

A new approach to the “apparent survival” problem: estimating true survival rates from mark–recapture studies

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Abstract. Survival estimates generated from live capture–mark–recapture studies may be negatively biased due to the permanent emigration of marked individuals from the study area. In the absence of a robust analytical solution, researchers typically sidestep this problem by simply reporting estimates using the term “apparent survival.” Here, we present a hierarchical Bayesian multistate model designed to estimate true survival by accounting for predicted rates of permanent emigration. Initially we use dispersal kernels to generate spatial projections of dispersal probability around each capture location. From these projections, we estimate emigration probability for each marked individual and use the resulting values to generate bias-adjusted survival estimates from individual capture histories. When tested using simulated data sets featuring variable detection probabilities, survival rates, and dispersal patterns, the model consistently eliminated negative biases shown by apparent survival estimates from standard models. When applied to a case study concerning juvenile survival in the endangered Cape Sable Seaside Sparrow (*Ammodramus maritimus mirabilis*), bias-adjusted survival estimates increased more than twofold above apparent survival estimates. Our approach is applicable to any capture–mark–recapture study design and should be particularly valuable for organisms with dispersive juvenile life stages.

Key words: *Ammodramus maritimus mirabilis*; Bayesian; Cape Sable Seaside Sparrow; demography; dispersal; emigration rates; hierarchical multistate models; juvenile survival.

INTRODUCTION

Accurate estimates of survival are essential in almost all branches of ecology. Researchers typically estimate survival rates using capture–mark–recapture (CMR) sampling protocols, applying analytical techniques derived from the Cormack–Jolly–Seber (CJS) modeling framework (Cormack 1964, Jolly 1965, Seber 1965). Over many years, CMR methodology has been refined to resolve various confounding issues including variation in detection probability and temporary emigration (Pollock et al. 1990, Lebreton et al. 1992). However, one confounding factor remains something of an “elephant in the room” for survival analysis from live-recapture CMR data: permanent emigration from the study area (Marshall et al. 2004, Zimmerman et al. 2007, Cooper et al. 2008, Horton and Letcher 2008). While temporary emigration can be accounted for using the “robust approach” to data sampling and analysis (Pollock et al. 1990), few widely applicable methods are available to differentiate permanent emigration from mortality

under live-recapture CMR sampling (Marshall et al. 2004). In lieu of a working solution to this problem, it has become customary to report CJS-based estimates using the term “apparent survival,” offering a simple acknowledgment of the uncertainty associated with permanent emigration (Lebreton et al. 1992).

If the geographical limits of a finite study area correspond perfectly with those of the population of interest (e.g., an island population), the conflation of mortality and permanent emigration may be sensible; permanent emigrants genuinely represent functional losses to the focal population. If the study area is nested within a wider population of interest, however, emigrants surviving outside the study area may continue to contribute to population processes. In these circumstances, mortality and emigration have diametrically opposite implications for population dynamics. Evidently, lumping these opposing components within the same parameter will give a misleading impression of true survival within the target population. If these “apparent” survival estimates are used to make further inferences about population dynamics (e.g., in population viability analysis), resultant conclusions may be flawed and misleading.

This issue draws together two allied but disparate avenues of inquiry associated with CMR sampling: survival estimation and dispersal modeling. Despite their close interrelation, the analytical methods used within these two fields have evolved largely in isolation;

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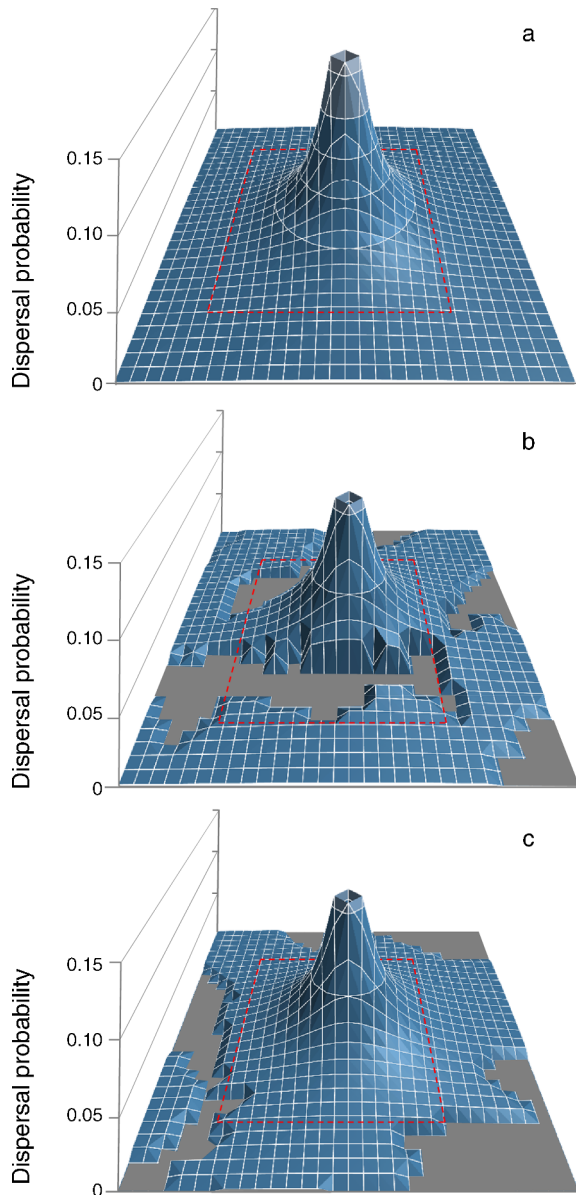


FIG. 1. Hypothetical examples of probability density surfaces describing dispersal probability around a single capture location within a study plot (delimited by broken red line), generated from a lognormal distribution. Surfaces reflect environments of varying heterogeneity: (a) homogeneous environment in which dispersal probability is independent of environmental conditions; (b) heterogeneous environment comprising suitable and unsuitable habitats (zero dispersal probability in the latter), where heterogeneity is adequately sampled within the study plot; (c) heterogeneous environment where the plot is poorly representative of heterogeneity within the wider landscape, so that a dispersal kernel modeled from plot-specific data may be a poor predictor of movements outside the plot.

researchers interested in survival have focused largely on developing the CJS framework (Lebreton et al. 1992), while those studying dispersal have focused on applying kernel-based distributional models (Kot et al. 1996,

Fujiwara et al. 2006). Few attempts have been made to combine these fields in order to draw inferences about survival and permanent emigration (but see Baker et al. 1995, Cooper et al. 2008). Here, we present a Bayesian approach in which information on survival and dispersal is combined in order to account for permanent emigration probability within finite-plot CMR data. We test the model using simulated data sets representative of typical finite-plot studies, and present a case study concerning juvenile survival in the endangered Cape Sable Seaside Sparrow (*Ammodramus maritimus mirabilis*).

METHODS

Using dispersal kernels to estimate emigration probability

In finite-plot capture–mark–recapture (CMR) studies, recaptures provide information on dispersive movements up to a theoretical limit corresponding with the maximum distance between two points in the sampled area (Baker et al. 1995). By fitting a distributional model (kernel) to these data, it is possible to generate spatially explicit predictions of dispersal probability around a given capture location (Kot et al. 1996, Van Houtan et al. 2010). Our approach is to apply these predictions as supplementary information in the process of estimating survival from capture histories.

To illustrate, we consider a scenario in which CMR sampling occurs in a single finite study plot within the range of a dispersive species. For simplicity, we assume that dispersal occurs in discrete periods between sampling events, and that emigration from the study plot is always permanent (e.g., in the case of species with high natal dispersal). In this scenario the probability of recapture $P(x)$ at time t of an individual marked within the plot at time $t - 1$ is composed of the survival probability S , the detection probability p (for an individual within the plot), and the probability that a surviving individual will remain in the plot at time t , which we term the residence probability r ; thus,

$$P(x)_t = S_r p_t. \quad (1)$$

We cannot estimate r directly from CMR data as it is completely confounded with mortality. Hence, in a classical CJS (Cormack–Jolly–Seber) model the probability of recapture collapses to the product of p and the apparent survival rate ϕ (i.e., the probability of surviving and remaining within the study area; Lebreton et al. 1992). However, if we assume dispersal is random in direction (and survival probability is similar inside and outside the plot), we can simply use a one-dimensional dispersal kernel to estimate r by generating a probability density surface around the capture location (Fig. 1). The kernel is estimated by estimating the parameters of a distribution function (e.g., Gaussian, Cauchy, lognormal) that best fits the distribution of observed dispersal events (Kot et al. 1996, Fujiwara et al. 2006). If dispersal direction is nonrandom, two-dimensional kernels may be used to model directional bias. We estimate r using the cumulative

density function (CDF) of the kernel, calculating the proportion of the total cumulative probability density falling within the study plot. The probability of emigration is simply $1 - r$. For kernels with unbounded support, an appropriate cutoff distance may be necessary in order to feasibly estimate r in a geographical information system (e.g., projecting up to 99.99% of the cumulative probability density around a capture location).

The validity of this approach hinges on how well the dispersal kernel predicts the true distribution of dispersal events in space. Dispersal probability is likely to vary in both space and time, and may be strongly influenced by factors such as habitat quality, patchiness, and barriers to movement (Schneider 2003, Schooley and Wiens 2004). If this heterogeneity is adequately represented within the study plot, a plot-specific kernel may be valid across the wider landscape (e.g., Fig. 1b). However, if environmental conditions outside the study plot differ widely from those within, settlement patterns outside the plot may be difficult to predict using models derived from within-plot data (e.g., Fig. 1c). The modeling approach described in the next section assumes that meaningful kernel-based predictions of spatial dispersal probability can be generated for the system in question.

The emigration model

Our model is an extension of the Bayesian CJS model developed by Calvert et al. (2009), adopting a hierarchical structure to model heterogeneity across discrete random variables (e.g., sites, years). We describe parameter notation for hierarchical structuring around years (index y), although the model can easily be generalized to other structures. In this parameterization, we assume that dispersal occurs between sampling periods, and that emigration is always permanent. The model can be readily extended to account for temporary emigration (provided that data can be partitioned into secondary sampling periods, i.e., days or weeks within years) by including an additional level of parameter indexing, estimating detection probabilities in a manner analogous to the robust approach (see Appendix A; Pollock et al. 1990, Calvert et al. 2009).

Following initial capture, marking, and release, individuals (i) belong either to one of K observable states representing living individuals within the study area, or an unobservable state $K + 1$ representing individuals that are dead or have permanently emigrated. All model parameters and variables are defined in Table 1. The model is separated into two elements: (1) a standard CJS-based hierarchical model that concerns individual capture histories, and (2) a hidden Markov process that concerns residence probabilities estimated through dispersal-kernel analysis. The CJS-based model adopts a state-space parameterization, separating the likelihood of observed individual capture histories ($x_{i,y}$) into process and observation components. The process component estimates apparent survival and transitions

between true underlying states ($z_{i,y}$), while the observation component estimates detection probabilities for individuals in observable states (denoted by the binary indicator $w_{i,y}$). The likelihood for the CJS-based model takes the following general form:

$$P\{x | \phi, \Psi, p\} = P\{z, w | \phi, \Psi, p\} = \prod_{i=1}^N \prod_{y=c_i+1}^Y P\{z_{i,y} | z_{i,y-1} \phi_y^a \Psi_y^{a,b}\} \times P\{w_{i,y} | z_{i,y} p_y^b\} \quad (2)$$

where $a = z_{i,y-1}$ and $b = z_{i,y}$. Note that the model conditions on time at first capture for each individual. The process component of the CJS-based model is defined by a categorical distribution with probabilities given thus:

$$P(z_{i,y} = b | z_{i,y-1} = a) = \begin{cases} \phi_y^a \Psi_y^{a,b} & a = 1, \dots, K \quad b = 1, \dots, K \\ 1 - \phi_y^a & a = 1, \dots, K \quad b = K + 1 \\ 1 & a = K + 1 \quad b = K + 1 \\ 0 & a = K + 1 \quad b = 1, \dots, K \end{cases} \quad (3)$$

where the top row represents probabilities associated with transitions between the K observable states (e.g., study areas), while the second row represents the probability of transition to the unobservable state (mortality plus permanent emigration). The remaining rows ensure that individuals in the unobservable state remain there permanently. The observation component is a Bernoulli process determined by the probability of detection of an individual (indicated by the data structure containing $w_{i,y}$ values), conditional on its true state $z_{i,y}$. Probabilities are defined thus:

$$P(w_{i,y} | z_{i,y} = a) = \begin{cases} p_y^a & a = 1, \dots, K \\ 0 & a = K + 1 \end{cases} \quad (4)$$

where the top row represents detection probabilities for each observable state and the bottom row dictates that detection is impossible for individuals in the unobservable state (apparent mortality). The hidden Markov process is computed simultaneously with the CJS-based model, decomposing apparent mortality (i.e., transitions to state $K + 1$) into true mortality and permanent emigration. The process is based on the notion that the true survival probability S_y for a marked sample of individuals in a finite study area is related to the apparent survival rate ϕ_y and the residence probability r_y :

$$S_y = \frac{\phi_y}{r_y} \quad (5)$$

Using a set of kernel-derived estimates of r for each individual and capture occasion, we rearrange Eq. 5 into a likelihood function where S^* , an estimate of S , is derived using the apparent survival estimate ϕ_y taken from the CJS-based model, with values of r modeled as a normal distribution with mean estimated thus:

TABLE 1. Descriptions of model parameters and data structures used in the Bayesian multistate model incorporating information on emigration probability.

Parameter or data structure	Definition
S_t^a	Probability that an individual in state a at time t survives to time $t + 1$
ϕ_t^a	Probability that an individual in state a at time t survives to time $t + 1$ and does not permanently emigrate from the study area
$\Psi_t^{a,b}$	Probability that an individual in state a at time t will be in state b at time $t + 1$ given that it survives to $t + 1$
p_t^a	Probability that an individual in state a at time t will be detected at time t
$x_{i,t}$	Observed state of individual i at time t
$z_{i,t}$	True state of individual i at time t
$w_{i,t}$	Binary indicator of whether individual i was observed at time t
$r_{i,t}$	Estimated probability that individual i observed at time t will remain within the study area at time $t + 1$, given that it survives to $t + 1$
c_i	Time of first capture for individual i
K	Total number of observable states

$$P\{r_{i,y} | x_{i,y} = a\} = \begin{cases} \frac{\phi_y^a}{S_y^{*a}} & a = 1, \dots, K \\ 0 & a = K + 1. \end{cases} \quad (6)$$

The function is conditional on the observed state of the individual $x_{i,y}$, reflecting the limitation that r values can only be generated when the state and location of the individual were observed in the preceding time period.

Parameter values at each hierarchical level (e.g., years) are assumed to form a random sample drawn from a “hyperprior” distribution (Carlin and Louis 1996). In order to ensure that parameter values are bounded between 0 and 1, we specify hyperprior distributions on the logit scale. Following Calvert et al. (2009), we use diffuse conjugate normal distributions for parameter means and gamma distributions for parameter precisions τ (used in WinBUGS [Lunn et al. 2000], rather than variance $1/\tau$). For observable state transition probabilities Ψ , parameter values must sum to 1 for each observable state. As such, in a model with K possible state transitions, hyperpriors are specified for $K - 1$ transitions, with the K th transition being defined as one minus the sum of all other transitions. As our focus is on unbiased parameter estimation, we do not directly address the issues of model goodness of fit or model selection directly in this study, although both are discussed in Appendix A.

Testing model performance with simulated data

We used a stochastic simulation process to generate realistic data sets with six years of mark-recapture sampling in a single study plot (full details in Appendix B). We incorporated two age classes (juvenile and adult), and restricted dispersal to juveniles so that all dispersive movements occurred in the first year of life. Dispersal was simulated as a one-dimensional process where individuals were assigned random capture locations relative to the plot boundary, moving out to a distance sampled from a lognormal distribution with fixed or time-varying parameters. We generated 25 data sets for each of eight scenarios combining variation in

recapture probability, true juvenile survival rate and dispersal distribution (see Appendix B for details). Sample sizes were fixed at $N = 100$ juveniles captured and released per year.

To analyze each data set we estimated individual-specific residence probabilities $r_{i,y}$ from spatial projections of a lognormal dispersal-kernel cumulative density function with parameters corresponding with the mean underlying dispersal distribution ($\mu = 5$, $\sigma = 2$). The resulting $r_{i,y}$ values and sampled capture histories were then used to fit the emigration model in WinBUGS version 1.4 (Lunn et al. 2000) using the code given in Appendix C. We used the Gelman-Rubin diagnostic (Gelman and Rubin 1992) to assess convergence based on three chains for each scenario, setting a precautionary burn-in run of 10 000 iterations and estimating parameters based on 50 000 subsequent iterations.

We also examined model performance when residence probability (r) was estimated using a dispersal kernel derived from right-censored data, as expected in typical finite plot studies where long-distance movements are detected infrequently. We compared three scenarios of varying study plot size, capturing the shortest 25%, 50%, and 75% of dispersal events. We generated 25 data sets for each scenario and estimated kernel parameters for each data set (including only within-plot recaptures) using maximum-likelihood routines in the *fitdistr* function in R version 2.9.2.³ We used $r_{i,y}$ values estimated from each kernel to fit the emigration model. We then repeated each simulation allowing some recaptures to occur within a narrow range of distances corresponding to the 90% and 95% limits of the true cumulative density function of the kernel. This scenario was therefore akin to a study design with two plots located within the dispersal range of a target species, allowing the detection of a small proportion of long-distance dispersal events (i.e., those occurring between disparate plots).

³ <http://www.r-project.org>



PLATE 1. A male Cape Sable Seaside Sparrow sings from the seasonally flooded marl prairie of Everglades National Park, Florida, USA. Long-term monitoring has provided a detailed understanding of the ecology of this threatened species, but the estimation of survival rates has been hampered by uncertainties associated with the dispersal of marked individuals beyond study plot boundaries. Our methods provide a means of controlling for this uncertainty, using information derived from observed dispersal events. Photo credit: J. J. Gilroy.

Field-based case study: Cape Sable Seaside Sparrow

Between 1998 and 2007, intensive capture–mark–recapture monitoring was conducted in eight finite plots (5.5 km² in total) across the Cape Sable Seaside Sparrow’s range in southern Florida, USA (Van Houtan et al. 2010; see Plate 1). Robust-approach apparent survival estimates for these data were presented by Boulton et al. (2009); we revisit their data set to evaluate the potential effect of permanent emigration on juvenile survival estimates. We estimated residence probabilities using a published juvenile dispersal kernel generated from the same data set (Van Houtan et al. 2010). We mapped habitat suitability (treated as a dichotomous variable) using occupancy data from annual breeding season point counts conducted at 1-km intervals throughout the known range (Van Houtan et al. 2010), and generated kernel projections representing two dispersal hypotheses: (1) dispersal probability independent of habitat suitability and (2) dispersal constrained to suitable habitat (see Appendix D). We used both sets of residence probability estimates to fit the Bayesian emigration model with age-specific survival parameters (juvenile or adult, $K = 2$), using the

uninformative priors and convergence diagnostics described for simulated data sets.

RESULTS

Survival estimates from the emigration model closely approximated true values across all simulated scenarios, while the equivalent standard CJS model consistently produced negatively biased estimates (Fig. 2a, b). Year-specific estimates showed little evidence of parameter “shrinkage” towards the mean (Calvert et al. 2009, Appendix E), suggesting that interannual variation was captured effectively by the emigration model given the sample sizes we simulated ($n = 100$ individuals marked per year). The model was robust to temporal variation in emigration probability, with little change in mean squared error rates relative to time-constant dispersal scenarios (Appendix F). Negative bias increased significantly when kernels derived from right-censored data were used to estimate residence probability, particularly when only short-distance dispersal events were captured within the study plot (Fig. 2c). However, bias was reduced for all plot sizes when recaptures were allowed to occur within a small proportion of the true kernel tail (i.e., long-distance events), analogous to a multi-plot study design (Fig. 2d).

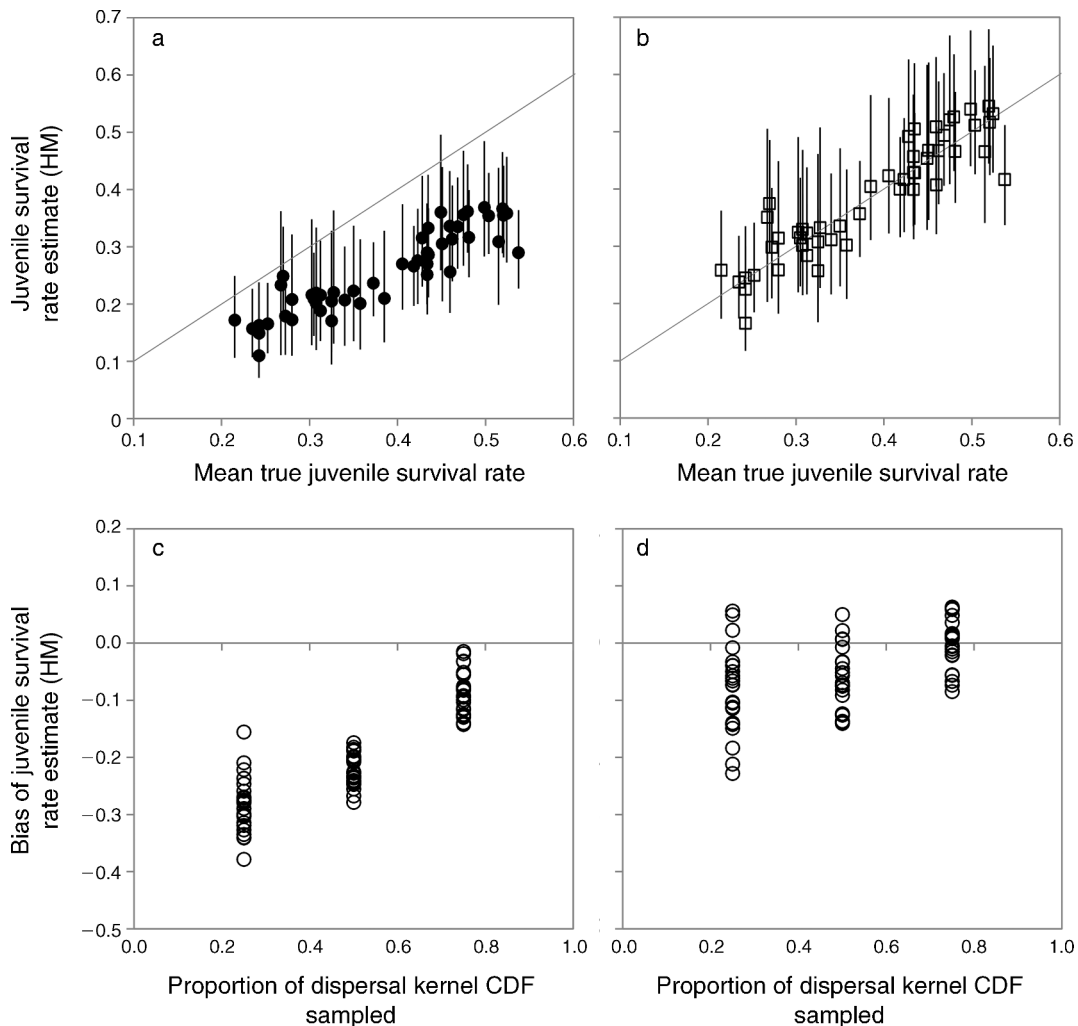


FIG. 2. Performance of the Bayesian emigration model against simulated capture-history data sets. The upper panels show correlations between mean true survival rates and model estimates (posterior means and 95% credible intervals) for a dispersive age class, showing (a) estimates from the standard Cormack-Jolly-Seber survival model (solid circles) and (b) estimates from the emigration model (open squares). The diagonal lines indicate perfect correlation. The lower panels show biases calculated from emigration-model survival estimates (posterior median minus true value) when ill-fitting dispersal kernels were used to estimate residence probability. Kernels were modeled for each simulated data set using recaptures from plots with a maximum dimension equating to the 25th, 50th, and 75th percentiles of the cumulative distribution function (CDF) of the true dispersal distribution. In panel (c), sampling occurred only within the study plot; in panel (d), recaptures were allowed within a small proportion of the tail of the true dispersal distribution (between the 90th and 95th percentiles), analogous to a second study plot. All data sets shown were simulated with low recapture probability ($P = 0.5$) and fixed dispersal distributions; “HM” stands for hierarchical mean.

For the Cape Sable Seaside Sparrow data set (Boulton et al. 2009, Van Houtan et al. 2010), spatial kernel projection yielded individual residence probability estimates ranging from 0.276 to 0.725 (mean 0.528, 95% CI 0.305–0.699) under an assumption that dispersal probability was independent of habitat suitability. When dispersal probability was constrained to suitable habitats, estimates ranged from 0.264 to 0.690 (mean 0.518, 95% CI 0.290–0.649), indicating that these assumptions had negligible impact on the estimation of emigration probability. The juvenile survival estimate from the emigration model assuming habitat independence (0.339 ± 0.078 , mean \pm SD) was more than double that of the

standard CJS model (0.151 ± 0.055), and showed a significantly wider 95% credible interval (0.191–0.585 for the emigration model, 0.094–0.240 for CJS), reflecting increased uncertainty once permanent emigration was taken into account. Results changed little when the model was fitted using kernel projections with habitat-dependent dispersal, producing a slightly higher mean juvenile survival rate of 0.342 ± 0.082 . Annual survival estimates and 95% credible intervals are given in Appendix G.

DISCUSSION

Since the inception of analytical methods for survival estimation from live-recapture data, researchers have

struggled to develop widely applicable methods to deal with the confounding issue of permanent emigration (Marshall et al. 2004, Zimmerman et al. 2007, Cooper et al. 2008). By combining information on survival and dispersal within a Bayesian framework, we were able to generate unbiased estimates of survival despite high rates of permanent emigration. Our model performed consistently across simulated scenarios of varying detection probability, survival rate, and dispersal probability. Fundamentally, the model is similar to other hierarchical applications of the CJS family (Gimenez et al. 2007, Calvert et al. 2009), and is relatively simple to implement. It generates standard apparent survival estimates (from the CJS-based model component) alongside true survival estimates accounting for emigration probability, so no information is lost relative to traditional survival models. Rather, valuable information is gained on the likely impact of permanent emigration on survival estimates within a given study system.

In real-world CMR studies, we anticipate that application of our model may be hindered by inadequate sampling of the true dispersal distribution (Schneider 2003, Cooper et al. 2008). Our simulations suggested that the inclusion of even small numbers of long-distance dispersal events can dramatically improve kernel fit, reducing bias in subsequent survival estimates. This result was unsurprising given that the distribution we used to simulate dispersal (lognormal) exhibits an inverse power law tail, and therefore shows self-similarity across spatial scales, allowing adequate modeling from restricted samples (Halley and Inchausti 2002). Inverse power law distributions are thought to occur frequently among dispersive organisms (Brown et al. 2002), and have been detected in numerous birds (Van Houtan et al. 2007) and butterflies (Fric and Konvicka 2007). Study designs involving multiple plots are likely to be highly beneficial in these cases, as the detection of even small numbers of long-distance movements between plots should facilitate accurate kernel fitting (Halley and Inchausti 2002, Cooper et al. 2008). Direct modeling of spatial variation in detection probability within the kernel likelihood function will also act to reduce bias associated with right censorship (Van Houtan et al. 2010), while nonparametric kernels might be more appropriate in sampling designs with severe right censorship. Whichever approach is taken, extreme care should be exercised when selecting models used to represent dispersal; gross errors such as the selection of an inappropriate model family for the dispersal kernel might lead to highly misleading estimates of emigration probability. In cases where there is considerable uncertainty in selecting the best model to represent dispersal, increased spatial sampling effort may be the most sensible approach to generating robust survival estimates.

While the problem of sampling the full distribution of dispersal distances can be addressed through appropriate study design and analysis, environmental heteroge-

neity presents a greater challenge to robust estimation of survival and dispersal (Ovaskainen et al. 2008). As dispersal is an emergent phenomenon reflecting interactions between an organism and its environment, a kernel generated from CMR data may only be truly meaningful within the conditions occurring in the sampled area (Schneider 2003). Owing to the lack of data beyond plot boundaries, predictions of emigration probability must ultimately rely on uninformed assumptions about dispersal behavior with respect to environmental variation. One way to account for this uncertainty is by constructing models representing different plausible hypotheses about off-plot dispersal. In the sparrow analysis, we compared scenarios where dispersal was assumed to be dependent or independent of habitat variation. In fact, survival and emigration estimates for the sparrow varied little between these divergent scenarios, reflecting the low relative impact of long-distance dispersal events (i.e., those reaching unsuitable habitats) on the overall probability of emigration for any given individual. Rather, emigration probability was largely dependent on the likelihood of short-distance movements carrying individuals to areas of suitable habitat just outside the study plot bounds.

In the absence of data on permanent emigration, we have no means of testing hypotheses relating to emigration rates. As such, probability density surfaces generated under our approach are more akin to best guesses than to data-based inferences. While relatively crude, we believe our approach represents a step in the right direction towards a better integration of survival and dispersal within empirical demographic models. We anticipate that further advances will be made via extensions to our approach, particularly if dispersal-kernel estimation can be directly incorporated within a spatially explicit CJS model (e.g., Saracco et al. 2010). We encourage researchers to make maximum use of the information at hand within capture-history data, and take advantage of the highly flexible range of tools available for demographic modeling within the Bayesian framework. We hope our model will provide a basis for further advances in the field of survival estimation in study systems where permanent emigration is likely to occur.

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SUPPLEMENTAL MATERIAL

Appendix A

Approaches to incorporating temporary emigration (*Ecological Archives* E093-134-A1).

Appendix B

Details of the data-simulation process and data-quality scenarios (*Ecological Archives* E093-134-A2).

Appendix C

Example WinBUGS code for the emigration model (*Ecological Archives* E093-134-A3).

Appendix D

Maps of sparrow spatial kernel projections (*Ecological Archives* E093-134-A4).

Appendix E

Comparison of juvenile survival parameter estimates from the Cormack-Jolly-Seber model and the emigration model, using simulated data (*Ecological Archives* E093-134-A5).

Appendix F

Mean squared error values for juvenile survival parameter estimates from the Cormack-Jolly-Seber model and the emigration model, using simulated data (*Ecological Archives* E093-134-A6).

Appendix G

Cape Sable Seaside Sparrow juvenile survival estimates (*Ecological Archives* E093-134-A7).