

Estimating abundance of an open population with an N -mixture model using auxiliary data on animal movements

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Abstract. Accurate assessment of abundance forms a central challenge in population ecology and wildlife management. Many statistical techniques have been developed to estimate population sizes because populations change over time and space and to correct for the bias resulting from animals that are present in a study area but not observed. The mobility of individuals makes it difficult to design sampling procedures that account for movement into and out of areas with fixed jurisdictional boundaries. Aerial surveys are the gold standard used to obtain data of large mobile species in geographic regions with harsh terrain, but these surveys can be prohibitively expensive and dangerous. Estimating abundance with ground-based census methods have practical advantages, but it can be difficult to simultaneously account for temporary emigration and observer error to avoid biased results. Contemporary research in population ecology increasingly relies on telemetry observations of the states and locations of individuals to gain insight on vital rates, animal movements, and population abundance. Analytical models that use observations of movements to improve estimates of abundance have not been developed. Here we build upon existing multi-state mark–recapture methods using a hierarchical N -mixture model with multiple sources of data, including telemetry data on locations of individuals, to improve estimates of population sizes. We used a state-space approach to model animal movements to approximate the number of marked animals present within the study area at any observation period, thereby accounting for a frequently changing number of marked individuals. We illustrate the approach using data on a population of elk (*Cervus elaphus nelsoni*) in Northern Colorado, USA. We demonstrate substantial improvement compared to existing abundance estimation methods and corroborate our results from the ground based surveys with estimates from aerial surveys during the same seasons. We develop a hierarchical Bayesian N -mixture model using multiple sources of data on abundance, movement and survival to estimate the population size of a mobile species that uses remote conservation areas. The model improves accuracy of inference relative to previous methods for estimating abundance of open populations.

Key words: abundance; *Cervus elaphus nelsoni*; elk; hierarchical Bayesian statistics; multi-state mark–recapture; N -mixture model; population size; wildlife.

INTRODUCTION

Estimating abundance forms a central challenge in population ecology and wildlife management (Seber 1982). The growth or decline of populations over time reflects changes in movement and survival. We developed a model to simultaneously estimate abundance, survival, and movement probabilities, to inform decisions on managing a population within areas defined by fixed jurisdictional boundaries. Large mobile animals can move into and out of these areas, creating challenges for abundance estimation and, hence, complicate decisions on population management.

It is imperative that population estimates account for the inevitable bias that results from animals that are present but

not seen. Failing to account for detectability means that differences in population estimates from year to year may result from errors in observing the population rather than from differences in the population itself. Many methods have been proposed to account for the problem of imperfect detection in estimates of animal abundance. These include mark–recapture (Pollock 1982, Nichols 1992, Kendall et al. 1997), removal sampling (White and Leffler 1982), and distance sampling (Buckland 2001). All of these methods use design-based procedures for estimating the probability of detecting individuals given that they are present. Detection probabilities, in turn, are used to account for individuals that are present but not counted, thereby correcting for “undercounting” bias.

There are many sources of variability that have been accounted for in mark–recapture estimators, including individual heterogeneity, environmental heterogeneity, time dependence, behavior, and combinations of all of these (Kendall 1999, Borchers et al., 2002). The estimation of the detection probability can be confounded by the fact that only a proportion of individuals in a population is available for sampling at any given time (Kendall 1999). Many mark–recapture

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estimators have been developed to adjust for mobility of species because movements in space can be substantially broader than the geographic regions that are surveyed. Temporary emigration can lead to biased estimates of abundance, resulting from underestimates of the probability of detection (p) and a corresponding overestimation of the total population size (N) (Nichols and Kendall 1995, Kendall et al. 1997). Different types of movement can lead to a variable number of individuals that are available to sample at any given time and may confound estimates across multiple surveys (Kendall 1999). Knowledge of the total population that uses these static regions can help inform management actions that target animals within fixed boundaries.

Research in population ecology increasingly relies on telemetry observations of the locations and states of individuals over time to gain insight on vital rates and behavior. However, there is no analytical approach for using these data to improve inference on animal abundance (Barker et al. 2017). We developed a hierarchical Bayesian model for estimating population sizes in a mark–recapture framework, using an N -mixture model coupled with location data on animal movement and survival. The method provides inference based on the posterior distribution of the average abundance of animals in a sequence of counts within a specified area without assuming that the area is closed to immigration, emigration, or mortality. We used very high frequency (VHF) telemetry collars and subsequent location information collected on a weekly timescale to model the temporary movement patterns of individuals into and out of the study region to estimate abundance in an open population (Chandler et al. 2011, Dail and Madsen 2011, Ivan et al. 2013) without making assumptions regarding individual home ranges or spatial distributions (Royle et al. 2014).

We used a model-based approach to estimate overall average abundances across multiple years and simultaneously estimate demographic parameters that provide important information about the state of the surveyed population. We estimated survival probabilities on weekly and annual time scales and we estimated transition probabilities that reflect movements among multiple areas within the surveyed region, which allowed us to assess the connectivity of various subgroups of the population. Our novel approach makes use of multiple sources of commonly collected data, thereby providing a complete summary of the state of the population during a specific period of time.

MATERIALS AND METHODS

Overview of modeling approach

Observations of locations of animals are prone to error and frequently include missing observations, motivating the use of a state-space approach to obtain posterior distributions of the true locations. We separate observed telemetry location data from an underlying true location of each collared individual. A general state space approach can be described as the conditional probability of observations (Y) given a true state (X) and a set of parameters governing the uncertainty with the data (θ_d)

$$[Y|X, \theta_d] \tag{1}$$

where the brackets denote a probability distribution. We can link our knowledge of the ecological system to the observations using a model for the latent state (X) and parameters (θ_p) governing its behavior such that

$$[X|\theta_p]. \tag{2}$$

We separated an underlying Markovian movement process model from a data model specified for location observations. Using this hierarchical structure, we were able to estimate the number of marked individuals that were available in the sample area during any week we surveyed the population. The movement model informs the true, unobserved locations of marked individuals, which allows us to know, with estimates of uncertainty, the true number of marked individuals within the study area.

We coupled the movement model with a mark–recapture estimator of independently collected count data from repeated surveys. The observed counts (n) can be modeled with a conditional probability distribution that depends on the total population size (N) and some function of detectability ($f(X)$), that we derived from the movement model true states. In general, a model combining the movement with census is described as

$$[n|N, f(X)]. \tag{3}$$

The data (n) consist of counts of the total number of individuals within the survey region as well as observations of the number of marked individuals within encountered groups. We also used additional secondary information to account for imperfectly recorded resighted marks, by calibrating the resights with telemetry data collected to verify this separate detection process. We combined the estimates of the true number of marked individuals within the region of interest with the estimated number of resighted marks, to determine the probability of detecting an individual in an N -mixture model (Eq. 3). We used a Bayesian approach implemented in JAGS (Plummer 2014) to approximate posterior distributions of model parameters “(see Supporting Information).”

Model development for marked individuals

We first considered the general scenario of repeatedly sampling a population of N individuals for $t = 1, \dots, T$ surveys. A subset of the population has been subjected to capture, in which individuals representative of the population are marked, and subsequently recaptured or resighted during T occasions.

We know that the total population size will likely change between surveys because of temporary emigration, immigration, and mortality. Using a hierarchical structure, we were able to capture sampling error resulting from temporal variation in abundance within the study area, as well as accounting for observation error resulting from failing to count animals that were present but not observed. Thus, a sample of n_t individuals is distributed as a binomial random variable such that

$$n_t \sim \text{binomial}(N_t, p_t) \tag{4}$$

$$N_t \sim \text{Poisson}(\mu) \tag{5}$$

$$\mu \sim \text{gamma}(\alpha, \beta) \tag{6}$$

where N_t is the total population size during sample t and μ is the overall average number of individuals that use the study area during the sampling intervals. The detection probability $p_t = R_t/M_t$ is defined as the ratio of the number of resighted marks (R_t) out of the total number of marked individuals (M_t), during the t th survey, similar to the classical Lincoln-Petersen estimator (Otis et al. 1978, Seber 1982). Auxiliary data must be used to determine p_t to avoid identifiability problems, because both N_t and p_t are unknown.

We explicitly modeled the movement behavior of marked individuals using location data collected with telemetry, and, in turn, we estimated the true number of marked individuals available for sampling during census. We made the assumption that closure only applies on the time scale of the location data intervals. Additional assumptions include that detection does not vary with any environmental heterogeneity, and that individuals do not alter behavior resulting from the initial capture.

Elk in Rocky Mountain National Park

The method we offer is general, and could apply to any species that moves in and out of a static study area during repeated surveys across a season. We developed the approach to provide estimates of population sizes corresponding to a fixed spatial domain targeted by management. Estimates reflect the number of individuals that use this domain, rather than a spatially constant population size, because environmental impact is based on the use of the conservation area.

We illustrate the approach using data on the wintering elk population in the Estes Valley, which consists of lower elevation areas on the eastern side of Rocky Mountain National Park (RMNP) and in the adjacent town of Estes Park, Colorado (EP). Management decisions based on abundance are made annually and require an estimate for the average number of elk using the park during the winter.

Aerial survey methods were used to survey elk in RMNP for 20 yr (1994–2014), however, the high costs and dangerous conditions of flying over the eastern slope of the Rocky Mountains during the winter motivated a change to ground survey methods. We used weekly ground VHF telemetry data collected throughout the winter months to determine the number of marked animals available in the region during ground surveys, where total counts of groups and counts of marked individuals were made along 10 road transects to obtain the abundance of elk in both RMNP and EP.

We developed this model to understand movements of elk across static park boundaries, as well as to develop a ground-based survey method that could be repeated multiple times during the winter season to understand temporal variation in elk abundance on the winter range within RMNP and EP.

Data

Approximately 20 volunteers drove road transects on the winter range of RMNP and EP. The volunteers recorded counts (y_{n_t}) of elk groups, as well as the number of collared elk present (m_t) during three days during the first or second week of each month of winter (November–March). The average total number of elk per day within each week,

rounded to the nearest integer, (n_t) were used as data in the N -mixture model of Eq. 4 to account for sampling variability within survey weeks.

We used the weekly ground telemetry locations of approximately 150 collars that were deployed by the National Park Service, and Colorado Parks and Wildlife (Fig. 1) to correct for animal movements across park boundaries in the model described below. The dates of collar deployment for each collar are known.

Movement model

Ideally, we would know the true locations of these collared elk every week, although realistically, the true state of the collared elk location was not always observed perfectly. We used a hierarchical, state space model to account for the movement of elk among three possible locations. We also incorporate observations of the marked individual’s status, alive or dead.

First, we describe a process model of the underlying true condition of the collared elk. We define a vector of seven mutually exclusive categories, or “true states” (Table 1). The three location categories indicate that the i th elk is either alive or dead within RMNP, EP, or outside the study area (generally the foothills). These areas can be seen in Fig. 1 with all telemetry observations throughout the winters from 2011 to 2015.

We used a vector of the true states ($\mathbf{x}_{i,t}$) to represent the true, unobserved location and condition of the i th collared animal at week t of winter. Individuals were denoted as out of the study if they were not yet collared or had died during a previous week of winter. A matrix of across winter histories of the state of the i th individual, \mathbf{X}_i , consists of a collection of the true state vectors across all time points. Thus, each column of \mathbf{X}_i represents a weekly time point for $i = 1, \dots, I$ collared elk. We assume a Markovian movement model, such that the probability of an elk moving from one state to another depends on the state of the elk during the previous point in time. The probabilities of the individual moving among states are described in Eq. 7.

$$\Theta = \begin{pmatrix} \phi\pi_{1,1} & \phi(1-\pi_{2,2})\pi_{2,1} & \phi(1-\pi_{3,3})(1-\pi_{3,2}) & 0 & 0 & 0 \\ \phi(1-\pi_{1,1})\pi_{1,2} & \phi\pi_{2,2} & \phi(1-\pi_{3,3})\pi_{3,2} & 0 & 0 & 0 \\ \phi(1-\pi_{1,1})(1-\pi_{1,2}) & \phi(1-\pi_{2,2})(1-\pi_{2,1}) & \phi\pi_{3,3} & 0 & 0 & 0 \\ (1-\phi)\pi_{1,1} & (1-\phi)(1-\pi_{2,2})\pi_{2,1} & (1-\phi)(1-\pi_{3,3})(1-\pi_{3,2}) & 0 & 0 & 0 \\ (1-\phi)(1-\pi_{1,1})\pi_{1,2} & (1-\phi)\pi_{2,2} & (1-\phi)(1-\pi_{3,3})\pi_{3,2} & 0 & 0 & 0 \\ (1-\phi)(1-\pi_{1,1})(1-\pi_{1,2}) & (1-\phi)(1-\pi_{2,2})(1-\pi_{2,1}) & (1-\phi)\pi_{3,3} & 1 & 1 & 1 \end{pmatrix} \quad (7)$$

Element	Definition
$\pi_{1,1}$	Probability that an animal in RMNP at time t stays in RMNP at time $t + 1$
$\pi_{1,2}$	Conditional on the animal moving from RMNP, it moves to EP
$\pi_{2,2}$	Probability that an animal in EP at time t remains in EP at time $t + 1$
$\pi_{2,1}$	Conditional on the animal moving from EP, it moves to RMNP
$\pi_{3,3}$	Probability that an animal outside the Estes Valley at time t remains outside at $t + 1$
$\pi_{3,2}$	Conditional on the animal moving from outside the Estes Valley, it moves to EP

We define a constant weekly survival probability ϕ independent of movement and inclusive of harvest and incorporate this probability into the transition matrix. A multinomial distribution was used to model the true latent state of the animal at time $t - 1$ where

$$\mathbf{x}_{i,t} \sim \text{multinomial}(1, \Theta \mathbf{x}_{i,t-1}) \quad (8)$$

using the transition matrix Θ (Eq. 7).

If we could actually observe these true states of the elk, then estimating the movement and abundance would be unnecessary because we would already know the status of

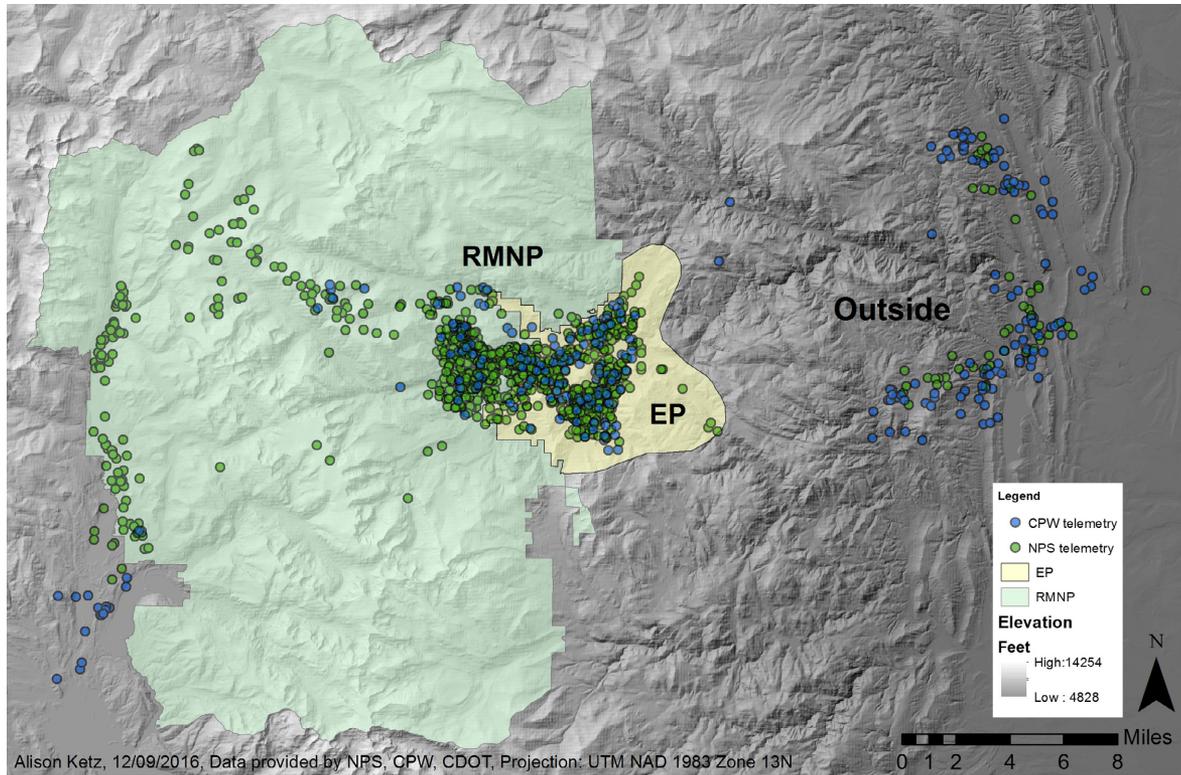


FIG. 1. Observed telemetry location data over time are represented by points. The green area represents Rocky Mountain National Park (RMNP) and the yellow region represents the town of Estes Park (EP). Telemetry locations were collected by two government agencies, the National Park Service (NPS; green points) and Colorado Parks and Wildlife (CPW; blue points). 1 mile = 1.6 km.

the population without uncertainty. However, there is uncertainty in the observation process: the true state (\mathbf{X}) was related to the observed state (\mathbf{Y}) through telemetry data (Table 1).

TABLE 1. We define a vector $\mathbf{x}_{i,t}$ with a 1 in one of seven mutually exclusive true states of the i th collared elk during the t th week of winter, with zeros elsewhere. We define a vector $\mathbf{y}_{i,t}$ with a 1 in one of ten mutually exclusive observed states of the i th collared elk during the t th week of winter, with zeros elsewhere.

Element j	Definition
$x_{1,t}$	alive in RMNP
$x_{2,t}$	alive in EP
$x_{3,t}$	alive outside of Estes Valley
$x_{4,t}$	dead in RMNP
$x_{5,t}$	dead in EP
$x_{6,t}$	dead outside of Estes Valley
$x_{7,t}$	out of study
$y_{1,t}$	observed alive in RMNP
$y_{2,t}$	observed alive in EP
$y_{3,t}$	observed alive along RMNP/EP boundary
$y_{4,t}$	observed alive outside the Estes Valley
$y_{5,t}$	observed alive, but no information on location is obtained
$y_{6,t}$	observed dead in RMNP
$y_{7,t}$	observed dead in EP
$y_{8,t}$	observed dead outside the Estes Valley
$y_{9,t}$	unobserved
$y_{10,t}$	out of study

Note: RMNP, Rocky Mountain National Park; EP, Estes Park.

A multinomial distribution was used to model the set of possible outcomes of observable states that arise from the underlying latent process. We link the observations of the state of the collared elk to the true states of the elk using a detection matrix \mathbf{D} such that

$$\mathbf{y}_{i,t} \sim \text{multinomial}(1, \mathbf{D}\mathbf{x}_{i,t}) \tag{9}$$

$$\mathbf{D} = \begin{pmatrix} p_s p_o p_d & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & p_s p_o p_d & 0 & 0 & 0 & 0 & 0 & 0 \\ p_s p_o (1 - p_d) & p_s p_o (1 - p_d) & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & p_s p_o & 0 & 0 & 0 & 0 & 0 \\ p_s (1 - p_o) & p_s (1 - p_o) & p_s (1 - p_o) & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & p_s & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & p_s & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & p_s & 0 \\ 1 - p_s & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix} \tag{10}$$

Parameter	Definition
p_s	Probability that the individual is observed.
p_o	Conditional on being observed, the probability that information on location is obtained.
p_d	Conditional on being observed with location information, the probability if it is in RMNP or EP.

where p_s is the probability that the individual is observed, p_o is the probability that information on location is obtained, conditional on the individual being observed, and p_d is the probability of the individual being in RMNP or EP, conditional on the individual being observed and on location information being obtained.

The number of marked individuals that could possibly be seen during ground census were calculated using the sum of the state vectors for the two geographic regions of interest during week t . The true number of collared elk in RMNP is $\sum_i x_{1,i,t}$ and for EP it is $\sum_i x_{2,i,t}$. Recall that $x_{1,i,t}$ represents whether the i th collared elk during the t th week of winter is either alive and in RMNP (1) or not (0). Similarly, the state of the elk with regard to EP ($x_{2,i,t}$) is either a 1 (present) or 0

(not present). We defined the number of marks (M_t) equal to the summation of the state vectors for the corresponding region of interest. Thus, the denominator for the detection probability in Eq. 4 for the elk in RMNP is $\sum_i x_{1,i,t}$ and similarly, the denominator in the detection probability for the elk in EP is $\sum_i x_{2,i,t}$. Movements between RMNP and EP are not independent because these states are mutually exclusive. However, because we explicitly model the movement across these regions, we do not need to incorporate the correlation between the abundance estimates for each area.

Perfectly observed resights of collars is a typical assumption of mark–recapture estimators. Estimates of population sizes are quite sensitive to violations of this assumption. One of the strengths of the Bayesian approach for learning about model parameters is that it is straightforward to alter the model to accommodate idiosyncrasies in the data, in this case, the failure to observe all marks that were present. The National Park Service deployed brown telemetry collars within RMNP to make collars less visible to park visitors. However, this meant that observers counting elk were not always able to see all collars present in a group. There were obvious errors in the number of marks observed during the ground count (m_t) leading to potentially serious biases in estimates of population size. This was particularly problematic when the elk were aggregated into large groups, which is common for calf and cow herds during winter. We collected data and developed a calibration model to account for the collars that were present but overlooked (Appendix S3).

Model fitting

Flat uniform prior distributions with support from zero to one were chosen for movement, survival, and detection probabilities. One ground count survey from the second year of study was omitted from the analysis due to inaccurate counting. The prior distribution for the average across winter mean of elk in both RMNP and EP was specified as $\text{gamma}(3, 0.01)$, which is minimally informative (Hobbs and Hooten 2015), and was based on prior information from previous years of study that the average number of elk was approximately in the low to mid hundreds, in the range of 200–400 individuals in either area (Ketz et al. 2016). Sensitivity of the over-winter population sizes to the influence of this prior was determined by refitting one year using a completely flat prior distribution for the over-winter means ($\text{gamma}(0.01, 0.01)$) in Appendix S4.

The full hierarchical Bayesian model, with the corresponding directed acyclic graph, as well as the joint and posterior distributions are provided in Appendix S1 and Appendix S2. We verified that parameters could be accurately recovered during model fitting using simulations based on known parameters. The model was fit using JAGS (Plummer 2014) with the *dclone* package (Sólymos 2010) for parallel computation of the *rjags* package (Plummer 2013) in R (R Core Team 2016). Three chains consisting of 200,000 Markov chain Monte Carlo iterations with a burn-in of 50,000 iterations were generated (Data S1).

Trace plots, ACF plots, and the Gelman-Rubin (Gelman et al. 2014) diagnostics indicated convergence of virtually all of the marginal posterior distributions of model parameters and latent states. Convergence problems arose for the

approximation of the posterior distributions of three of the model parameters, namely for the derived probability of detection from one of the months during the first year of study, and for two of the derived monthly probabilities of detection during the second year of the study. However, in all instances, the across winter average population size of elk successfully converged, so inference for this parameter is valid. After one monthly survey from the third year of the study was removed, posterior predictive checks showed no evidence of lack of fit (Gelman et al. 2014) for all years.

Model comparisons

We compared our method with three additional models of abundance that are commonly used for open populations. Ideally, we could obtain the abundance of this population without using mark–recapture data for cost-effective future ground surveys. We considered the Dail-Madsen (DM) model because it was developed for unmarked open populations, but with our survey design we could only specify 10 replicate sites using the road transects, which is an inadequate number of spatial replicates for this model. A small number of survey sites is often the case in ecological data, which is why our model is an improvement on the DM model. Nevertheless, we used the DM model to obtain posterior distributions of the average number of individuals in the combined survey region (RMNP and EP) for each year, using the 10 road transects and 15 surveys of counts from each winter.

The Jolly-Seber multi-state approach for estimating abundance of marked open populations provides a suite of possible estimators for abundance using the mark–recapture telemetry data, including the Arnason-Schwartz model and its variants (Jolly 1965, Seber and Manly 1985, Schwarz and Arnason 1996, Kéry and Schaub 2011). We obtained results with the multi-state Jolly-Seber approach by approximating distributions of abundances across winter for each year separately using the Bayesian restricted dynamic occupancy parameterization (Royle and Dorazio 2008, Kéry and Schaub 2011). This parameterization provides the same “superpopulation” sizes as the Arnason-Schwartz model, but is computationally much faster (Kéry and Schaub 2011). The Jolly-Seber approach depends on numerous assumptions, including random initial captures, that could be violated in our survey. However, failing to meet assumptions of the JS models is quite common and demonstrates the flexibility of our approach.

We then developed a mark–recapture N -mixture model very similar to Pollock’s robust design in a Bayesian framework (Pollock 1982, Kendall et al. 1997), without adjusting the number of marked individuals using the state-space model of telemetry data. We specified a primary sampling period for each of the five months of winter, in which temporary emigration was permitted. We assumed closure within the ground survey weeks (secondary samples) where we used three repeated count surveys and used the proportion of resighted marks to the total number of marks for the detection probability. We did not correct the number of marks available for sampling using the auxiliary telemetry data. All of these models were approximated using MCMC and standard diagnostics indicated convergence of all posterior distributions (Data S2).

RESULTS

The estimated population sizes in RMNP and EP were substantially lower than the historical estimates of over-abundant elk on the winter range (Hess 1993, Lubow et al. 2002, Ketz et al. 2016; Fig. 2 and Table 2). The median of the posterior distribution of the population size in the study area as a whole ranged from a low of 488 individuals in 2012 with an equal-tailed Bayesian credible interval (BCI = 462, 515), to a high in 2014, with a median of 825, (BCI = 747, 918) individuals (Table 2 and Fig. 2).

The number of elk that used RMNP more than doubled between 2012 and 2013, from 171 (BCI = 158, 187) to 422 (BCI = 372, 478) individuals. Increases in the population on this time scale were more likely to result from the fluid connectivity of the sub herds that also use other areas, such as EP or the foothills during the winter than from increased recruitment of the same animals within RMNP. These results highlight the fact that movement between RMNP, EP, and the foothills is an important process that must be accounted for during abundance estimation.

Posterior distributions of the process model parameters were generated for each year of the study separately, and showed little influence from the prior distributions because the posteriors differed from the priors (Appendix S4). Results were identical when a completely flat prior was used ($\mu \sim \text{gamma}(0.01, 0.01)$) compared to when a minimally informative prior was ($\mu \sim \text{gamma}(3, 0.01)$) (Appendix S4) for one year of the study. For populations that may be rare, or where little prior information is known, a flat prior could be used and will only result in slower convergence of MCMC chains. The weekly survival probabilities were transformed into annual estimates of survival, using the transformation ϕ^T (Noon and Sauer 1992), where T was the number of weeks of winter telemetry observations within each year. Median annual survival probabilities increased during the first four years of the study, and decreased during the last year (Table 3).

Movement probabilities were consistent among all years and had a similar trend within years (Appendix S4). For example, in 2015, collared individuals that were in RMNP were more likely to remain (median $\pi_{11} = 0.88$ [BCI = 0.86, 0.9]) than they were to leave (median $1 - \pi_{11} = 0.12$ [BCI = 0.1, 0.14]). Similarly, the median probability that a collared individual that was in EP at time t (π_{22}), would stay was 0.85 (BCI = 0.83, 0.88). Although collared individuals were more likely to remain in their location based on these transition probabilities, movement between these areas, as well as outside of the study region was occurring because the mass of probability (>0.999) in the posterior distributions of movement parameters (π) did not include 1.

The probability of detecting a collared individual (p_s) decreased throughout the years of the study (Appendix S4: Table S1). Low probabilities of detecting the marked individuals (p_s) justifies the use of the state space approach for modeling telemetry data, where missing data are treated as unknown parameters and the posterior distributions of the true locations can be approximated. After an individual was detected, information about the location of that individual was likely obtained with posterior median detection probabilities $p_d = p_v = 1$.

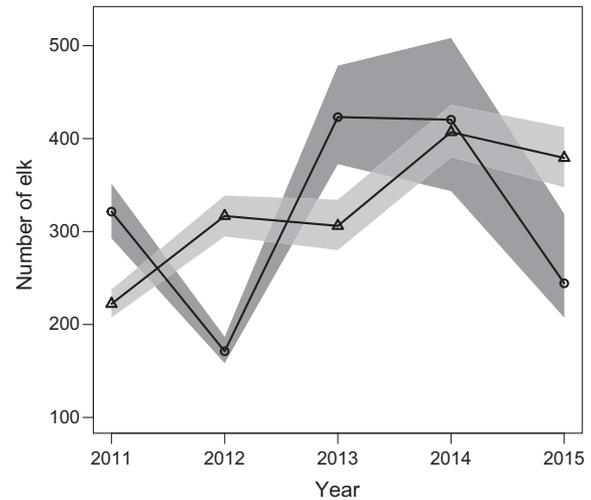


FIG. 2. The median number of elk using Rocky Mountain National Park, μ_{RMNP} (circles), and in the town of Estes Park, μ_{EP} (triangles), shows the population during five winters. The 95% Bayesian credible intervals for RMNP (dark gray) and EP (light gray) are the shaded regions.

We found an inverse relationship between herd size and collar detectability, such that the probability of missing marks within a sighted group decreased by -0.0099 , ($SD = 0.0041$) as herd size increased with each additional elk (Appendix S3: Fig. S1). The observed proportions of collared elk accurately detected during ground counts in both RMNP and EP show high variability in sightability, ranging from 0.13 to 1.0.

Summary statistics of the posterior distributions for the average number of elk in the winter range of the Estes Valley showed the altered inference that occurred when different models and different data of the same population were used (Table 4). The Jolly-Seber model, which only considered

TABLE 2. Five years of the average number of elk on the winter range from 2011 through 2015 for RMNP (μ_{RMNP}), EP (μ_{EP}), and the Estes Valley as a whole (μ_{VAL}).

Parameter (year)	Mean	Median	SD	0.025	0.975
μ_{RMNP}					
2011	321	321	15.1	293	352
2012	171	171	7.2	158	187
2013	423	422	27.1	372	478
2014	420	418	42.1	344	508
2015	244	238	28.3	207	319
μ_{EP}					
2011	222	222	7.7	207	238
2012	317	317	11.4	295	339
2013	306	306	13.9	280	334
2014	407	406	14.3	380	436
2015	379	379	16.4	348	412
μ_{VAL}					
2011	544	543	16.9	511	577
2012	488	488	13.5	462	515
2013	729	729	29.0	674	788
2014	827	825	43.7	747	918
2015	623	619	32.2	573	702

Note: The right two columns represent the 0.025 and 0.975 quantiles of the marginal posterior distributions of the estimated parameters.

abundance using the telemetry data, had the lowest mean population sizes, with medians below the ground count population totals. The open population Dail-Madsen model posterior means, using only the ground count data, were nearly nine times greater than the Jolly-Seber model posterior means. When observation error of the telemetry data were ignored, the posterior means of the average overwinter number of elk were more than three times greater than the posterior means using the state-space model of movement of the telemetry data.

DISCUSSION

We developed a Bayesian hierarchical model that exploited multiple sources of data to estimate animal abundance when scales of animal movement are greater than the fixed spatial domain of management decisions. We illustrated the use of our approach to obtain the average over-winter population sizes of elk on the winter range of the Estes Valley during five years of surveys (see Fig. 2 and Table 2). We used movement data to improve inference for animal abundance within a fixed study area and used auxiliary detection data to calibrate missed resights. Abundance estimators typically only provide information about the size of a population, however, our model also provided inference for multiple demographic population parameters that can be useful for management.

Movements of animals across management jurisdictions pose challenges for estimating population sizes because the scale of inference often fails to correspond to the scale at which decisions are made. For example, movements can occur on large geographic scales, such as the seasonal migration of elk from the alpine during summer to lower valleys during winter (Hess 1993). Movements can also occur on small geographic space and time scales, such as movements among the conservation area of RMNP, the nearby town of Estes Park, and the foothills, throughout winter. These smaller scale movements can confound efforts to accurately estimate population sizes because the number of individuals using the managed areas varies. We explicitly modeled movements with a Markovian process model coupled with a multinomial data model of telemetry location data. Thus, we were able to accurately estimate the number of marked individuals available for sampling during any given survey. The movement probabilities showed a consistent trend; elk were more likely to remain in their location from one week to the next, than to move to other areas. Nevertheless, study area boundary movements were sufficiently occurring to necessitate accounting for these small scale movements in the model.

TABLE 3. Annual survival (ϕ^T) estimates derived from a constant weekly survival estimated from the weekly telemetry data.

Year	Mean	Median	SD	0.025	0.975
2011	0.866	0.871	0.047	0.763	0.943
2012	0.927	0.929	0.025	0.872	0.968
2013	0.927	0.929	0.021	0.880	0.963
2014	0.971	0.973	0.014	0.937	0.992
2015	0.961	0.964	0.017	0.922	0.987

Note: The right two column headings represent the 0.025 and 0.975 quantiles of the marginal posterior distributions.

TABLE 4. Summary statistics of the posterior distributions of the average overwinter population sizes (μ_{VAL}) of elk in Rocky Mountain National Park and Estes Park for 2011 to 2015 using multiple models, including the open population Lincoln-Peterson style model described above (LP-move), the Dail-Madsen model (DM), the model similar to Pollock's robust design (Robust), and the Jolly-Seber model (JS).

Model (year)	Mean	Median	SD	0.025	0.975
LP-move					
2011	544	543	16.94	511	577
2012	488	488	13.50	462	515
2013	729	729	29.01	674	788
2014	827	825	43.71	747	918
2015	623	619	32.17	573	702
DM					
2011	9,049	9,045	266.19	8,544	9,584
2012	9,223	9,218	255.37	8,740	9,735
2013	8,477	8,472	249.63	8,007	8,978
2014	8,842	8,837	249.48	8,371	9,343
2015	8,599	8,594	251.92	8,124	9,105
Robust					
2011	1,378	1,378	20.72	1,338	1,419
2012	2,832	2,832	37.37	2,760	2,906
2013	2,708	2,708	40.09	2,631	2,788
2014	3,067	3,067	39.29	2,991	3,145
2015	2,741	2,741	38.33	2,667	2,817
JS					
2011	79	79	0.93	78	81
2012	139	139	1.61	137	143
2013	149	149	1.67	147	153
2014	140	139	2.34	136	145
2015	139	139	2.14	135	144

Note: The right two columns represent the equal-tailed Bayesian 95% credible intervals.

Median annual survival probabilities during the later years of this study (Table 3) resembled those of Brodie et al. (2013), who estimated annual elk survival of 0.95 in elk populations without predators, and 0.94 in elk populations that were not hunted. However, the low survival probability for the first year, 0.87 (BCI = 0.76, 0.94) is similar to the estimated survival probability in Monello et al. (2014) of 0.85 (BCI = 0.75, 0.93), with overlapping credible intervals. The low probability of survival is likely due to the fact that all of the elk were captured and collared in RMNP, and a high proportion of collared elk wintered in the park during that year. The increase in annual survival for subsequent years may be due to the inclusion of elk that were captured and collared outside the park, inclusion of elk that wintered in areas other than RMNP, and the greater elk population expanding into new habitat use areas outside the park, where sources of mortality differ and chronic wasting disease prevalence has been found to be lower (B. Kraft, R. Monello, M. Miller, L. Wolfe, unpublished data).

Elk aggregate into large herds during winter, particularly for calf and cow groups. These large groups can prevent observers from resighting marks, which in turn, can lead to biased overestimates of the population size. We were able to calibrate the resighted marks using auxiliary telemetry data collected during ground census and adjusting for imperfect detection of resights. Ideally, these auxiliary data could be collected throughout the study, but we were only able to

collect these observations during a small fraction of ground surveys and then applied the results to all of the surveys across all years. In some cases, we might be overcompensating for missed resights, as reflected in the high probabilities of detection within the N -mixture model during some of the winter survey weeks, which then led to convergence problems in the MCMC samplers. The average population sizes across all winter months were not sensitive to this over-compensation because the estimates borrowed strength from the repeated surveys and hierarchical structure of the model (Hobbs and Hooten 2015). We obtained population sizes during each month of winter, however, given the convergence diagnostics, we suggest caution interpreting these statistics.

We assumed that the probability of detection was constant among all collared elk, despite the fact that brightly colored collars deployed by Colorado Parks and Wildlife were more readily visible to ground count volunteers than the brown

collars deployed by the National Park Service. Additionally, the telemetry data were based on collars deployed only on adult female elk. We applied the estimates of the probability of detection in the abundance estimator to data consisting of all sex and stage classes. This is a realistic assumption for juveniles and yearling males, because juveniles, yearling males, and adult females aggregate into large herds during winter. Adult males form separate groups and typically have lower probabilities of detection. Because adult males comprise a relatively small proportion of the overall population that uses RMNP and EP, assuming a constant probability of detection for all classes is unlikely to have a substantial influence on overall population size predictions.

Elk population sizes in RMNP varied throughout the years of the study (Fig. 3). This variation could result from variable snow depth, moisture regimes (there were drought conditions through 2013), forage conditions, development in the town of

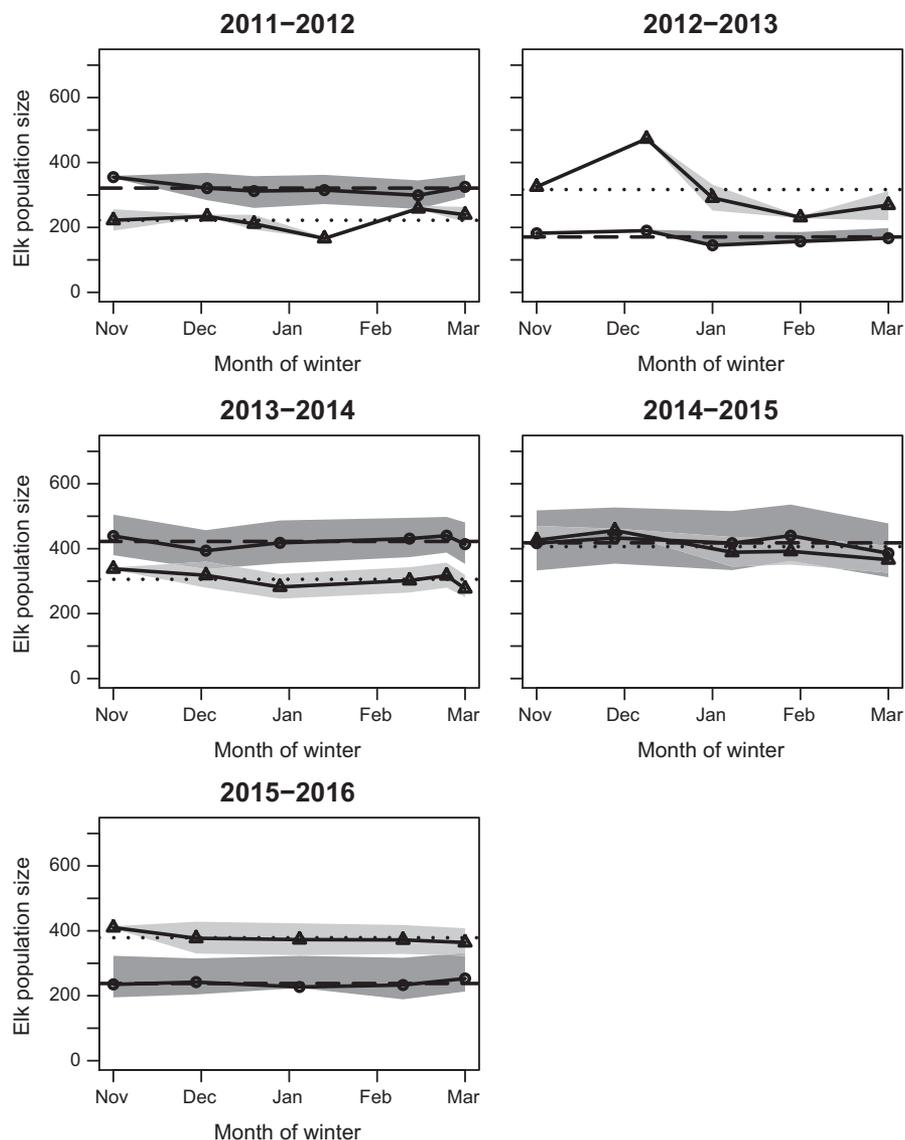


FIG. 3. The median number of elk using Rocky Mountain National Park throughout winter (circles), and in the town of Estes Park (triangles), shows the population during five seasons. The 95% Bayesian credible intervals for RMNP (dark gray) and EP (light gray) are the shaded regions. The lines with small dashes represent the across winter averages in RMNP, μ_{RMNP} , while the lines with large dashes represent the across winter averages of elk in EP, μ_{EP} .

Estes Park, and increased fenced areas in the park winter range. The estimated number of elk in the Estes Valley, Colorado was much lower than historical estimates (Lubow et al. 2002), due to several reasons including a population reduction prescribed in the elk and vegetation management plan (National Park Service 2007) and a subsequent increase in the number of elk that winter outside of the Estes Valley in the foothills. The population of elk in RMNP was lowest during the second season of the study, during the 2012–2013 winter, with the median of the marginal posterior of $\mu_{\text{RMNP}} = 171$ (BCI = 158, 187). This estimate was lower than a suggested minimum limit of 200 elk as described by recent ecosystem models developed for the winter range (National Park Service 2007). Subsequent increases were likely due to a larger number of elk remaining in the Estes Valley and RMNP during winter, vs. going to the foothills, rather than resulting from greater survival or recruitment.

Aerial surveys were used to census the elk in RMNP annually from 1994 to 2014. These surveys were expensive, dangerous, and required staff to be constantly available throughout winter to exploit rare periods of weather suitable for flying. Expense and limited opportunity for flying prevented multiple samples so that during most years, only a single survey was made. Overwinter variability in population size was necessarily ignored during these years. Ground based census methods, consisting of monthly counts throughout winter, permitted estimates of sampling variation. However, ground surveys had their own set of limitations, such as the restriction of observations to occur close to accessible roads, and difficulty in properly training volunteers. The National Park Service repeated samples to minimize the impact of these potential problems. Annual aerial surveys that were corrected using a sightability model (Lubow 2015, *unpublished report*) were

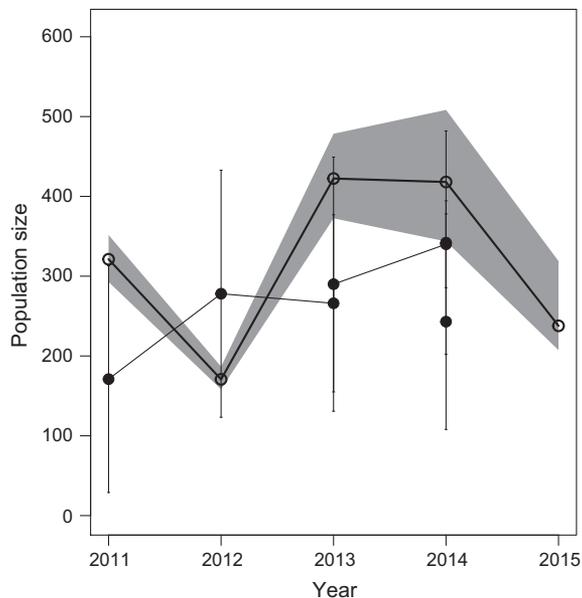


FIG. 4. Medians of the posterior distributions of the overwinter population sizes in Rocky Mountain National Park (open circles), with equal-tailed Bayesian credible intervals (gray shaded region). Estimated number of elk for each aerial survey based on the sightability model of Lubow et al. (2002) (solid circles). Vertical bars are ± 2 standard errors. No aerial surveys occurred in 2015.

similar to the medians of the posterior distributions of population sizes based on the N -mixture model used here (Fig. 4).

Multiple models showed unrealistic results of the overwinter means of abundance across the years of the study (Table 4). The Dail-Madsen model led to posterior means that were unrealistically high, and the Jolly-Seber model led to posterior means that were unrealistically low. Not accounting for temporary emigration, observation error of the telemetry data, and observation error of the resighted marks also led to unrealistically high mean abundance. While population sizes obtained using alternative models and different data are naturally expected to differ, the substantial variability in posterior means was surprising, and shows the difficulty of implementation of ground based methods for surveys of large mobile wildlife species.

Using a Bayesian approach enabled us to address sources of uncertainty in both the ecological processes as well as measurement error. We were able to bring together multiple commonly collected data sources, and account for their corresponding variability. Our approach is particularly useful for supporting estimates of abundance of mobile animals that move in and out of conservation areas.

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