

Estimating demographic parameters using a combination of known-fate and open N -mixture models

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Abstract. Accurate estimates of demographic parameters are required to infer appropriate ecological relationships and inform management actions. Known-fate data from marked individuals are commonly used to estimate survival rates, whereas N -mixture models use count data from unmarked individuals to estimate multiple demographic parameters. However, a joint approach combining the strengths of both analytical tools has not been developed. Here we develop an integrated model combining known-fate and open N -mixture models, allowing the estimation of detection probability, recruitment, and the joint estimation of survival. We demonstrate our approach through both simulations and an applied example using four years of known-fate and pack count data for wolves (*Canis lupus*). Simulation results indicated that the integrated model reliably recovered parameters with no evidence of bias, and survival estimates were more precise under the joint model. Results from the applied example indicated that the marked sample of wolves was biased toward individuals with higher apparent survival rates than the unmarked pack mates, suggesting that joint estimates may be more representative of the overall population. Our integrated model is a practical approach for reducing bias while increasing precision and the amount of information gained from mark–resight data sets. We provide implementations in both the BUGS language and an R package.

Key words: *Canis lupus*; detection probability; Gates of the Arctic National Park, Alaska, USA; integrated model; known-fate models; mark–resight data; N -mixture models; recruitment; survival; wolves.

INTRODUCTION

Population ecologists and managers require precise and unbiased estimates of demographic parameters to ensure proper inference (Skalski et al. 2005). Mark–recapture methods are commonly used to estimate survival and other parameters (Williams et al. 2002), with radio-marking being particularly useful because marked individuals can be relocated and fate (i.e., alive or dead) can be identified with near certainty (White and Garrott 1990). These field techniques are commonly used to collect survival data in a variety of species including waterfowl (Ringleman and Longcore 1982, Schmidt et al. 2006), ungulates (Adams et al. 1995, Johnson et al. 2010), and carnivores (Adams et al. 2008). Known-fate models (Pollock et al. 1989b) are typically used for analysis of this type of data and have a long history of development and application in the ecological literature (e.g., Kaplan and Meier 1958, Heisey and Fuller 1985, Pollock et al. 1989a). In the simplest case, data are limited to the marked individuals, which are assumed to be representative of the population, but may also include group members when detection can be

assumed to be 1.0 (e.g., ducklings associated with marked hens). In many cases, additional information (e.g., counts, spatial locations) for unmarked individuals are gathered during relocations of the marked sample, but these data are generally not used for estimating demographic rates (although see Johnson et al. 2010) because analytical methods for data from unmarked individuals are limited.

The development of N -mixture models (Royle 2004) has recently provided a method for extracting abundance information from count data that are generally considered to be of lower value. N -mixture models allow the estimation of abundance from repeated counts of unmarked individuals in a closed population by assuming that observed counts are a function of detection probability and abundance (Royle 2004, Chandler et al. 2011, Schmidt et al. 2013). More recently, open versions of the N -mixture model have also been developed (Dail and Madsen 2011, Zipkin et al. 2014b), relaxing the closure assumption and allowing the estimation of population dynamics parameters. This is achieved by assuming that the abundance, N_{it} , at each site i and time t has the Markov property so that N_{it} is dependent only on $N_{i,t-1}$. Abundance is then modeled as the sum of the number of individuals that survived at site i from time $t - 1$ to time t , and the number of

Manuscript received 3 March 2015; revised 18 May 2015; accepted 19 May 2015. Corresponding Editor: E. G. Cooch.

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individuals that were recruited at site i from time $t - 1$ to time t (Dail and Madsen 2011). Although mark-recapture and N -mixture methods are available for estimating demographic parameters using different data sets, separate analyses for each data set are inefficient.

A natural progression is the integration of a known-fate model based on relocations of radio-marked individuals with an open N -mixture model using counts of unmarked group members associated with marked individuals observed during radio relocations. The combination of data from multiple sources to improve inference has received much attention, largely due to the prospects for increasing precision, reducing required sample sizes, and estimating additional parameters (e.g., Borchers 2012, Sollmann et al. 2013). Integrated models (e.g., Besbeas et al. 2002, Schaub and Abadi 2012) are likely to be more efficient at large spatial scales (Zipkin et al. 2014a) and may be particularly useful for telemetry studies, which tend to be expensive both logistically and monetarily. For social species, most of the observed individuals are unmarked, but due to frequent relocation of radio-marked group members, much additional information on survival and recruitment in the form of repeated counts could be used. To our knowledge, an integrated model combining known-fate and open N -mixture models has not been developed, but a combined approach could increase the amount of demographic information available for a variety of past and future studies.

Here we present an approach combining known-fate and open N -mixture models to jointly estimate the survival parameter while also providing estimates of annual recruitment. This model uses capture histories from radio-collared individuals and associated counts of unmarked individuals observed with those that are marked. We expected that combining these two data types would result in more accurate and precise estimates, particularly of survival, and would allow the estimation of recruitment, which is often not possible using only the information from radio-marked individuals. We use simulations to assess the ability of our integrated model to recover parameters and demonstrate a simple approach for assessing bias in the marked sample. We also offer a practical example by applying our joint model to four years of previously published wolf (*Canis lupus*) survival and pack count data (see Adams et al. 2008).

MODEL DESCRIPTION

To share strength between the known-fate and open N -mixture data types, we combined a known-fate survival submodel and an open N -mixture submodel in a hierarchical fashion to estimate demographic parameters. First, for the known-fate submodel, we used the same basic structure as previously published hierarchical nest survival models (Royle and Dorazio 2008, Schmidt et al. 2010). Because fates are assumed to be known with certainty for known-fate individuals, detection proba-

bility is not estimated. Although many known-fate models are formulated at the individual level (e.g., Pollock et al. 1989b), here we assume there are negligible individual effects within known groups, so survival is constant between individuals within groups. However, shared covariates could be used to relax this assumption. We model the status of the m th known-fate individual of group i , at time t , Y_{mit} , as

$$[Y_{mit} | Y_{mi,t-1}] = \text{Bernoulli}(\omega_{i,t-1} \cdot Y_{mi,t-1}); \quad m = 1, \dots, M, i = 1, \dots, I, \text{ and } t = 2, \dots, T$$

where $[x | y]$ represents the conditional probability distribution of x given y , $\omega_{i,t-1}$ is the probability of survival from time $t - 1$ to t . The survival probabilities are modeled using

$$\text{logit } \omega_{i,t-1} = \mathbf{x}'_{i,t-1} \boldsymbol{\beta}$$

where $\mathbf{x}_{i,t-1}$ is a vector of known covariates and $\boldsymbol{\beta}$ are the associated coefficients.

In addition to the known-fate individuals in group i at time t , we also assume there are N_{it} additional individuals in the group. These additional individuals are composed of those that survived from the previous time, S_{it} , to the current time plus those that are recruited to the group at the current time, G_{it} . It may become necessary to replenish the sample of known-fate individuals due to accumulating deaths, so, the known-fate sample does not become extinct through the course of the study. Therefore, let R_{it} denote the known number of individuals removed from the general population at time t and placed into the known-fate sample.

The survivors are modeled via

$$[S_{it} | N_{i,t-1}] = \text{Binomial}(N_{i,t-1} - R_{i,t-1}, \omega_{i,t-1}^*)$$

where $\text{logit } \omega_{i,t-1}^* = \mathbf{x}'_{i,t-1} \boldsymbol{\beta}^*$.

To share information between the two data sets and see improvements to parameter inference we assume that some, if not all, elements of $\boldsymbol{\beta}$ are equal to $\boldsymbol{\beta}^*$. Following Dail and Madsen (2011), the recruited individuals are modeled with $[G_{it}] = \text{Poisson}(\gamma_{it})$ where γ_{it} is the recruitment rate parameter. To allow inclusion of covariate information or allow relationships between population size and recruitment, we can further parameterize the recruitment rate using

$$\text{log } \gamma_{it} = \mathbf{w}'_{it} \boldsymbol{\rho}.$$

Although we do not consider it in the simulations and wolf analysis in the following sections, setting $\mathbf{w}_{it} = (1, \log N_{i,t-1})'$ gives the "autoregressive" model of Dail and Madsen (2011). In reality, one might use $\log (N_{i,t-1} + \sum_m Y_{mi,t-1})$ to include those density effects of animals in the known-fate sample. But if the size of the known-fate group is small relative to the size of the general population, this will make little difference.

Finally, as with all open N -mixture data, the general population is usually not observed; thus a detection

model is necessary to model the observed abundance, n_{it} . Given the true abundance of the general population, we assume that the observation process represents a binomial sample, i.e., $[n_{it} | N_{it}] = \text{Binomial}(N_{it} - R_{it}, p_{it})$ where p_{it} is the probability of detecting one of the members of the group i in the general population at time t , and R_{it} are the number removed from the general population and transferred to the known-fate sample. Although we do not consider the case here, to more explicitly compensate for radio failures, an additional term representing individuals transitioning from the known-fate sample back to the unmarked sample could also be added. Here we formulate the model with removals counted before the detection process. In our opinion, this makes more sense because the process of sampling new known-fate individuals is probably more involved and invasive than the usual survey methodology for the open N -mixture detection process. Therefore, we do not want to model those individuals with a p_{it} detection probability. Analogous to the survival models, we parameterize the detection probability using

$$\text{logit } p_{it} = \mathbf{z}'_{it}\boldsymbol{\alpha}$$

where $\mathbf{z}_{it}$ is a vector of known covariates and $\boldsymbol{\alpha}$ are the associated coefficients.

Using the dynamic components of the model, we can derive the transition kernel of the abundance process using the appropriate convolution (Dail and Madsen 2011):

$$\begin{aligned} [N_{it} = k | N_{i,t-1} = j] \\ = \sum_{c=0}^{\min\{j-R_{i,t-1}, k\}} \text{Binomial}(c | j - R_{i,t-1}, \omega_{i,t-1}^*) \\ \times \text{Poisson}(k - c | \gamma_{it}). \end{aligned}$$

Note that our definition is slightly altered to account for the removals, R_{it} , transferred to the known-fate sample. We present both maximum-likelihood and Bayesian implementations of our model using programs R 3.1.0 (R Core Development Team 2014) and OpenBUGS 3.2.3 (Thomas et al. 2006). We created an R package *kfdnm* (*available online*)⁶ containing both maximum-likelihood and MCMC implementations (Appendix A) based on a novel hidden Markov model (HMM) formulation of the open N -mixture model. In addition, we also present the OpenBUGS code used for the applied example (see Supplement).

SIMULATIONS

Using both the *kfdnm* package and OpenBUGS, we ran two sets of simulations to assess the ability of our model to jointly estimate both survival and recruitment. We considered scenarios for a 5-year project with 10 revisits per year with the assumption that three

individuals in each of 20 groups carried radio marks at the beginning of each year. The initial number of unmarked individuals present in each group was drawn from a Poisson distribution with a mean of 4.5. At each monthly revisit, the fate of the marked individuals was observed with certainty and the true count of the unmarked group-mates was partially observed, assuming that the probability of detection was $p = 0.5$. We assumed that immigration and emigration did not occur. The number of recruits in each group was assumed to come from a Poisson distribution with a mean of 4.0, and the recruitment event was assumed to occur in the first time period each year. First we considered a scenario designed to separately estimate survival for both marked ($\omega_t^1 = 0.90$) and unmarked ($\omega_t^2 = 0.90$) individuals (i.e., ω_t not shared). This is analogous to fitting a known-fate model to data from the marked subset and a separate open N -mixture model to the repeated count data, thereby providing a test of the assumption that the marked sample is representative of the population of interest. We also simulated data where $\omega_t = 0.90$ for all individuals and survival was jointly estimated (i.e., ω_t was shared). We generated 200 data sets for each scenario and fit our model to each replicate set, saving the mean of the posterior of each parameter of interest to assess the ability of the model to recover the data-generating values.

The results of our simulations showed that the implementations in OpenBUGS and *kfdnm* recovered the data-generating parameter estimates under both scenarios considered (Appendix B). The accuracy of the estimates when survival was estimated separately indicates that using the model to test the assumption of representativeness of the marked sample is valid. In addition, when the survival parameter was estimated jointly using both data sources, estimates were accurate and more precise than when estimated separately (Appendix B). We also ran identical simulations in both WinBUGS 1.4.3 (Lunn et al. 2000) and JAGS 3.3.0 (Plummer 2003), but found that estimates were consistently biased when models were fit using either of these programs (see discussion, Appendix C).

APPLICATION: WOLF RADIOTELEMETRY DATA

The wolf population in Gates of the Arctic National Park and Preserve (GAAR), Alaska, was studied from the spring of 1987 to spring 1991 (see Adams et al. 2008). Radio-marked wolves were maintained in 14–19 packs between April 1987 and January 1990, declining to eight monitored packs by April 1991. Packs were relocated and individuals were counted throughout the year, although effort varied. In the original study, loss of wolves from the marked population was separated into mortality and emigration, and annual estimates were calculated for each using known-fate methods (Heisey and Fuller 1985). The maximum number of pups observed per pack in September–October on average each year was used as an estimate of annual recruitment.

⁶ <https://github.com/NMML/kfdnm/releases>

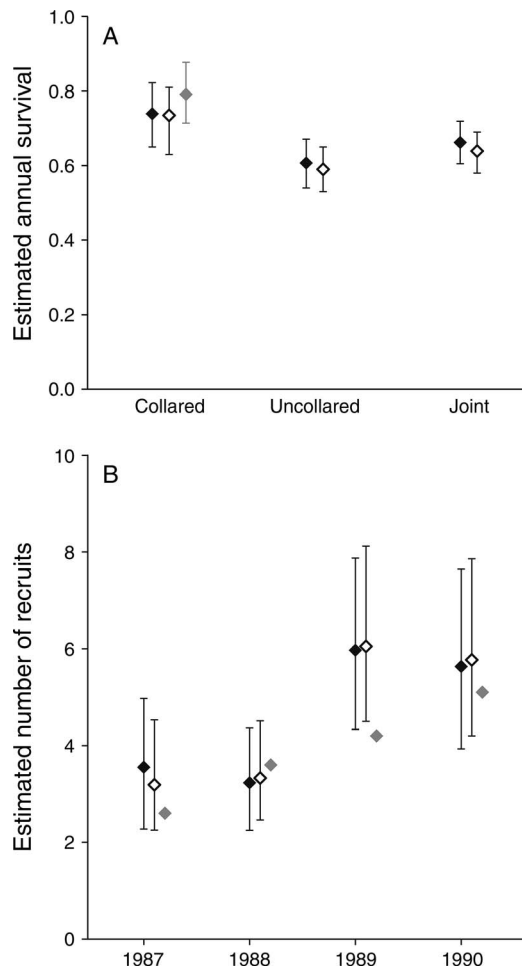


FIG. 1. (A) Estimated mean annual apparent survival probabilities (includes mortality and emigration) for the wolf population studied in Gates of the Arctic National Park and Preserve, Alaska, USA, 1987–1990. Two sets of estimates are shown: survival of collared and uncollared wolves estimated independently, and survival of all wolves estimated jointly. The solid symbols represent Bayesian estimates using OpenBUGS, the open symbols represent maximum likelihood estimates using the *kfndm* package, and the gray symbol represents the known-fate survival estimate (not including emigration) from Adams et al. (2008). (B) Estimated mean number of wolves added to each pack in May of each year, 1987–1990, assuming survival differed between groups. Gray symbols represent observed mean number of pups per pack on October 1 from Adams et al. (2008). The dark error bars represent 95% credible intervals for the Bayesian estimates and 95% confidence intervals for the maximum likelihood estimates.

We applied our model to the GAAR wolf data with the goals of identifying potential bias in the marked sample and providing a general comparison of survival and recruitment estimates to those based on known-fate methods and direct observations. Final survival estimates were based on data pooled across age, sex, and years, largely due to limited sample sizes (for further details, see Adams et al. 2008).

Our estimates of survival are interpreted as apparent survival because we could not distinguish between losses due to mortality vs. emigration for the unmarked individuals. During many months, radio-marked wolves were relocated multiple times, although we consolidated the data to a single observation for each month using the highest observed count as the best observation of the unmarked individuals. We assumed that overcounting did not occur. If a radio-marked wolf could not be relocated due to a lack of signal, it was right-censored; Adams et al. (2008) treated these as dispersers. Not all packs were located during each month, resulting in many missing values. When multiple records of the same number of individuals within a pack were recorded during a single month under good sighting conditions, we assumed $p = 1.0$ for that time period. Although “perfect” counts are not required, their inclusion improved estimation. Otherwise, we assumed detection probability was constant across months. We also assumed survival probability was constant across months and years, but allowed recruitment rate to vary by year. Recruitment, defined as additions of individuals to a pack, was assumed to occur during May when pups are typically born. Therefore, recruitment only occurred during the first month of the biological year (1 May of the current year through 30 April of the following year). We assumed that immigration did not occur.

We fit two versions of the model to the GAAR data using both OpenBUGS and *kfndm*. We estimated survival separately for the marked and unmarked individuals in the first version of the model; in the second, we jointly estimated survival. We found that annual survival rates were lower in the unmarked sample than in the marked sample when estimated separately for the two groups (Fig. 1A). Estimates for the marked sample alone were very similar to those from Adams et al. (2008), as expected (Fig. 1A). Results from the joint model showed that survival for the sampled population (marked and unmarked) probably was lower than that based solely on the collared sample (Fig. 1A). The estimated numbers of individuals added during May were generally larger than observed average pup counts and were less precise in later years, corresponding to reduced numbers of relocations and reduced numbers of packs in the sample (Fig. 1B). Together, our results suggest that apparent survival was lower in the overall population as compared to the marked population alone and recruitment estimates were similar to observed mean pup counts.

We also fit a model in which survival varied across months smoothly in the same pattern between collared and uncollared animals, but, the two groups were assumed to have different overall survival rate. This model was constructed using b-splines to form the x_{it} with the *bs(...)* function (using all function defaults) of the R package *splines*. Then an additional intercept parameter was added for the known-fate population. This allowed sharing of information on the annual

pattern of survival among groups, despite the assumption that annual rates differed. We included this as a simple example demonstrating how covariate information could be shared among groups to improve estimation, even if survival rates differed. We fit this model using both MLE and MCMC methods using the *kfdnm* package to explore variation in survival throughout the year and compare estimates of precision between the two formulations. These results suggested that monthly survival rates declined until late winter before increasing into spring (Fig. 2). They also showed that the estimates from the Bayesian implementation were more precise and that other covariates could be used in a similar manner to share information between groups and improve estimation when bias in the marked sample is suspected.

DISCUSSION

Through simulations and a practical example, we demonstrated that by combining known-fate data with count data from associated group mates, unbiased estimates of survival and recruitment can be produced that are more accurate and precise than is possible using typical known-fate approaches. Many researchers employing radio tags collect associated count data during relocations of marked animals. Here we have shown how these additional data can be directly included in the analysis to reduce bias and increase precision, indicating that auxiliary data should generally be collected when sampling marked individuals (Pollock 2002, Lindberg 2012). We also provided a straightforward approach for assessing bias in the marked sample by separately estimating survival for the marked and unmarked samples. Even if such bias exists, the inclusion of covariates can be used to share information among groups to improve estimation. In addition, the ability to directly estimate recruitment is appealing and could further increase the amount of information gained from these studies. Overall, we expect that many projects utilizing known-fate methods to assess survival rates in group-dwelling animals would benefit from our integrated analytical approach.

The results of our simulations demonstrated that our model performed well. Under each scenario, the model reliably recovered the true parameter values, and while it may not be surprising that precision increased when survival was estimated jointly, these results confirm that increases in precision are possible when count data are also utilized. Interestingly, when attempting to use either the WinBUGS or JAGS software packages, estimates were consistently biased relative to the generated values for reasons that were not apparent. Identical model code showed no evidence of bias when fit using OpenBUGS or the *kfdnm* R package. This finding is consistent with that of Kéry and Schaub (2012:410), who reported that efforts to fit the open *N*-mixture model in WinBUGS were unsuccessful. The patterns of bias that we observed were similar to those found by Zipkin et al. (2014b) for a

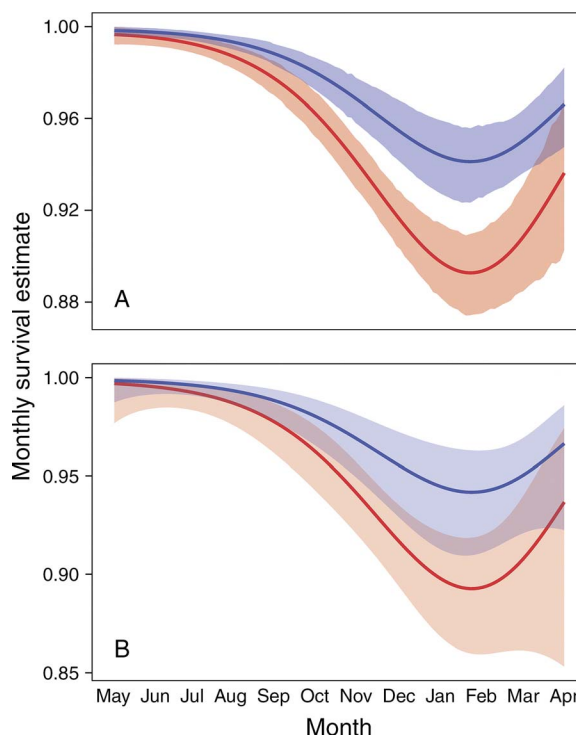


FIG. 2. Estimated average monthly survival rate for collared (blue) and uncollared (red) wolves in the study population in Gates of the Arctic National Park and Preserve, Alaska, 1987–1990. (A) Bayesian and (B) maximum-likelihood estimates are presented to allow a comparison of estimates of precision (colored bands represent 95% intervals). Results are based on a model assuming a common pattern in survival across months for both collared and uncollared wolves, with overall rates differing between the two groups. Models were fit using the *kfdnm* R package.

stage-structured open *N*-mixture model fit using JAGS, possibly providing an alternate explanation for the skewed estimates they observed. Although further work will be required to determine the cause of the problem, we thought the potential for unexplained bias when using some implementations of the BUGS language may be of interest to others working with similar models.

Although our estimates of survival are not directly comparable to those of Adams et al. (2008), our apparent survival estimates for the marked sample alone were similar and consistent with differences in application of the available data (e.g., treatment of emigrants), thus suggesting our results overall are analogous. We did find that the magnitude of the bias in estimated apparent survival rates between the marked and unmarked sample was fairly large ($\omega_{\text{annual}}^1 = 0.74$ vs. $\omega_{\text{annual}}^2 = 0.61$). The finding of some sample bias is not surprising because adults that are less likely to be lost from the population through emigration are commonly targeted for capture and marking. Bias induced by capture heterogeneity (Fletcher et al. 2012) or individual heterogeneity (Lindberg et al. 2013) can have implications for assessing population growth rates. We expect

that sample bias and marking effects (Murray and Fuller 2000) could be substantial in many settings, possibly leading to inappropriate conclusions and comparisons among populations. Our model relaxes the assumption of a representative sample of marked individuals and provides inference to the entire population. We found fewer differences in estimated recruitment between our work and that of Adams et al. (2008), although our estimates tended to be higher because they represent the average number of individuals added to each pack in May, rather than those surviving until direct observations occurred (June–October).

The combination of multiple data sources to improve estimation is an active area of development and promises to increase the amount of demographic information that can be extracted from commonly collected field data (e.g., Kéry and Schaub 2012, Bird et al. 2014). While we have demonstrated how count and known-fate data may be combined to improve inference, the inclusion of other data sources and demographic parameters is also possible. For example, composition data or information on movement rates could be incorporated to help estimate cohort-specific survival and immigration/emigration rates, respectively (e.g., Zipkin et al. 2014b; Hostetler and Chandler 2015). For simplicity, we did not include covariates or pup counts in our demonstration, although they could be added for other applications. Our simple example using a shared spline function demonstrated how the inclusion of covariates could be used to share information among groups. In other situations, additional count and mark-resight data sources may be available (e.g., Johnson et al. 2010) and could also be incorporated. One of the advantages of our approach was that the incorporation of an open *N*-mixture model allowed us to estimate recruitment from repeated counts of unmarked individuals, without requiring direct observations of young. The use of a nest survival model also made the incorporation of ragged data (i.e., capture histories of uneven length) straightforward. The choice of which integrated modeling approach to use is largely dependent on the data streams available and the objectives of a particular project, although models incorporating the open *N*-mixture model can add substantial flexibility.

Further extensions of our model could include the incorporation of the robust design if shorter closed periods were sampled between open periods. The stage-structured model of Zipkin et al. (2014b) may also benefit from the inclusion of known-fate data when available. It is also possible that other models could be used in place of the known-fate model, with similar benefits for other types of studies (e.g., distance sampling; Sollmann et al. 2015). The integration of mark-recapture or distance sampling models with open *N*-mixture models should provide opportunities to improve ecological inference in a variety of settings and will help to increase our knowledge of population dynamics. As a general approach, explicitly combining

data sources can provide a much more complete picture of the population dynamics of a species than would be possible through independent analytical efforts.

ACKNOWLEDGMENTS

Funding for this work was provided by the U.S. National Park Service's Inventory and Monitoring Program through the Central Alaska Network. The findings and conclusions expressed by authors do not necessarily reflect the opinions of the funding agencies and institutions with which the authors are affiliated, except for the U.S. Geological Survey. This report was reviewed and approved by the U.S. Geological Survey under their Fundamental Science Practices policy (<http://www.usgs.gov/fsp/>). Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–C and the Supplement are available online: <http://dx.doi.org/10.1890/15-0385.1.sm>