METHODS, TOOLS, AND TECHNOLOGIES

Bayesian mark–recapture–resight–recovery models: increasing user flexibility in the BUGS language

THOMAS V. RIECKE [iD],[1,2,3],† DAN GIBSON [iD],[4] ALAN G. LEACH,[2] MARK S. LINDBERG,[5]
MICHAEL SCHAUB [iD],[3] AND JAMES S. SEDINGER[2]

[1]*Program in Ecology, Evolution, and Conservation Biology, University of Nevada, Reno, Reno, Nevada 89557 USA*
[2]*Department of Natural Resources and Environmental Science, University of Nevada, Reno, Reno, Nevada 89557 USA*
[3]*Swiss Ornithological Institute, Sempach 6204 Switzerland*
[4]*Department of Fish and Wildlife Conservation, Virginia Tech University, Blacksburg, Virginia 24060 USA*
[5]*Institute of Arctic Biology and Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks, Alaska 99709 USA*

Abstract.   Estimating demographic parameters of interest is a critical component of applied conservation biology and evolutionary ecology, where demographic models and demographic data have become increasingly complex over the last several decades. These advances have been spurred by the development and use of information theoretic approaches, programs such as MARK and SURGE, and Bayesian inference. The use of Bayesian analyses has also become increasingly popular, where WinBUGS, JAGS, Stan, and NIMBLE provide increased user flexibility. Despite recent advances in Bayesian demographic modeling, some capture–recapture models that have been implemented in Program MARK remain unavailable to quantitative ecologists that wish to use Bayesian modeling approaches. We provide novel parameterizations of capture–mark–recapture–resight–recovery models implemented in Program MARK that have not yet been implemented in the BUGS language. Simulations show that the models described herein provide accurate parameter estimates. Our parameterizations of these models can easily be extended to estimate additional parameters such as entry probability, additional live states, or cause-specific mortality rates. Additionally, implementing these models in a Bayesian framework allows users to readily estimate parameters as mixtures, incorporate random individual or temporal variation, and use informative priors to assist with parameter estimation.

† **E-mail:** thomasvanceriecke@gmail.com

INTRODUCTION

An understanding of the causal mechanisms underlying population trends and individual fitness is a primary purpose of applied and evolutionary ecology. Demographic data are often the foundation of our understanding of these mechanisms, where the most effective applied management actions specifically target problematic demographic components, and these data expand our understanding of life-history theory and individual fitness (Stearns 1992, Cam et al. 2002, Gimenez and Gaillard 2018, Gimenez et al. 2018). However, there is often substantial uncertainty when estimating demographic parameters given imperfect observations of demographic

processes. Thus, models that allow researchers to accurately estimate demographic parameters of interest are critically important; such models can be used to estimate true and apparent survival, site fidelity, movement and harvest rates, breeding propensity, and relationships between these parameters and environmental and individual covariates (Brownie and Pollock 1985, Kendall et al. 1997, 2013, Cam et al. 2002, Gimenez et al. 2018).

Over time, demographic models have become increasingly complex. Capture–mark–recapture (Cormack 1964, Jolly 1965, Seber 1965) and capture–mark–recovery models (Seber 1970, Brownie and Pollock 1985) were originally developed to estimate survival. Following the development of these model types, researchers developed robust design models that allowed for the estimation of individual heterogeneity in detection probability (Pollock and Raveling 1982). This model was subsequently expanded to estimate recruitment and immigration (Nichols and Pollock 1990), as well as temporary emigration or breeding probability (Kendall et al. 1995, 1997). Concurrently, multistate or multistrata models were developed to estimate movement among discrete sites or transitions among states (Hestbeck et al. 1991, Brownie et al. 1993), and capture–mark–recapture and capture–mark–recovery models were combined to estimate site fidelity (Burnham 1993). These advances were rapidly followed by the inclusion of auxiliary live resights and dead recoveries during survival intervals (Barker 1997), the integration of the robust design with Burnham's live-dead model (Lindberg et al. 2001), and the integration of both dead recoveries and auxiliary resights simultaneously (Barker and White 2004, Barker et al. 2004, Kendall et al. 2013). The implementation of these model types in programs such as MARK (White and Burnham 1999) and E-SURGE (Choquet et al. 2009) has dramatically expanded inference in ecology and evolution, and the continued development of multi-event (Schofield et al. 2009) and various spatial capture–recapture models (Royle et al. 2013) will undoubtedly lead to further advances.

Recently, Bayesian parameterizations of demographic models have become increasingly popular (King et al. 2010), where the flexibility of BUGS and JAGS (Lunn et al. 2000, Plummer 2003, Gimenez et al. 2009), Stan (Gelman et al. 2015), and NIMBLE (de Valpine et al. 2017) allows researchers to effectively incorporate additional parameter uncertainty and prior information. For instance, quantitative ecologists can use information from previous studies to affect inference when sample sizes are small, or estimate demographic parameters as mixtures or distributions (Kéry and Schaub 2012, Gimenez et al. 2018). Further, it is relatively straightforward to include other data types in Bayesian capture–recapture, matrix, or integrated population models (Kéry and Schaub 2012). Recent advances in Bayesian demographic modeling include the development of live–dead models (Kéry and Schaub 2012, novel parameterizations of the robust design (Riecke et al. 2018, Gibson et al. 2018), and various multistate and multi-event models (Schofield et al. 2009). However, Bayesian parameterizations of the models developed by Barker (1997), Lindberg et al. (2001), and Kendall et al. (2013) have not previously been published or developed to our knowledge (although see Robinson et al. 2020 for a partial Bayesian implementation of the Barker 1997 model). Implementing these models in the BUGS language would provide increased flexibility to researchers interested in modeling demographic parameters, or the joint modeling of demographic components and abundance (Schaub and Kéry 2021). Thus, in this manuscript we use a state-space framework (King 2012) to parameterize and test the some of the most complex existing capture–mark–recapture–resight–recovery models available in Program MARK (Barker 1997, Lindberg et al. 2001, Kendall et al. 2013) in the BUGS language using simulated data, expanding the tools currently available to quantitative ecologists.

METHODS

We simulated capture–mark–recapture–resight–recovery data using a multistate approach (Lebreton et al. 2009, Kéry and Schaub 2012) following Kendall et al. (2013) that required simulating nine parameters (Table 1): (1) true survival from primary occasion t to $t+1$ (ϕ_t), (2) site fidelity from primary occasion t to $t+1$ (F_t), (3) the probability of availability for encounter during primary occasion $t+1$ given availability

Table 1. Parameters and the distributions used to generate capture–mark–recapture–recovery–resight data to test Bayesian parameterizations of Barker (1997), Lindberg et al. (2001), and Kendall et al. (2013).

Parameter	θ	Distribution	Model
True survival	ϕ	Uniform(0.7, 0.9)	B,L,K
Site fidelity	F	Uniform(0.9, 0.99)	B,L,K
Breeding propensity for breeders in $t-1$	γ''	Uniform(0.6, 0.95)	L,K
Breeding propensity for non-breeders in $t-1$	γ'	$\gamma'' = \gamma'$	L,K
Secondary occasion detection probability	p_j	Uniform(0.15, 0.35)	L,K
Primary occasion detection probability	p^*	$p^* = 1 - \prod_{j=1}^{J}\left(1-p_j\right)$	B,L,K
Non-breeding detection probability	R	Uniform(0.15, 0.45)	B,K
Non-breeding detection probability given mortality	R'	$R' = \frac{R}{2}$	B,K
Recovery and reporting probability given mortality	r	Uniform(0.05, 0.5)	B,L,K

Notes: Letters indicate estimation in different capture–mark–recapture–recovery–resight model types, where *B* denotes estimation in Barker (1997), *L* denotes estimation in Lindberg et al. (2001), and *K* denotes estimation in Kendall et al. (2013).

during primary occasion t (γ''_t), (4) the probability of availability for encounter during primary occasion $t+1$ given that an individual was not available during primary occasion t (γ'_t), (5) reencounter probability during secondary occasions (j) within each primary occasion ($p_{t,j}$), (6) reencounter probability during each primary occasion (p^*_t), (7) reencounter probability between primary occasions t and $t+1$ (R_t), (8) reencounter probability between primary occasions t and $t+1$ (R'_t) prior to mortality ($1-\phi$) between reencounter and primary occasion $t+1$, and (9) recovery probability of individuals that died between primary occasion t and $t+1$ (r_t; Table 1). For each iteration of our simulation, we generated time invariant demographic and observation parameters from uniform distributions for parameters ϕ, F, $\gamma = \gamma'' = \gamma'$, p, R, and r. We derived primary occasion detection probability (p^*) as a function of secondary occasion (j) detection probabilities (Lindberg et al. 2001, Kendall et al. 2013), $p^* = 1 - \prod_{j=1}^{J}\left(1-p_j\right)$. We also derived

non-breeding detection probability for individuals, which did not survive from breeding occasion t to breeding occasion $t+1$ (R') as a function of non-breeding detection probability for individuals that did survive the interval (R, Barker 1997, Kendall et al. 2013), where $R' = \frac{R}{2}$.

We then simulated individual state transitions among five latent states: (1) available for detection during primary occasion t, (2) temporarily unavailable for detection during primary occasion t, (3) permanently unavailable for detection during primary occasions, (4) recently dead, and (5) dead prior to the interval between t and $t+1$. We simulated the latent states of each individual using a state-transition matrix (**S**) populated with demographic parameters (Table 1) following Kendall et al. (2013), where rows represent states in primary occasion t, and columns represent states in primary occasion $t+1$.

$$s_{i,t} = \begin{bmatrix} \phi F\gamma'' & \phi F(1-\gamma'') & \phi(1-F) & 1-\phi & 0 \\ \phi F\gamma' & \phi F(1-\gamma') & \phi(1-F) & 1-\phi & 0 \\ 0 & 0 & \phi & 1-\phi & 0 \\ 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 1 \end{bmatrix}$$

(1)

We then simulated a robust-design observation process (i.e., resight and recapture) during a portion of the year assumed to be closed, and simulated auxiliary live resights and dead recoveries (i.e., resight and recovery) during the "open" interval between t and $t+1$ (e.g., Kendall et al. 2013, Leach et al. 2020), given five possible types of observations: (1) detected during primary occasion t given primary occasion detection probability, p^*, and resighted in the interval between primary occasions $t-1$ and t given a resighting probability, R; (2) detected during primary occasion t, but not resighted in the preceding interval; (3) not detected during primary occasion t, but resighted during the preceding interval; (4) not detected during primary occasion t or the preceding interval; and (5) recently dead, recovered, and reported to researchers. We defined a state-observation matrix (**O**) populated with appropriate nuisance (i.e., observation) parameters (Table 1) for each possibility following Kendall et al. (2013),

$$
o_{i,t} = \begin{bmatrix} p^*R & p^*(1-R) & (1-p^*)R & (1-p^*)(1-R) & 0 \\ 0 & 0 & R & (1-R) & 0 \\ 0 & 0 & R & (1-R) & 0 \\ 0 & 0 & R'(1-r) & (1-R')(1-r) & r \\ 0 & 0 & 0 & 1 & 0 \end{bmatrix}
\tag{2}
$$

We simulated a single dataset for each iteration of the simulation and then selectively removed data given the parameterizations of each model

incorporate six latent states into our novel parameterization: (1) available for detection during primary occasion t; (2) temporarily unavailable for detection during primary occasion t; (3) permanently unavailable for detection during primary occasions; (4) died during the interval between $t-1$ and t and recovered (r); (5) died during the interval between $t-1$ and t, resighted (R'), but not recovered ($1-r$); and (6) dead, absorbing. We then populated the state-transition matrix with the appropriate demographic and observation parameters (see Eq. 3 and Table 1).

$$
\Psi_{i,t} = \begin{bmatrix} \phi F\gamma'' & \phi F(1-\gamma'') & \phi(1-F) & (1-\phi)r & (1-\phi)R'(1-r) & (1-\phi)(1-R')(1-r) \\ \phi F\gamma' & \phi F(1-\gamma') & \phi(1-F) & (1-\phi)r & (1-\phi)R'(1-r) & (1-\phi)(1-R')(1-r) \\ 0 & 0 & \phi & (1-\phi)r & (1-\phi)R'(1-r) & (1-\phi)(1-R')(1-r) \\ 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}
\tag{3}
$$

of interest. To create data for the model developed by Barker (1997), we excluded the robust design data. To create data for the model developed by Lindberg et al. (2001), we excluded the live-resight data (R and R') collected during the interval between t and $t+1$. We retained all data for the model proposed by Kendall et al. (2013). Thus, we used the exact same simulation and datasets to estimate the parameters described in Barker (1997), Lindberg et al. (2001), and Kendall et al. (2013). We ran 100 simulations in which we initially released 100 marked individuals and then released an additional 50 marked individuals per primary occasion for the subsequent 14 occasions ($T = 15$).

To analyze our simulated data, we reparameterized the models of Barker (1997), Lindberg et al. (2001), and Kendall et al. (2013). We first constructed a state-transition matrix (Ψ), where rows represent an individual's latent state in primary occasion t, and columns represent an individual's latent state in time $t+1$. Kéry and Schaub (2012) demonstrated that it is necessary to include observation or nuisance parameters associated with mortality (e.g., r) in the state-transition matrix rather than the observation matrix for Seber (1970) band-recovery models. Therefore, we

To estimate the remaining nuisance or observation parameters, we constructed an observation matrix (Ω), where rows represent an individual's latent state in primary occasion t. This matrix is nearly identical to the matrix used to simulate the data (**O**), except that the probabilities of observation for individuals in latent states four and five were fixed as these parameters were estimated in the state-transition matrix (Ψ; Kéry and Schaub 2012),

$$
\omega_{i,t} = \begin{bmatrix} p^*R & p^*(1-R) & (1-p^*)R & (1-p^*)(1-R) & 0 \\ 0 & 0 & R & (1-R) & 0 \\ 0 & 0 & R & (1-R) & 0 \\ 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 \end{bmatrix}
\tag{4}
$$

We followed Riecke et al. (2018) to estimate p^*, or primary occasion detection probability. To obtain estimates from the model proposed by Barker (1997), we fixed $\gamma'' = \gamma' = 1$ to ensure parameter identifiability and removed the robust design structure in the model to estimate a single p rather than the more complex p^*. To obtain estimates from the model proposed by Lindberg

et al. (2001), we fixed $R = R' = 0$. We chose vague priors for all demographic and nuisance parameters $(\boldsymbol{\theta})$, where $\boldsymbol{\theta} \sim \text{Uniform}(0, 1)$. We simulated data using R 4.0.3 (R Core Team 2018), and all analyses (Supplementary Material) were conducted in JAGS (Plummer 2003) using the jagsUI package (Kellner 2016). We sampled from six MCMC chains for 25,000 iterations with an adaptive phase of 1000 iterations for each model for the simulated data. We discarded the first 15,000 iterations and retained every fifth saved iteration. We saved medians and 95% Bayesian credible intervals for each parameter for each simulation, and report the normalized mean signed difference and parameter calibration (Little 2006, Williams and Hooten 2016) for each parameter.

RESULTS

The Barker (1997), Lindberg et al. (2001), and Kendall et al. (2013) models required approximately 30, 25, and 30 min to run, respectively, on an HP desktop computer with a 10-core Intel i9-10900 processor (2.8 GHz) and 32 GB of RAM. All estimates of model parameters were centered around the true values used to generate the data (Figs. 1 and 2; Table 2), despite relatively small sample sizes for models of this complexity. Parameter coverage was adequate, where true parameter values were included in the 95% Bayesian credible intervals of modeled demographic parameters in $\geq 94\%$ of simulations (Table 2).

DISCUSSION

We demonstrate that the models described by Barker (1997), Lindberg et al. (2001), and Kendall et al. (2013) can be effectively implemented and fit in the BUGS language if users modify the state-transition and observation matrices (Eqs. 3 and 4, Figs. 1 and 2, Table 2). This allows quantitative ecologists to implement these complex mark–recapture–recovery–resight models in Bayesian frameworks using the BUGS language. We note that generalized m-array parameterizations have recently been developed for multistate models (Schaub and Kéry 2021), and a helpful guide to marginalizing discrete latent states has also recently been published (Yackulic et al. 2020). Both of these advances greatly reduce computational requirements for the models

described in this manuscript when individual covariates are not required. Our code (Data S1) can also be easily modified by other researchers to conduct power analyses tailored to their study system.

Here, we explain three minor inconsistencies between parameter estimates and the true values used to generate the data. First, while parameter constancy was excellent for estimates of p^* (Table 2) from the models developed by Lindberg et al. (2001) and Kendall et al. (2013), coverage was slightly lower than expected. We attribute this to our use of a fully conditional likelihood for the secondary capture occasions as demonstrated in Riecke et al. (2018). Second, the estimates of p^* from the model developed by Barker (1997) were lower than the true values used to generate the data. Importantly, we fixed $\gamma'' = \gamma' = 1$ to ensure parameter identifiability when using the model developed by Barker (1997), which does not include a robust design component. Thus, estimates of p^* from the Barker (1997) model in this simulation study are the product of primary occasion detection probability given presence (p^*) and the probability of presence (γ). Finally, while parameter constancy was also excellent for estimates of R', we observed substantial variance around the true values used to generate the data (Fig. 2). R', or the probability of resighting an individual during the interval between t and $t+1$ that does not survive the entire interval, is notoriously difficult to estimate (Kendall et al. 2013) and is often fixed to zero (Leach et al. 2020). Thus, we simply attribute this variance to the fairly small number of releases in the simulated data. Importantly, these minor inconsistencies were expected and did not influence constancy or coverage of demographic parameters.

The continued development of novel models and effective and efficient parameterizations of existing models will be critical for an enhanced understanding of ecological processes. The models described in this manuscript can easily be extended to estimate temporal or individual covariates, examine parameters at multiple sites, estimate demographic and observation parameters as mixtures or distributions (Kéry and Schaub 2012, Schaub and Kéry 2021), incorporate state uncertainty and allow for misclassification
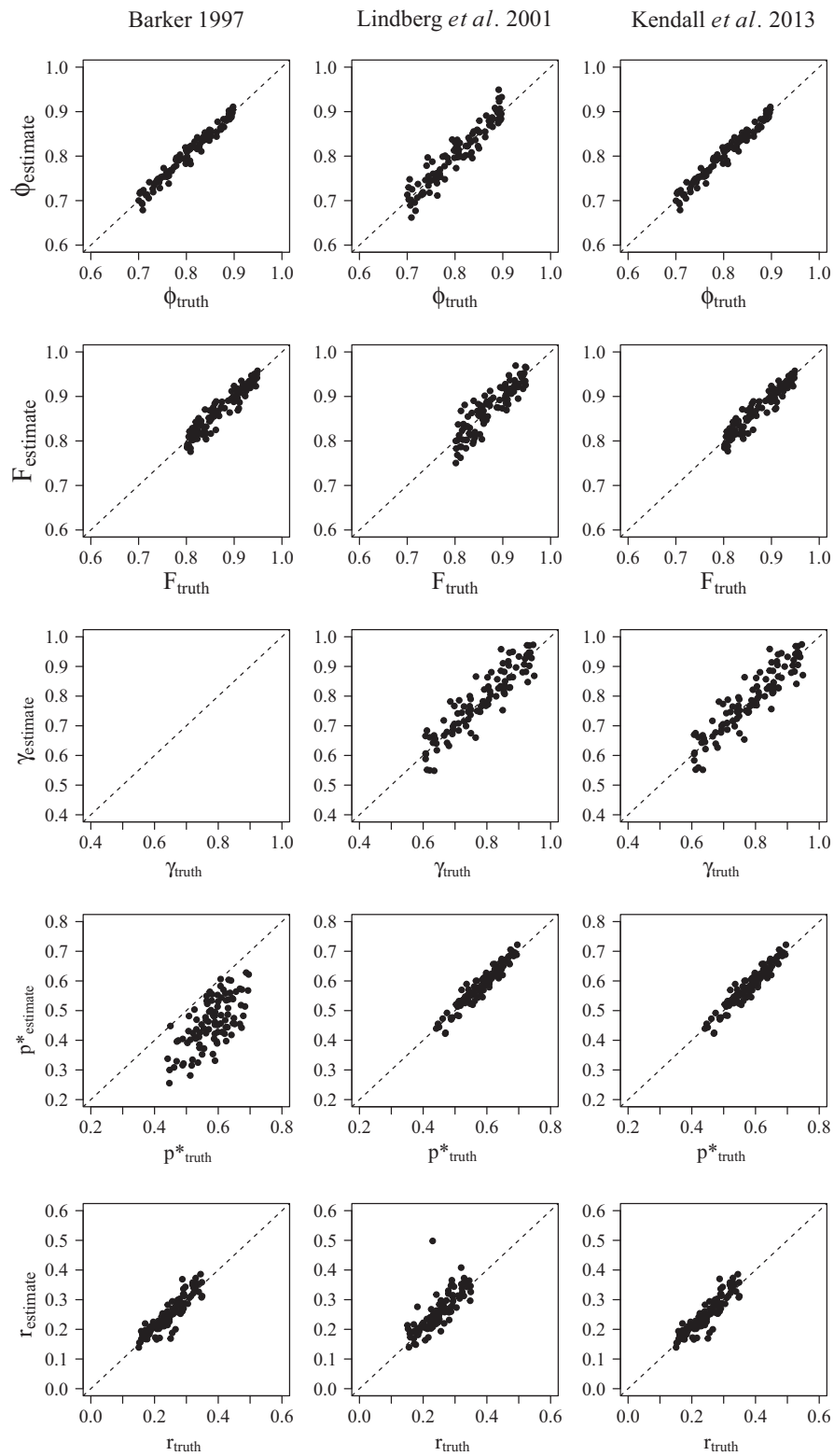
Fig. 1. Medians of posterior distributions for estimates of survival (φ), site fidelity (*F*), breeding probability (γ),

(Fig. 1. *Continued*)

primary occasion detection probability (p^*), and band reporting probability (r) from Bayesian parameterizations of the models developed by Barker (1997), Lindberg et al. (2001), and Kendall et al. (2013) plotted against the true values used to simulate the capture–recapture–resight–recovery data.

(Kendall et al. 2003, Conn and Cooch 2009, Pradel 2009), or estimate correlations and share information among parameters using multivariate normal distributions (Riecke et al. 2019). Further, these models can now be readily incorporated into integrated population models (Schaub and Kéry 2021) or other joint analyses,

such as using mark–recapture–resight–recovery and radio-, satellite-, or GPS-telemetry data simultaneously (e.g., Soisalo and Cavalcanti 2006). As the availability of citizen science data (i.e., auxiliary resights) increases, and joint analysis methods continue to expand, researchers will benefit tremendously by using models that can
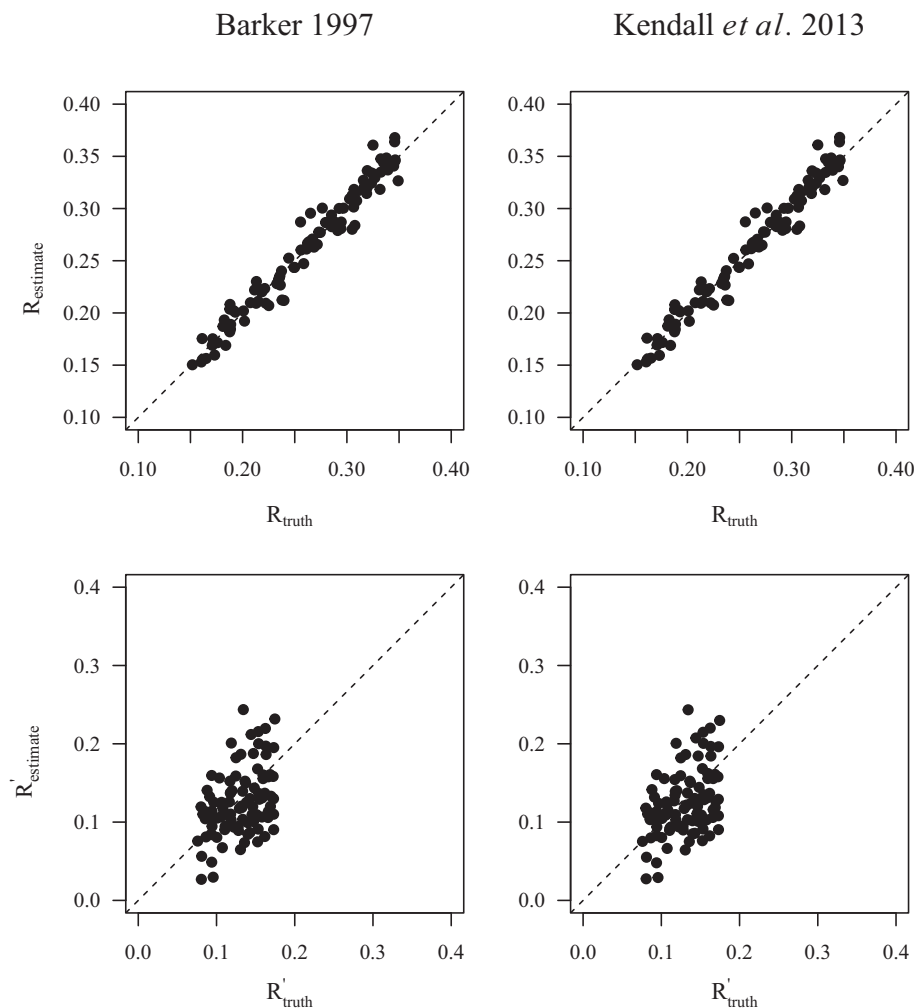

Fig. 2. Medians of posterior distributions for estimates of resighting probability (R), and resighting probability given mortality (R') between primary occasion t and primary occasion $t + 1$ from Bayesian parameterizations of the models developed by Barker (1997) and Kendall et al. (2013) plotted against the true values used to simulate the capture–recapture–resight–recovery data.

Table 2. Mean difference between parameter estimates and the true values used to simulate capture–mark–recapture–recovery–resight data to test Bayesian parameterizations of Barker (1997), Lindberg et al. (2001), and Kendall et al. (2013) from 100 simulations.

Parameter	Barker (1997)	Lindberg et al. (2001)	Kendall et al. (2013)
ϕ	0.001 (1.00)	0.001 (1.00)	0.001 (0.95)
F	−0.003 (0.96)	−0.001 (0.97)	−0.003 (0.96)
γ	—	0.001 (0.95)	0.001 (0.94)
p^*	−0.122 (0.12)	0.002 (0.83)	0.002 (0.83)
r	0.003 (0.93)	0.011 (0.94)	0.003 (0.92)
R	0.001 (0.96)	—	0.001 (0.97)
R'	−0.005 (0.96)	—	−0.005 (0.96)

Notes: Parameter coverage (i.e., the proportion of simulations that included the true value in the 95% Bayesian credible intervals) is also included in parentheses. Note that only a single estimate for γ is included, as $\gamma'' = \gamma'$ in our simulations, and that γ was fixed to 1 for the model developed by Barker (1997). Entries marked — are not estimated in the respective models.

incorporate multiple data types (e.g., Sun et al. 2019, Gamble et al. 2020). The joint capture–recapture–resight–recovery model parameterizations described in this manuscript increase the number of demographic parameters that can be estimated (Burnham 1993, Barker 1997, Lindberg et al. 2001, Kendall et al. 2013), enhance parameter precision, and allow for improved ecological and evolutionary inference.

Acknowledgments

Literature Cited

Barker, R. J. 1997. Joint modeling of live-recapture, tag-resight, and tag-recovery data. Biometrics 53:666–677.

Barker, R. J., K. P. Burnham, and G. C. White. 2004. Encounter history modeling of joint mark-recapture, tag-resighting and tag-recovery data under temporary emigration. Statistica Sinica 14:1037–1055.

Barker, R. J., and G. C. White. 2004. Towards the mother–of–all–models: customised construction of the mark–recapture likelihood function. Animal Biodiversity and Conservation 27:177–185.

Brownie, C., J. Hines, J. Nichols, K. Pollock, and J. Hestbeck. 1993. Capture-recapture studies for multiple strata including non-Markovian transitions. Biometrics 49:1173–1187.

Brownie, C., and K. H. Pollock. 1985. Analysis of multiple capture-recapture data using band-recovery methods. Biometrics 41:411–420.

Burnham, K. P. 1993. A theory for combined analysis of ring recovery and recapture data. Pages 199–213 *in* P. M. North, and J.-D. Lebreton, editors. Marked individuals in the study of bird populations. Birkhäuser, Bäsel, Switzerland.

Cam, E., W. A. Link, E. G. Cooch, J.-Y. Monnat, and E. Danchin. 2002. Individual covariation in life-history traits: seeing the trees despite the forest. The American Naturalist 159:96–105.

Choquet, R., L. Rouan, and R. Pradel. 2009. Program E-SURGE: a software application for fitting multi-event models. Pages 845–865 *in* D. L. Thomson, E. G. Cooch, and M. J. Conroy, editors. Modeling demographic processes in marked populations. Springer, New York, New York, USA.

Conn, P. B., and E. G. Cooch. 2009. Multistate capture–recapture analysis under imperfect state observation: an application to disease models. Journal of Applied Ecology 46:486–492.

Cormack, R. 1964. Estimates of survival from the sighting of marked animals. Biometrika 51:429–438.

de Valpine, P., D. Turek, C. J. Paciorek, C. Anderson-Bergman, D. T. Lang, and R. Bodik. 2017. Programming with models: writing statistical algorithms for general model structures with NIMBLE. Journal of Computational and Graphical Statistics 26:403–413.

Gamble, A., R. Garnier, T. Chambert, O. Gimenez, and T. Boulinier. 2020. Next-generation serology: integrating cross-sectional and capture–recapture approaches to infer disease dynamics. Ecology 101: e02923.

Gelman, A., D. Lee, and J. Guo. 2015. Stan: a probabilistic programming language for Bayesian inference and optimization. Journal of Educational and Behavioral Statistics 40:530–543.

Gibson, D., T. V. Riecke, T. Keyes, C. Depkin, J. Fraser, and D. H. Catlin. 2018. Application of Bayesian robust design model to assess the impacts of a hurricane on shorebird demography. Ecosphere 9: e02334.

Gimenez, O., S. J. Bonner, R. King, R. A. Parker, S. P. Brooks, L. E. Jamieson, V. Grosbois, B. J. Morgan, and L. Thomas. 2009. WinBUGS for population ecologists: Bayesian modeling using Markov Chain Monte Carlo methods. Pages 883–915 *in* D. L.

Thomson, E. G. Cooch, and M. J. Conroy, editors. Modeling demographic processes in marked populations. Springer, New York, New York, USA.

Gimenez, O., E. Cam, and J.-M. Gaillard. 2018. Individual heterogeneity and capture–recapture models: What, why and how? Oikos 127:664–686.

Gimenez, O., and J.-M. Gaillard. 2018. Estimating individual fitness in the wild using capture–recapture data. Population Ecology 60:101–109.

Hestbeck, J. B., J. D. Nichols, and R. A. Malecki. 1991. Estimates of movement and site fidelity using mark-resight data of wintering Canada geese. Ecology 72:523–533.

Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika 52:225–247.

Kellner, K. 2016. jagsUI: a wrapper around "rjags" to streamline "JAGS" analyses. R package version 1.4.2. https://CRAN.R-project.org/package=jagsUI (accessed November 17, 2020).

Kendall, W. L., R. J. Barker, G. C. White, M. S. Lindberg, C. A. Langtimm, and C. L. Peñaloza. 2013. Combining dead recovery, auxiliary observations and robust design data to estimate demographic parameters from marked individuals. Methods in Ecology and Evolution 4:828–835.

Kendall, W. L., J. E. Hines, and J. D. Nichols. 2003. Adjusting multistate capture–recapture models for misclassification bias: manatee breeding proportions. Ecology 84:1058–1066.

Kendall, W. L., J. D. Nichols, and J. E. Hines. 1997. Estimating temporary emigration using capture–recapture data with Pollock's robust design. Ecology 78:563–578.

Kendall, W. L., K. H. Pollock, and C. Brownie. 1995. A likelihood-based approach to capture-recapture estimation of demographic parameters under the robust design. Biometrics 51:293–308.

Kéry, M., and M. Schaub. 2012. Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic Press, Waltham, Massachusetts, USA.

King, R. 2012. A review of Bayesian state-space modelling of capture–recapture–recovery data. Interface Focus 2:190–204.

King, R., B. Morgan, O. Gimenez, and S. Brooks. 2010. Bayesian analysis for population ecology. CRC Press, Boca Raton, Florida, USA.

Leach, A. G., T. V. Riecke, J. S. Sedinger, D. H. Ward, and S. Boyd. 2020. Mate fidelity improves survival and breeding propensity of a long-lived bird. Journal of Animal Ecology 89:2290–2299.

Lebreton, J.-D., J. D. Nichols, R. J. Barker, R. Pradel, and J. A. Spendelow. 2009. Modeling individual animal histories with multistate capture–recapture models. Advances in Ecological Research 41:87–173.

Lindberg, M., W. Kendall, J. Hines, and M. G. Anderson. 2001. Combining band recovery data and Pollock's robust design to model temporary and permanent emigration. Biometrics 57:273–281.

Little, R. J. 2006. Calibrated Bayes: a Bayes/frequentist roadmap. The American Statistician 60:213–223.

Lunn, D. J., A. Thomas, N. Best, and D. Spiegelhalter. 2000. WinBUGS-a Bayesian modelling framework: concepts, structure, and extensibility. Statistics and Computing 10:325–337.

Nichols, J. D., and K. H. Pollock. 1990. Estimation of recruitment from immigration versus in situ reproduction using Pollock's robust design. Ecology 71:21–26.

Plummer, M. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. *In* Proceedings of the 3rd International Workshop on Distributed Statistical Computing, Volume 124. Vienna, Austria.

Pollock, K. H., and D. G. Raveling. 1982. Assumptions of modern band-recovery models, with emphasis on heterogeneous survival rates. The Journal of Wildlife Management 46:88–98.

Pradel, R. 2009. The stakes of capture–recapture models with state uncertainty. Pages 781–795 *in* D. L. Thomson, E. G. Cooch, and M. J. Conroy, editors. Modeling demographic processes in marked populations. Springer, New York, New York, USA.

R Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Riecke, T. V., A. G. Leach, D. Gibson, and J. S. Sedinger. 2018. Parameterizing the robust design in the BUGS language: lifetime carry-over effects of environmental conditions during growth on a long-lived bird. Methods in Ecology and Evolution 9:2294–2305.

Riecke, T. V., B. S. Sedinger, P. J. Williams, A. G. Leach, and J. S. Sedinger. 2019. Estimating correlations among demographic parameters in population models. Ecology and Evolution 9:13521–13531.

Robinson, S. G., D. Gibson, T. V. Riecke, J. D. Fraser, H. A. Bellman, A. DeRose-Wilson, S. M. Karpanty, K. M. Walker, and D. H. Catlin. 2020. Piping Plover population increase after Hurricane Sandy mediated by immigration and reproductive output. The Condor 122:duaa041.

Royle, J. A., R. B. Chandler, R. Sollmann, and B. Gardner. 2013. Spatial capture-recapture. Academic Press, Waltham, Massachusetts, USA.

Schaub, M., and M. Kéry. 2021. Integrated population models. Theory and ecological applications with R and JAGS. Academic Press, Waltham, Massachusetts, USA.

Schofield, M. R., R. J. Barker, and D. I. MacKenzie. 2009. Flexible hierarchical mark-recapture modeling for open populations using WinBUGS. Environmental and Ecological Statistics 16:369–387.

Seber, G. A. 1965. A note on the multiple-recapture census. Biometrika 52:249–259.

Seber, G. 1970. Estimating time-specific survival and reporting rates for adult birds from band returns. Biometrika 57:313–318.

Soisalo, M. K., and S. M. Cavalcanti. 2006. Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture–recapture sampling in combination with GPS radio-telemetry. Biological Conservation 129:487–496.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, London, UK.

Sun, C. C., J. A. Royle, and A. K. Fuller. 2019. Incorporating citizen science data in spatially explicit integrated population models. Ecology 100: e02777.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:S120–S139.

Williams, P. J., and M. B. Hooten. 2016. Combining statistical inference and decisions in ecology. Ecological Applications 26:1930–1942.

Yackulic, C. B., M. Dodrill, M. Dzul, J. S. Sanderlin, and J. A. Reid. 2020. A need for speed in Bayesian population models: a practical guide to marginalizing and recovering discrete latent states. Ecological Applications 30:e02112.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3810/full