into account, abundance is likely to be underestimated. Conversely, our methods were susceptible to sampling bias that could have inflated estimates of abundance. Overall, we suspect the amount of effort exerted in a grid cell may have reflected the a priori estimated probability of capturing a mountain lion; rather than more effort resulting in a greater probability of detecting a mountain lion, a higher probability of detecting a mountain lion resulted in more effort being expended. This type of survey will potentially bias density estimates high (as indicated by our simulations). Indeed our models with effort in the detection function generated the greatest estimates of mountain lions for the Blackfoot. Sampling of random transects in addition to areas where mountain lions were known to occur may have provided additional information to allow for unbiased estimates. Though statistical methodology can potentially correct for differences in detection probability and survey effort, sampling bias can compromise estimates especially if that bias is unstated.

The methodology presented here is flexible enough to accommodate search patterns that can result in grid cells being characterized as surveyed or not surveyed. Previous results indicate that the selection of grid cell size should reflect the ecology and movement ability of the species (Thompson et al. 2012). Cells should be large enough to minimize resampling of an individual because of spatial autocorrelation of hair, scat, or track samples, and yet small enough to avoid the negative bias in population estimation resulting from a failure to account for individual heterogeneity (Dorazio and Royle 2003, Thompson et al. 2012).

Our results indicate that genetic sampling combined with spatial locations of captures provides a promising method for estimating population sizes of animals that are difficult to sample with systematic sampling methods. Repeated systematic surveys conducted in traditional mark–recapture studies would likely have led to very low capture and recapture rates for the mountain lion population, thus increasing our estimation error. Estimates of abundance for harvested wildlife populations are useful for assessing the impacts of management actions such as different harvest quotas, or season lengths. Additionally, periodic population estimates can help determine the value of population indices, the accuracy of population models, and allow managers to evaluate population trends.

MANAGEMENT IMPLICATIONS

Snow tracking has been shown to be an effective technique to collect hair samples for multiple low density carnivores including lynx, mountain lions, and wolverine (McKelvey et al. 2006, Ulizio et al. 2006, Sawaya et al. 2011). Snow tracking inevitably involves a non-random search pattern as individual observers attempt to follow the path of the carnivore. The recent development of spatial capture–recapture models, including those developed here, provides managers with a flexible technique for estimating abundance of animals that are difficult to survey because of their elusive behavior or low density occurrences, while accounting for the spatial distribution of traps or animal detections. Without a methodology for accurately enumerating mountain lion populations across space, perceived densities of mountain lions may influence wildlife stakeholders' acceptance levels for mountain lions (Riley and Decker 2000). An effective way of estimating carnivore population sizes will help inform science-based decisions about predator harvest levels and will facilitate evaluations of different management policies and strategies on mountain lion populations.

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