

ORIGINAL RESEARCH

Estimating correlations among demographic parameters in population models

Thomas V. Riecke^{1,2}  | Benjamin S. Sedinger³  | Perry J. Williams² | Alan G. Leach² | James S. Sedinger²

¹Program in Ecology, Evolution, and Conservation Biology, University of Nevada, Reno, Nevada

²Department of Natural Resources and Environmental Science, University of Nevada, Reno, Nevada

³College of Natural Resources, University of Wisconsin-Stevens Point, Stevens Point, Wisconsin

Correspondence

Thomas V. Riecke, Program in Ecology, Evolution, and Conservation Biology, University of Nevada, Reno, NV 89557. Email: triecke@cabnr.unr.edu

Funding information

National Science Foundation, Grant/Award Number: DEB 0743152, DEB 1252656, DEB 9815383, OPP 0196406, OPP 9214970 and OPP 9985931; Delta Waterfowl; Institute for Wetland and Waterfowl Research, Ducks Unlimited Canada

Abstract

Estimating correlations among demographic parameters is critical to understanding population dynamics and life-history evolution, where correlations among parameters can inform our understanding of life-history trade-offs, result in effective applied conservation actions, and shed light on evolutionary ecology. The most common approaches rely on the multivariate normal distribution, and its conjugate inverse Wishart prior distribution. However, the inverse Wishart prior for the covariance matrix of multivariate normal distributions has a strong influence on posterior distributions. As an alternative to the inverse Wishart distribution, we individually parameterize the covariance matrix of a multivariate normal distribution to accurately estimate variances (σ^2) of, and process correlations (ρ) between, demographic parameters. We evaluate this approach using simulated capture-mark-recapture data. We then use this method to examine process correlations between adult and juvenile survival of black brent geese marked on the Yukon-Kuskokwim River Delta, Alaska (1988–2014). Our parameterization consistently outperformed the conjugate inverse Wishart prior for simulated data, where the means of posterior distributions estimated using an inverse Wishart prior were substantially different from the values used to simulate the data. Brent adult and juvenile annual apparent survival rates were strongly positively correlated ($\rho = 0.563$, 95% CRI 0.181–0.823), suggesting that habitat conditions have significant effects on both adult and juvenile survival. We provide robust simulation tools, and our methods can readily be expanded for use in other capture-recapture or capture-recovery frameworks. Further, our work reveals limits on the utility of these approaches when study duration or sample sizes are small.

KEYWORDS

black brent, *Branta bernicla nigricans*, capture-recapture, demography, fitness, hyperpriors, inverse Wishart, multivariate normal

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2019 The Authors. *Ecology and Evolution* published by John Wiley & Sons Ltd.

1 | INTRODUCTION

Capture–mark–recapture–resight and capture–mark–recovery data can be used to estimate demographic parameters such as true and apparent survival, site fidelity, movement and harvest rates, breeding propensity, demographic heterogeneity, and relationships among these parameters and environmental covariates (Brownie & Pollock, 1985; Cam, Link, Cooch, Monnat, & Danchin, 2002; Gimenez, Cam, & Gaillard, 2018; Kendall et al., 2013; Kendall, Nichols, & Hines, 1997). Estimating relationships between demographic parameters can lead to more effective conservation actions (Arnold, Afton, Anteau, Koons, & Nicolai, 2016; Servanty et al., 2010, 2011), where biologists might direct conservation actions toward demographic components which are intrinsically linked, such as pre- and post-fledging survival (Nicolai & Sedinger, 2012) or adjust anthropogenic harvest rates to affect population growth rates of wild organisms (Nichols, Runge, Johnson, & Williams, 2007; Péron, 2013; Runge et al., 2002; Williams & Johnson, 1995). Estimating relationships among demographic rates can also advance our understanding of individual heterogeneity, life-history trade-offs, and the evolution of life histories (Cam, Aubry, & Authier, 2016; Cam et al., 2002; Gimenez et al., 2018; Stearns, 1992).

Estimating correlations among demographic parameters has often proven challenging, because sampling correlations can obscure process correlations (Anderson & Burnham, 1976; Link & Barker, 2005). For instance, the estimation of band recovery probability is confounded with the estimation of survival (Anderson & Burnham, 1976), affecting inference on the relationship between survival and harvest. Previous methods have employed approaches to achieve independent samples by comparing estimates of survival from the marked sample with estimates of harvest of the total population (Anderson & Burnham, 1976) or by partitioning the capture–mark–recovery data (Nichols & Hines, 1983). Recently, work on the effects of harvest on survival has focused on understanding process correlations (ρ) between survival and harvest rates (Arnold et al., 2016; Bartzen & Dufour, 2017; Sedinger, White, Espinosa, Partee, & Braun, 2010), where a strong negative correlation suggests additive relationships between survival and harvest, and minimal or no correlation may be indicative of compensation or partial compensation, although these relationships are complex (Arnold et al., 2016; Péron, 2013). Others have focused on the correlation between natural mortality and harvest mortality (Péron, 2013; Servanty et al., 2010), where no correlation may be indicative of additive harvest, and a negative correlation may be indicative of compensatory harvest. Ecologists have both highlighted (Arnold et al., 2016; Péron, 2013; Servanty et al., 2010) and debated (Arnold, Afton, Anteau, Koons, & Nicolai, 2017; Lindberg, Boomer, Schmutz, & Walker, 2017) the utility of these approaches. Capture–recapture (Riecke, Leach, Gibson, & Sedinger, 2018) and integrated population models can also be used to examine covariation among parameters such as survival and breeding propensity. This allows researchers to examine life-history trade-offs at the individual or population level (Cam et al., 2002), as well as correlations among other demographic parameters

(Kindsvater et al., 2018; Koons, Arnold, & Schaub, 2017; Link & Barker, 2005; Schaub, Jakober, & Stauber, 2013). Conservation biologists can subsequently use these relationships to predict the potential of management actions to affect wildlife populations.

Bayesian hierarchical models allow for the separation of sampling and process correlations (Link & Barker, 2005). However, the choice of priors can dramatically impact posterior distributions and inference when using Bayesian models, where relatively uninformative priors are often favored (Link, Cam, Nichols, & Cooch, 2002) for objective Bayesian analyses. Further, conjugate priors are desirable computationally, because their full-conditional distributions are analytically tractable with a known distribution, and there is no need for Metropolis–Hastings updates or tuning. A conjugate prior for the covariance matrix ($K \times K$) of a multivariate normal distribution is the inverse Wishart distribution, where quantitative ecologists often use this distribution with degrees of freedom equal to $K + 1$ and a $K \times K$ identity matrix as a scale matrix (Haff, 1979; Kéry & Schaub, 2012; Péron, 2013; Wishart, 1928). Thus, for a bi-variate normal distribution,

$$y \sim \text{Normal}(\mu, \Sigma)$$

$$\Sigma = \begin{bmatrix} \sigma_1^2 & \sigma_1 \sigma_2 \rho_{1,2} \\ \sigma_1 \sigma_2 \rho_{1,2} & \sigma_2^2 \end{bmatrix}, \quad (1)$$

$$\Sigma^{-1} \sim \text{Wishart}(3, I),$$

where I is a 2×2 identity matrix. Critically, simulation work has revealed that the inverse Wishart prior is strongly informative for covariance matrices (Alvarez, Niemi, & Simpson, 2014). Specifically, the inverse Wishart prior can result in strong prior influence on the posterior distribution of variances and covariances, particularly when variances are small ($\sigma^2 < 0.25$), affecting the posterior distribution of correlations (Alvarez et al., 2014). The shape of the logistic link function, and life-history theory (Stearns, 1992), dictates that the standard deviations (σ), and consequently variances (σ^2), of demographic parameters of interest will typically be small (Gimenez et al., 2018). For instance, typical North American dabbling duck survival rates exhibit variances of approximately $\sigma^2 = 0.1$, where σ^2 is from Equation (1). Given the structure of covariance matrices, where the covariance is equal to the product of the square roots of the applicable variances, and a process correlation between the applicable parameters ($\sigma_i \sigma_j \rho_{i,j}$), the use of the Wishart, scaled inverse Wishart (O'Malley & Zaslavsky, 2008), or hierarchical half-t (Huang & Wand, 2013) priors for a precision matrix often leads to the underestimation of ρ . This has important implications for the interpretation of process correlations, affecting biological inference and management decisions.

To alleviate current issues regarding the estimation of ρ and σ^2 when using the logistic link and the inverse Wishart distribution, we propose individual parameterization for the components of the

covariance matrix when using multivariate normal distributions to estimate parameters.

$$y \sim \text{Normal}(\mu, \Sigma)$$

$$\Sigma = \begin{bmatrix} \sigma_1^2 & \sigma_1 \sigma_2 \rho_{1,2} \\ \sigma_1 \sigma_2 \rho_{1,2} & \sigma_2^2 \end{bmatrix}, \quad (2)$$

$$\sigma_i \sim \text{Uniform}(0, 5),$$

$$\rho_{ij} \sim \text{Uniform}(-1, 1),$$

This approach avoids introducing strong, undesirable effects on the posterior distributions via the prior distributions, such as the scaled inverse chi-square distribution implied for the variances when using the inverse Wishart distribution as a prior for the covariance matrix (Figure 1), or the implied correlations among σ and ρ (Alvarez et al., 2014, Figure 2). The inverse Wishart prior, as well as other derivatives of that prior, clearly leads to correlations among σ and ρ (Alvarez et al., 2014). Other hyperpriors for variances, such as the half-t, half-normal, or half-Cauchy, may be equally effective as a uniform prior. However, we strongly suggest careful consideration of the data, and the use of vague priors when modeling a covariance matrix.

To demonstrate the utility of our approach, we use simulated data, as well as a robust longitudinal dataset, capture-mark-recapture-resight data from female Pacific black brent geese (*Branta bernicla nigricans*; hereafter, brent) marked on the Yukon-Kuskokwim River Delta in Alaska (1988–2014). Brent breeding at the Tutakoke River Colony on the Yukon-Kuskokwim River Delta, Alaska, has been monitored from 1984 through the present (Leach et al., 2019; Sedinger, Flint, & Lindberg, 1995). Over the duration of the Tutakoke River Colony brent demographic project, researchers have collected data on every avian demographic component, where an enhanced understanding of process correlations among demographic components may lead to more effective management actions, and improve our understanding of demographic buffering and life-history trade-offs. We use multivariate normal distributions, and novel covariance matrix parameterizations for demographic parameters (Barnard, McCulloch, & Meng, 2000), to assess the relationships among adult and juvenile survival of brent to better understand life-history trade-offs and the demographic buffering hypothesis (Gaillard, Festa-Bianchet, Yoccoz, Loison, & Toigo, 2000; Pfister, 1998; Stearns, 1992), which predicts that vital rates with greater demographic sensitivities will have lower variances. Further, we simulate thousands of biologically plausible capture-mark-recapture datasets to explore the effects of prior influence on inference in the presence of parameter uncertainty and imperfect observation when truth is known. Our work has important implications for researchers using multivariate

normal distributions to estimate process correlations among demographic parameters of wild organisms, as well as research in other fields where inverse Wishart distributions are used as prior for covariance matrices for multivariate data (e.g., Multivariate spatial models, Gelfand, Diggle, Guttorp, & Fuentes, 2010; Bayesian structural equation models).

2 | METHODS

2.1 | Capture-mark-recapture data simulation

We simulated capture-mark-recapture datasets using mean annual adult apparent survival probabilities of 0.73 ($\mu_{\phi_{ad}} = 1, \sigma_{\phi_{ad}}^2 = 0.1$ on the real scale), and mean annual juvenile survival probabilities of 0.27 ($\mu_{\phi_{juv}} = -1, \sigma_{\phi_{juv}}^2 = 0.1$ on the real scale; Table 1), to approximate adult

and juvenile survival probabilities for species with intermediate-paced life-history strategies. Our simulations and the R script we provide (Data availability statement) can be easily modified to assess relationships for species with slower or faster paced life-history strategies. To assess our ability to estimate process correlations (ρ), we used fixed variances of 0.1 for adult and juvenile survival rates, and randomly generated a process correlation between adult and juvenile survival for each simulation (v) using a uniform distribution to represent all possible relationships between these two demographic parameters,

$$\rho_v \sim \text{Uniform}(-1, 1), \text{ for } v = 1, \dots, V,$$

$$\sigma_{\phi_{ad}}^2 = \sigma_{\phi_{juv}}^2 = 0.1,$$

$$\text{logit}(\Phi) \sim \text{Normal}(\mu_{\phi}, \Sigma), \quad (3)$$

To generate capture-mark-recapture data, we first simulated each individual's latent state ($z_{i,t}$) given its initial release occasion (τ_i), initial age-class (juvenile or adult), number of release occasions (T), and time-varying survival probabilities (Φ),

$$\Sigma = \begin{pmatrix} \sigma_{\phi_{ad}}^2 & \sigma_{\phi_{ad}} \sigma_{\phi_{juv}} \rho \\ \sigma_{\phi_{ad}} \sigma_{\phi_{juv}} \rho & \sigma_{\phi_{juv}}^2 \end{pmatrix}$$

$$z_{i,t} \sim \begin{cases} \text{Bernoulli}(\phi_{i,t}), & z_{i,t-1} = 1 \\ 0, & z_{i,t-1} = 0 \end{cases}, \text{ for } t = \tau_i, \dots, T. \quad (4)$$

We then simulated capture histories for each individual ($y_{i,t}$) given its current latent state ($z_{i,t}$) and a detection probability ($p = .5$),

$$y_{i,t} \sim \begin{cases} \text{Bernoulli}(p), & z_{i,t} = 1 \\ 0, & z_{i,t} = 0 \end{cases}, \text{ for } t = \tau_i + 1, \dots, T. \quad (5)$$

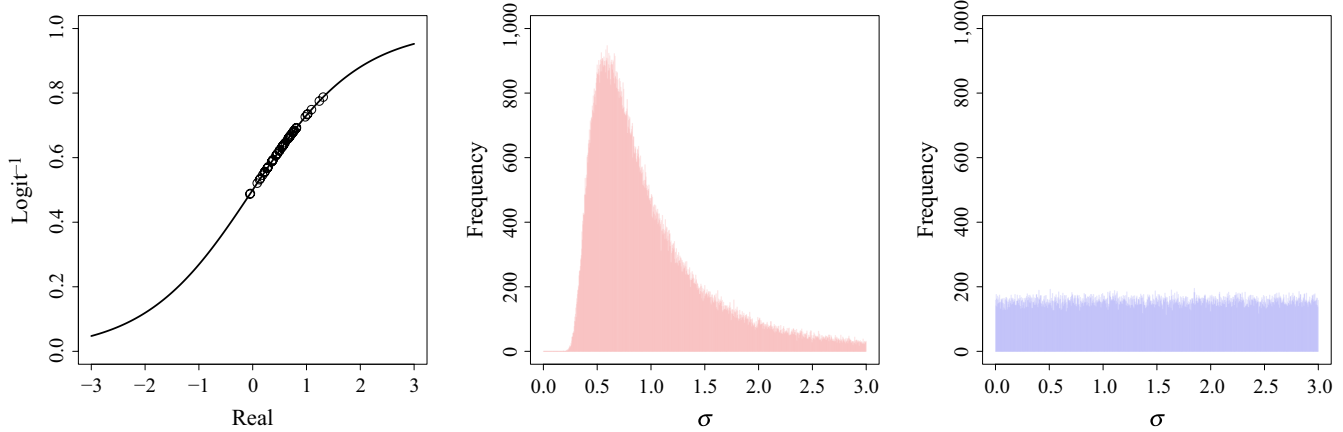


FIGURE 1 Fifty randomly generated annual survival probabilities given mean survival (μ_s) of 0.5 and a variance (σ_s^2) of 0.1 on the real scale and their respective positions on the inverse logit link function (left). Additionally, we plot prior distributions for the standard deviation of survival probabilities from a Wishart prior with an identity scale matrix and degrees of freedom equal to $K + 1$ (center), and from a uniform prior with a lower bound of 0, and an upper bound of 5 (right), where the uniform prior is clearly less informative for variances of demographic parameters

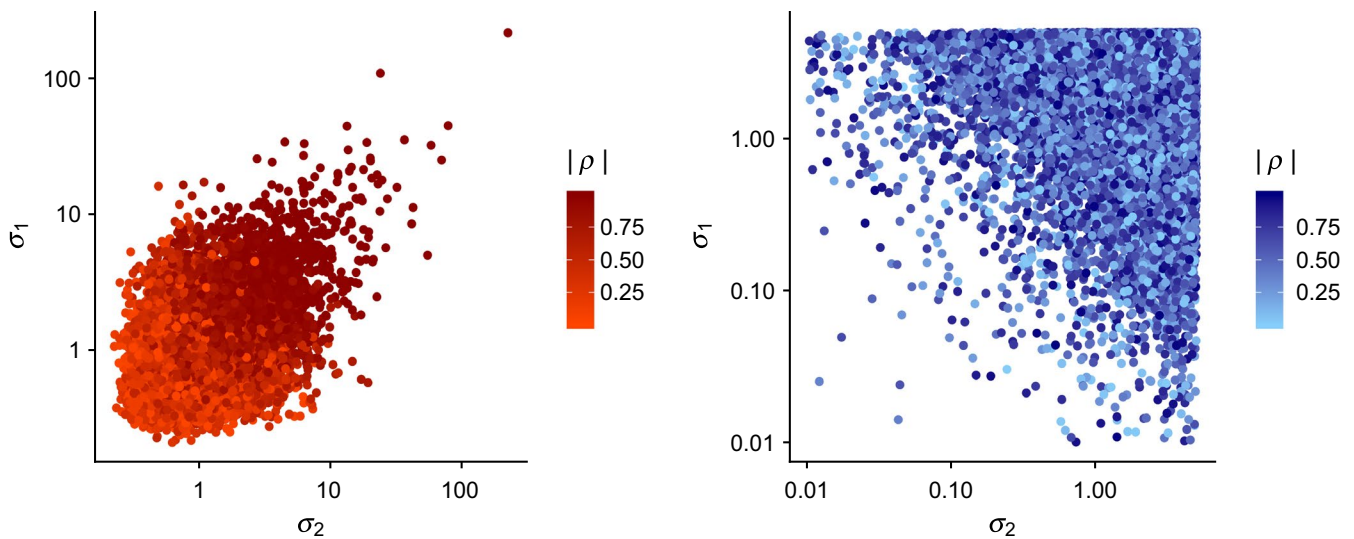


FIGURE 2 Correlations among standard deviations (σ_k) and process correlations (ρ) drawn from an inverse Wishart prior with an identity scale matrix and degrees of freedom equal to $K + 1$ (left), and from a multivariate normal distribution where hyperpriors of the covariance matrix were individually specified, where we used a half-normal distribution with a variance of ten for the standard deviations, and a uniform prior with lower and upper bounds of -1 and 1 for the process correlation (right). Note the strong correlation between values of (σ_k) and values of (ρ) when using the inverse Wishart prior

We simulated 1,000 populations and capture-mark-recapture datasets for each pairwise comparison of 10, 20, and 30 occasions, and 100, 1,000, and 5,000 releases per occasion, for a total of 9,000 simulated capture-mark-recapture datasets.

2.2 | Analyzing the simulated data

For each simulated dataset, we built age-specific Bayesian CJS models (Cormack, 1964; Jolly, 1965; Seber, 1965), identical to the model used to simulate the data. We first modeled each individual's latent state ($z_{i,t}$) given its release occasion (τ_i) and age at release, given

Equation (4). We then modeled each individual's capture history as a function of its latent state, given Equation (5). For computational efficiency, we structured the capture-mark-recapture data in m arrays for juveniles and adults (Data availability statement). To examine process correlations between adult (ϕ_{ad}) and juvenile (ϕ_{juv}) survival, we drew occasion specific adult and juvenile survival probabilities from a multivariate normal distribution,

$$\text{logit}(\Phi) \sim \text{Normal}(\mu, \Sigma), \tag{6}$$

where $\mu = (\mu_{\phi_{ad}}, \mu_{\phi_{juv}})$ and $\Phi = (\phi_{ad,t}, \phi_{juv,t})$. We specified vague priors for the means of adult and juvenile survival,

TABLE 1 Parameter values used to simulate data for capture–mark–recapture models

Model	Symbol	Parameter value
Parameter	θ	
Mean adult survival	$\mu_{\phi_{ad}}$	1
Temporal variance in adult survival	$\sigma_{\phi_{ad}}^2$	0.1
Mean juvenile survival	$\mu_{\phi_{juv}}$	-0.5
Temporal variance in juvenile survival	$\sigma_{\phi_{juv}}^2$	0.1
Process correlation	$\rho_{\phi_{ad}, \phi_{juv}}$	Uniform (-1, 1)
Detection probability	p	0.5

$$\begin{aligned} \mu_{\phi_{ad}} &\sim \text{Normal}(0,1), \\ \mu_{\phi_{juv}} &\sim \text{Normal}(0,1). \end{aligned} \quad (7)$$

We then used two approaches to estimate the covariance matrix (Σ). First, we modeled the precision matrix (Σ^{-1}) of the multivariate normal distribution with a Wishart prior (Equation 1). Second, we specified priors for the components of the covariance matrix (Equation 2).

2.3 | Brent capture–mark–recapture data collection

We captured brent by drive-trapping during brood-rearing and the adult remigial molt at the Tutakoke River Brent Colony in western Alaska (61.25°N, -165.62°W; Sedinger, Lindberg, Rextad, Chelgren, & Ward, 1997). We uniquely marked all encountered individuals with stainless steel or incoloy USGS rings and uniquely engraved plastic tarsal rings. Prior to ringing efforts each year, we monitored nests in 49 long-term, 50-m radius plots, and actively located nests of tarsal-ringed females at the colony (Sedinger et al., 1995). Following hatch, we observed adults and goslings from 3 to 4 m tall observation blinds throughout brood-rearing. We then captured adults, goslings, and second-year females (fledged the previous year) during the adult and second-year remigial molt, and prior to goslings gaining flight capabilities, with few exceptions. For this analysis, we constrained our encounter histories to include all adult (*ad*), second-year (*sy*), and juvenile (*juv*) females encountered at the nest, during brood-rearing, or during ringing drives from 1988 to 2014, for a total sample of 8,338 adult and second-year, and 12,630 juvenile, female brent.

2.4 | Brent capture–mark–recapture data analysis

We built models to estimate adult and juvenile survival, and the correlation between these parameters, in exactly the same way as for the simulated data with one exception. We modeled age-related and temporal heterogeneity in detection probability. Brent do not breed until after their second year, and they are less likely to be detected at

the breeding colony until this time. However, we do resight second-year females at the colony and recapture these individuals during ringing efforts. Thus, we modeled detection probabilities of second-year and adult brent separately based on age-class (k), where we estimated detection probability for both age-classes (p_k) as random variables drawn from a normal distribution with a mean (μ_{p_k}) and variance ($\sigma_{p_k}^2$),

$$\begin{aligned} \text{logit}(p_{k,t}) &= \beta_0 + \epsilon_{p_{k,t}}, \\ \beta_0 &\sim \text{Normal}(0,3), \\ \epsilon_{p_{k,t}} &\sim \text{Normal}(0, \sigma_{p_k}^2), \\ \sigma_{p_k} &\sim \text{Uniform}(0,3). \end{aligned} \quad (8)$$

We did not discriminate between adult and second-year survival probabilities, as previous analyses have not indicated variation in survival rates between these age-classes (Leach et al., 2019; Lindberg, Sedinger, & Lebreton, 2013; Sedinger, Herzog, & Ward, 2004). To examine process correlations between adult ($\phi_{ad,t}$) and juvenile ($\phi_{juv,t}$) survival, we drew survival parameters (Φ) from a multivariate normal distribution. We used identical approaches as those used for the simulated data to parameterize the covariance matrix, where we first modeled the precision matrix (Σ^{-1}) of the multivariate normal distribution with a Wishart prior (Equation 1). Second, we specified hyperpriors for the components of the covariance matrix (Equation 2).

2.5 | Computational details

We simulated data using R 3.5.1 (R Core Team, 2018), and all analyses were conducted in JAGS (Plummer, 2003) using the 'jagsUI' package (Kellner, 2016). We ran two MCMC chains of 25,000 iterations for each model for simulated data, where we discarded the first 15,000 iterations and retained every fifth saved iteration (Schaub & Fletcher, 2015). For the brent data, we ran two MCMC chains of 100,000 iterations, where we discarded the first 50,000 iterations and retained every fifth saved iteration.

3 | RESULTS

3.1 | Capture–mark–recapture simulation

When we used the same model to simulate and analyze the capture–mark–recapture data with an inverse Wishart prior on the covariance matrix of the multivariate normal distribution, the means of the posterior distributions of the process correlation (ρ) between adult and juvenile survival were different than the values used to simulate the data for all combinations of releases and occasions (Table 2). Further, 95% Bayesian credible intervals only covered truth for approximately 75% of simulations (Table 3). Critically, coverage declined as $|\rho|$ increased (Figure 3). However, when we used hyperpriors on the

TABLE 2 Mean absolute value of the difference between the simulated process correlation used to generate the data, and the mean of the posterior distributions of the estimated process correlations (ρ), as a function of the number of occasions (t), the number of individuals released per occasion (n), and the parameterization of the covariance matrix used for the capture–recapture models

Parameterization	Occasions		
	10	20	30
Releases			
Inverse Wishart			
100	0.426	0.346	0.325
1,000	0.329	0.227	0.197
5,000	0.280	0.163	0.147
Hyperpriors			
100	0.319	0.126	0.095
1,000	0.203	0.067	0.042
5,000	0.150	0.048	0.029

TABLE 3 The proportion of simulations (out of 1,000) for which the value of ρ used to simulate the capture–mark–recapture data was included in the 95% Bayesian credible interval of the estimate of ρ as a function of the number of occasions (t), the number of individuals released per occasion (n), and the parameterization of the covariance matrix used for the capture–recapture models

Parameterization	Occasions		
	10	20	30
Releases			
Inverse Wishart			
100	0.654	0.696	0.720
1,000	0.645	0.675	0.737
5,000	0.617	0.744	0.743
Hyperpriors			
100	0.966	0.996	0.999
1,000	0.986	0.999	1.000
5,000	0.986	0.997	0.996

individual components of the covariance matrix, matching the variances of the demographic parameters to the prior (Figure 1), bias in the estimation of ρ was reduced for all combinations of releases and occasions (Figure 3), and eliminated when data were sufficient to estimate these parameters (Table 2). Further, credible interval coverage was adequate for all combinations of releases and occasions (Table 3).

3.2 | Correlations among survival rates of female brent

When we used an inverse Wishart distribution as a prior for the covariance matrix, adult and juvenile survival of female brent were positively correlated ($\rho = 0.481$, 95% CRI 0.115–0.754; Figure 4), and the variance of juvenile survival ($\sigma_{\phi_{juv}}^2 = 0.685$, 95% CRI 0.380–1.251)

was significantly greater than the variance of adult survival ($\sigma_{\phi_{ad}}^2 = 0.194$, 95% CRI 0.103–0.369). When we used hyperpriors for components of the covariance matrix, which more accurately reflected the potential variance of demographic components in our simulations, we estimated a stronger correlation between adult and juvenile survival ($\rho = 0.563$, 95% CRI 0.181–0.823; Figure 4). Further, estimates of the variances of juvenile survival ($\sigma_{\phi_{juv}}^2 = 0.753$, 95% CRI

0.405–1.413) and adult survival ($\sigma_{\phi_{ad}}^2 = 0.156$, 95% CRI 0.073–0.326) also differed from the inverse Wishart parameterization (Figure 5), where the difference between the variances increased.

4 | DISCUSSION

4.1 | Implications for the estimation of process correlations

Our simulation results highlight two critical issues in the estimation of process correlations among demographic components. First, we demonstrate the influence of currently used prior distributions on biological inference due to the informative nature of the inverse Wishart prior for the variances and covariances of demographic parameters (Figure 1). The $\text{Wish}^{-1}(3, I_{2 \times 2})$ prior implies certain hyperpriors for the variances of, and correlations between, demographic parameters which strongly impact inference. We also illustrate the inherent link between the estimation of ρ and σ when using inverse Wishart priors, where there is an intrinsic link between prior values for variances and process correlations (Figure 2). Our simulations clearly reveal that these issues can be addressed by specifying hyperpriors for the individual components of a covariance matrix. Second, and critically, we show that analyses with few releases ($n < 100$) or of short duration ($t < 20$), may fail to accurately estimate the underlying process correlation among demographic components (Figure 3), even when appropriate priors are used. These approaches have important utility for examining relationships between survival and harvest. Further, they allow researchers to examine life-history trade-offs among demographic components at both the population and individual level. Quantitative ecologists can use similar approaches to examine individual covariation in life-history traits, such as survival and breeding probability (Cam et al., 2002), trade-offs between current and future reproductive allocation (Leach et al., 2019), or correlations among demographic parameters and abundance or environmental conditions.

4.2 | Implications for black brent populations

The estimated variance of adult survival rates was significantly less than the variance of juvenile survival rates (Figure 5). This is consistent with the demographic buffering hypothesis, where we would expect population growth rates of long-lived organisms to be most sensitive to adult survival (Gaillard et al., 2000; Pfister, 1998).

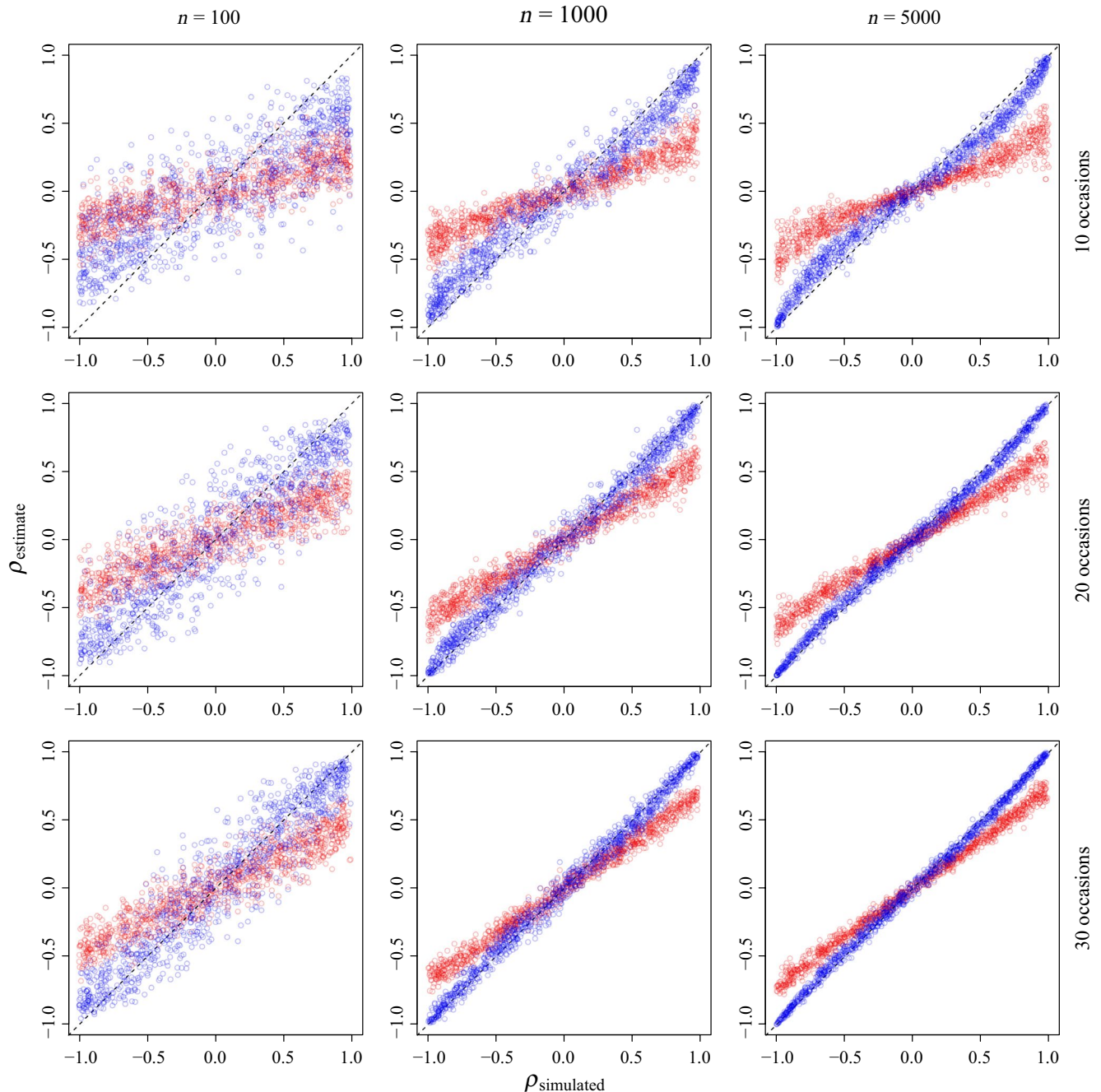


FIGURE 3 Means of the posterior distributions for process correlations (ρ) among adult (ϕ_{ad}) and juvenile (ϕ_{juv}) survival estimated from simulated capture–mark–recapture data using inverse Wishart (red) and hyperprior (blue) parameterizations for the covariance matrix of the multivariate normal distribution from which the parameters were estimated for different combinations of releases ($n = 100, 1,000, \text{ or } 5,000$) and occasions ($t = 10, 20, \text{ or } 30$). The dashed line represents 1:1 congruence between the simulated data and the estimate

Therefore, adult survival should be the most consistent demographic component and be buffered from environmental variation or reproductive allocation (Gaillard et al., 2000; Pfister, 1998). As predicted, and indicated by previous research (Leach et al., 2017), we observed positive correlations between adult and juvenile survival. Brent family groups remain together from hatch through late spring (Sedinger, Nicolai, Lensink, Wentworth, & Conant, 2007), where we would expect environmental variation which impacts adult survival

to affect juvenile survival as well, despite strong carry-over effects of environmental conditions during growth on first-year survival, and lifetime fitness, of juvenile brent (Riecke et al., 2018; Sedinger et al., 1995, 2007). Long-term declines in both adult (Leach et al., 2017; Riecke et al., 2018) and juvenile survival (Leach et al., 2017) have critical implications for brent populations, which are also experiencing declines in fecundity (Ward, Amundson, Stehn, & Dau, 2018) and population size (Sedinger, Riecke, Leach, & Ward, 2019).

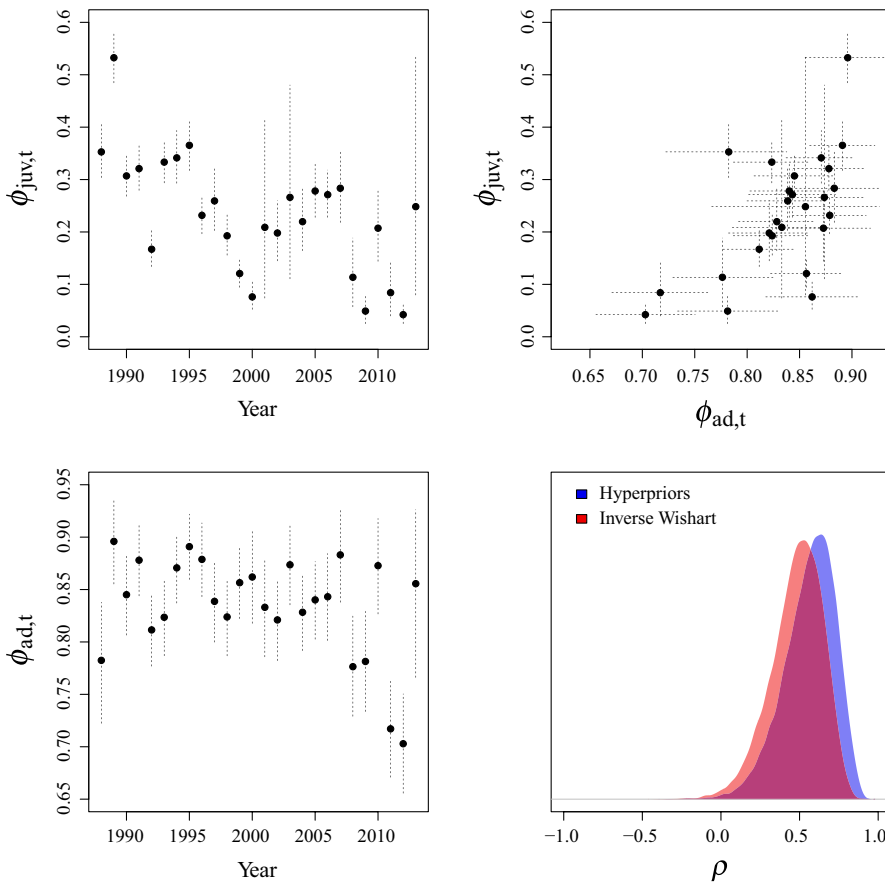


FIGURE 4 Means and 95% Bayesian credible intervals of adult (top left) and juvenile (bottom left) survival for black brent (*Branta bernicla nigricans*) marked on the Yukon–Kuskokwim River Delta, Alaska, 1988–2014. Further, we plot the correlation between these two parameters (top right), and the posterior distributions of the correlation (ρ) between these parameters from models using either an inverse Wishart prior (red), or hyperpriors (blue) for the covariance matrix components (bottom right)

4.3 | Implications for future research

We examine the behavior of multivariate normal distributions for demographic parameters in the presence of parameter uncertainty for a variety of biologically plausible scenarios. We suggest that investigators simulate data and conduct power analyses prior to drawing inference from their data. We provide simple R script to perform these analyses, where short-term (<10 years) datasets with small sample sizes (<100 releases per year) generally yield inaccurate

estimates of process correlations when using capture–mark–recapture or capture–mark–recovery data. Our work has important implications for previous (Péron, 2013; Servanty et al., 2010) and future research, and our parameterizations can be expanded to covariance matrices of $K \times K$ dimensions (Alvarez et al., 2014). Thus, our preliminary analyses highlight the power and importance of robust longitudinal datasets and the importance of model parameterization. Additionally, our simulations do not induce variation or heterogeneity in detection probability (p), where variation in these probabilities

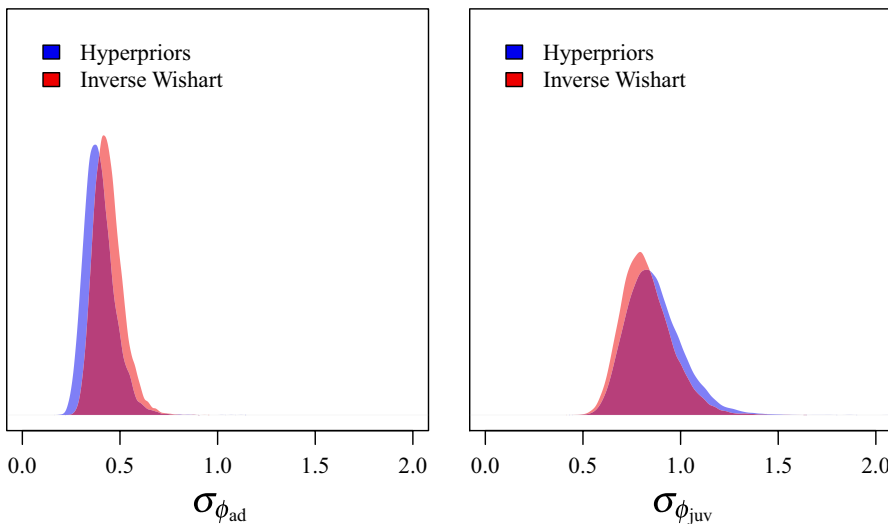


FIGURE 5 Density plots of the posterior distributions of variances (σ^2) of adult (left) and juvenile (right) survival for black brent (*Branta bernicla nigricans*) marked on the Yukon–Kuskokwim River Delta, Alaska, 1988–2014 from models with inverse Wishart priors on the covariance matrix (red), as well as models with hyperpriors on the individual components of the covariance matrix (blue)

can affect the absolute bias and precision of estimates of ρ (e.g., increased detection probabilities or recovery and reporting rates lead to increased precision and accuracy in the estimation of ρ).

These approaches have great utility for the future development of integrated population and capture-mark-recapture-recovery models, where quantitative ecologists can draw demographic parameters of interest from multivariate normal distributions within integrated population or capture-mark-recapture models to share information among demographic parameters. Finally, recent research (Alvarez et al., 2014) has revealed that the scaled inverse Wishart distribution (O'Malley & Zaslavsky, 2008) and hierarchical half-t prior distribution proposed by Huang and Wand (2013) are less informative than the inverse Wishart, although they experience similar issues, albeit at a lesser scale (Alvarez et al., 2014). We do not believe we have completely resolved this issue, and recent advances in Bayesian methods (Gelman, Lee, & Guo, 2015) may further our understanding. Finally, our simulations indicate that specifying hyperpriors for the components of a covariance matrix is significantly more effective than using the inverse Wishart distribution, or other recently developed approaches (Huang & Wand, 2013; O'Malley & Zaslavsky, 2008) for capture-mark-recapture and other demographic analyses, as the hyperprior approach leads to accurate estimates of process correlations and variances given sufficient sample sizes. These results have important implications for a variety of multivariate models in ecology.

ACKNOWLEDGMENTS

The authors thank the 200+ technicians, volunteers, and graduate students who collected data at the Tutakoke River Brent Colony during this study. TVR was supported by the Bonnycastle Fellowship in Wetland and Waterfowl Biology from the Institute for Wetland and Waterfowl Research, Ducks Unlimited Canada, the Dennis Raveling Scholarship from the California Waterfowl Association, and Delta Waterfowl. BSS was supported by Delta Waterfowl. Brent data collection efforts were supported by the Alaska Science Center, U. S. Geological Survey, Migratory Bird Management Region 7, U. S. Fish and Wildlife Service, Ducks Unlimited, the Morro Bay Brant Group, Phil Jebbia (in memory of Marnie Shepherd), and The National Science Foundation (OPP 9214970, DEB 9815383, OPP 9985931, OPP 0196406, DEB 0743152, and DEB 1252656). We would also like to thank two anonymous reviewers for providing positive contributions to the manuscript, as well as Martyn Plummer for developing the "dmnorm.vcov()" function in JAGS.

CONFLICT OF INTEREST

None declared.

AUTHOR CONTRIBUTIONS

J.S.S. conceived the capture-mark-resight-recapture study and has led data collection efforts through the course of the project. T.V.R., J.S.S., B.S.S., and A.G.L. collected data. T.V.R. and B.S.S. identified issues with existing parameterizations of these model types, with important contributions from all authors. T.V.R. designed the

simulation experiment, with important contributions from P.J.W., T.V.R., and J.S.S. led the writing of the manuscript. All authors contributed critically to manuscript revisions and gave final approval for publication.

ORCID

Thomas V. Riecke  <https://orcid.org/0000-0001-7998-5233>

Benjamin S. Sedinger  <https://orcid.org/0000-0002-1070-6109>

DATA AVAILABILITY STATEMENT

R script for simulating capture-mark-recapture data and analyzing the data in JAGS, and RDATA and R script for analyzing the Brent capture-mark-resight-recapture data, are archived at the Dryad Digital Repository (<https://doi.org/10.5061/dryad.dbrv15dws>) <https://datadryad.org/stash/share/jA19ZtMLZpLmIPIJDAGKfjJSVvALvfJQWlqWnlFH0E>.

REFERENCES

- Alvarez, I., Niemi, J., & Simpson, M. (2014). Bayesian inference for a covariance matrix. arXiv preprint. *arXiv*, 14084050.
- Anderson, D. R., & Burnham, K. P. (1976). *Population ecology of the mallard: VI. The effect of exploitation on survival*. Fish and Wildlife Service, Resource Publication No. 128. Washington, DC: Fish and Wildlife Service, US Department of the Interior.
- Arnold, T. W., Afton, A. D., Anteau, M. J., Koons, D. N., & Nicolai, C. A. (2016). Temporal variation in survival and recovery rates of lesser scaup. *The Journal of Wildlife Management*, 80, 850–861. <https://doi.org/10.1002/jwmg.21074>
- Arnold, T. W., Afton, A. D., Anteau, M. J., Koons, D. N., & Nicolai, C. A. (2017). Temporal variation in survival and recovery rates of lesser scaup: A response. *The Journal of Wildlife Management*, 81, 1142–1148. <https://doi.org/10.1002/jwmg.21315>
- Barnard, J., McCulloch, R., & Meng, X. L. (2000). Modeling covariance matrices in terms of standard deviations and correlations, with application to shrinkage. *Statistica Sinica*, 10(2000), 1281–1311.
- Bartzen, B., & Dufour, K. (2017). Northern pintail (*Anas acuta*) survival, recovery, and harvest rates derived from 55 years of banding in Prairie Canada, 1960–2014. *Avian Conservation and Ecology*, 12(2), 7.
- Brownie, C., & Pollock, K. H. (1985). Analysis of multiple capture-recapture data using band-recovery methods. *Biometrics*, 41, 411–420. <https://doi.org/10.2307/2530866>
- Cam, E., Aubry, L. M., & Authier, M. (2016). The conundrum of heterogeneities in life history studies. *Trends in Ecology, Evolution*, 31, 872–886. <https://doi.org/10.1016/j.tree.2016.08.002>
- Cam, E., Link, W. A., Cooch, E. G., Monnat, J. Y., & Danchin, E. (2002). Individual covariation in life-history traits: Seeing the trees despite the forest. *The American Naturalist*, 159, 96–105. <https://doi.org/10.1086/324126>
- Cormack, R. (1964). Estimates of survival from the sighting of marked animals. *Biometrika*, 51, 429–438. <https://doi.org/10.1093/biomet/51.3-4.429>
- Gaillard, J. M., Festa-Bianchet, M., Yoccoz, N., Loison, A., & Toigo, C. (2000). Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics*, 31, 367–393. <https://doi.org/10.1146/annurev.ecolsys.31.1.367>
- Gelfand, A. E., Diggle, P., Guttorp, P., & Fuentes, M. (2010). *Handbook of spatial statistics*. Boca Raton, FL: CRC Press.
- Gelman, A., Lee, D., & Guo, J. (2015). Stan: A probabilistic programming language for bayesian inference and optimization. *Journal of Educational and Behavioral Statistics*, 40, 530–543. <https://doi.org/10.3102/1076998615606113>

- Gimenez, O., Cam, E., & Gaillard, J. M. (2018). Individual heterogeneity and capture-recapture models: What, why and how? *Oikos*, 127, 664–686. <https://doi.org/10.1111/oik.04532>
- Haff, L. (1979). An identity for the wishart distribution with applications. *Journal of Multivariate Analysis*, 9, 531–544. [https://doi.org/10.1016/0047-259X\(79\)90056-3](https://doi.org/10.1016/0047-259X(79)90056-3)
- Huang, A., & Wand, M. P. (2013). Simple marginally noninformative prior distributions for covariance matrices. *Bayesian Analysis*, 8, 439–452. <https://doi.org/10.1214/13-BA815>
- Jolly, G. M. (1965). Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika*, 52, 225–247. <https://doi.org/10.1093/biomet/52.1-2.225>
- Kellner, K. (2016). *jagsUI: A wrapper around 'rjags' to streamline 'JAGS' analyses (Version 1.4.4)*. Retrieved from <https://cran.r-project.org/web/packages/jagsUI/index.html>
- Kendall, W. L., Barker, R. J., White, G. C., Lindberg, M. S., Langtimm, C. A., & Peñaloza, C. L. (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. <https://doi.org/10.1111/2041-210X.12077>
- Kendall, W. L., Nichols, J. D., & Hines, J. E. (1997). Estimating temporary emigration using capture-recapture data with pollock's robust design. *Ecology*, 78, 563–578.
- Kéry, M., & Schaub, M. (2012). *Bayesian population analysis using WinBUGS: A hierarchical perspective*. Waltham, MA: Academic Press.
- Kindsvater, H. K., Dulvy, N. K., Horswill, C., Juan-Jordá, M. J., Mangel, M., & Matthiopoulos, J. (2018). Overcoming the data crisis in biodiversity conservation. *Trends in Ecology, Evolution*, 33(9), 676–688. <https://doi.org/10.1016/j.tree.2018.06.004>
- Koons, D. N., Arnold, T. W., & Schaub, M. (2017). Understanding the demographic drivers of realized population growth rates. *Ecological Applications*, 27, 2102–2115. <https://doi.org/10.1002/eap.1594>
- Leach, A. G., Sedinger, J. S., Riecke, T. V., Van Dellen, A. W., Ward, D. H., & Boyd, W. S. (2019). Brood size affects future reproduction in a long-lived bird with precocial young. *The American Naturalist*, 193, 458–471. <https://doi.org/10.1086/701783>
- Leach, A. G., Ward, D. H., Sedinger, J. S., Lindberg, M. S., Boyd, W. S., Hupp, J. W., & Ritchie, R. J. (2017). Declining survival of black Brant from subarctic and arctic breeding areas. *The Journal of Wildlife Management*, 81, 1210–1218. <https://doi.org/10.1002/jwmg.21284>
- Lindberg, M. S., Boomer, G. S., Schmutz, J. A., & Walker, J. A. (2017). A comment on “temporal variation in survival and recovery rates of lesser scaup”. *The Journal of Wildlife Management*, 81, 1138–1141. <https://doi.org/10.1002/jwmg.21250>
- Lindberg, M. S., Sedinger, J. S., & Lebreton, J. D. (2013). Individual heterogeneity in black Brant survival and recruitment with implications for harvest dynamics. *Ecology and Evolution*, 3, 4045–4056. <https://doi.org/10.1002/ece3.767>
- Link, W. A., & Barker, R. J. (2005). Modeling association among demographic parameters in analysis of open population capture-recapture data. *Biometrics*, 61, 46–54. <https://doi.org/10.1111/j.0006-341X.2005.030906.x>
- Link, W. A., Cam, E., Nichols, J. D., & Cooch, E. G. (2002). Of bugs and birds: Markov chain Monte Carlo for hierarchical modeling in wildlife research. *The Journal of Wildlife Management*, 66(2), 277–291. <https://doi.org/10.2307/3803160>
- Nichols, J. D., & Hines, J. E. (1983). The relationship between harvest and survival rates of mallards: A straightforward approach with partitioned data sets. *The Journal of Wildlife Management*, 47, 334–348. <https://doi.org/10.2307/3808506>
- Nichols, J. D., Runge, M. C., Johnson, F. A., & Williams, B. K. (2007). Adaptive harvest management of North American waterfowl populations: A brief history and future prospects. *Journal of Ornithology*, 148, 343–349. <https://doi.org/10.1007/s10336-007-0256-8>
- Nicolai, C. A., & Sedinger, J. S. (2012). Are there trade-offs between pre- and post-fledging survival in black Brant geese? *Journal of Animal Ecology*, 81, 788–797. <https://doi.org/10.1111/j.1365-2656.2012.01952.x>
- O'Malley, A. J., & Zaslavsky, A. M. (2008). Domain-level covariance analysis for multilevel survey data with structured nonresponse. *Journal of the American Statistical Association*, 103, 1405–1418. <https://doi.org/10.1198/016214508000000724>
- Péron, G. (2013). Compensation and additivity of anthropogenic mortality: Life-history effects and review of methods. *Journal of Animal Ecology*, 82, 408–417. <https://doi.org/10.1111/1365-2656.12014>
- Pfister, C. A. (1998). Patterns of variance in stage-structured populations: Evolutionary predictions and ecological implications. *Proceedings of the National Academy of Sciences of the United States of America*, 95, 213–218. <https://doi.org/10.1073/pnas.95.1.213>
- Plummer, M. (2003). *JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling*. Proceedings of the 3rd international workshop on distributed statistical computing, p. 125. Wien, Austria: Technische Universität Wien.
- R Core Team (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Riecke, T. V., Leach, A. G., Gibson, D., & Sedinger, J. S. (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. <https://doi.org/10.1111/2041-210X.13065>
- Runge, M. C., Johnson, F. A., Dubovsky, J. A., Kendall, W. L., Lawrence, J., & Gammonley, J. (2002). *A revised protocol for the adaptive harvest management of mid-continent mallards* (28 pp). Washington, DC: Fish and Wildlife Service, US Dept Interior. Retrieved from <http://migratorybirds.fws.gov/reports/ahm02/MCMrevise2002.pdf>
- Schaub, M., & Fletcher, D. (2015). Estimating immigration using a Bayesian integrated population model: choice of parametrization and priors. *Environmental and Ecological Statistics*, 25, 535–549.
- Schaub, M., Jakober, H., & Stauber, W. (2013). Strong contribution of immigration to local population regulation: Evidence from a migratory passerine. *Ecology*, 94, 1828–1838. <https://doi.org/10.1890/12-1395.1>
- Seber, G. A. (1965). A note on the multiple-recapture census. *Biometrika*, 52, 249–259. <https://doi.org/10.1093/biomet/52.1-2.249>
- Sedinger, J. S., Flint, P. L., & Lindberg, M. S. (1995). Environmental influence on life-history traits: Growth, survival, and fecundity in black Brant (*Branta bernicla*). *Ecology*, 76, 2404–2414. <https://doi.org/10.2307/2265816>
- Sedinger, J. S., Herzog, M. P., & Ward, D. H. (2004). Early environment and recruitment of black Brant (*Branta bernicla nigricans*) into the breeding population. *The Auk*, 121, 68–73. [https://doi.org/10.1642/0004-8038\(2004\)121\[0068:EEAROB\]2.0.CO;2](https://doi.org/10.1642/0004-8038(2004)121[0068:EEAROB]2.0.CO;2)
- Sedinger, J. S., Lindberg, M. S., Rexstad, E. A., Chelgren, N. D., & Ward, D. H. (1997). Testing for handling bias in survival estimation for black brant. *Journal of Wildlife Management*, 61, 782–791.
- Sedinger, J. S., Nicolai, C. A., Lensink, C. J., Wentworth, C., & Conant, B. (2007). Black Brant harvest, density dependence, and survival: A record of population dynamics. *The Journal of Wildlife Management*, 71, 496–506. <https://doi.org/10.2193/2005-768>
- Sedinger, J. S., Riecke, T. V., Leach, A. G., & Ward, D. H. (2019). The black Brant population is declining based on mark recapture. *The Journal of Wildlife Management*, 83, 627–637. <https://doi.org/10.1002/jwmg.21620>
- Sedinger, J. S., White, G. C., Espinosa, S., Partee, E. T., & Braun, C. E. (2010). Assessing compensatory versus additive harvest mortality: An example using greater sage-grouse. *The Journal of Wildlife Management*, 74, 326–332. <https://doi.org/10.2193/2009-071>
- Servanty, S., Choquet, R., Baubet, É., Brandt, S., Gaillard, J.-M., Schaub, M., ... Gimenez, O. (2010). Assessing whether mortality is additive using marked animals: A bayesian state-space modeling approach. *Ecology*, 91, 1916–1923. <https://doi.org/10.1890/09-1931.1>

- Servanty, S., Gaillard, J. M., Ronchi, F., Focardi, S., Baubet, É., & Gimenez, O. (2011). Influence of harvesting pressure on demographic tactics: Implications for wildlife management. *Journal of Applied Ecology*, *48*, 835–843. <https://doi.org/10.1111/j.1365-2664.2011.02017.x>
- Stearns, S. C. (1992). *The evolution of life histories*. London, UK: Oxford University Press.
- Ward, D. H., Amundson, C. L., Stehn, R. A., & Dau, C. P. (2018). Long-term trends in fall age ratios of black Brant. *The Journal of Wildlife Management*, *82*, 362–373. <https://doi.org/10.1002/jwmg.21388>
- Williams, B. K., & Johnson, F. A. (1995). Adaptive management and the regulation of waterfowl harvests. *Wildlife Society Bulletin*, *1973-2006*(23), 430–436.
- Wishart, J. (1928). The generalised product moment distribution in samples from a normal multivariate population. *Biometrika*, *20A*, 32–52. <https://doi.org/10.1093/biomet/20A.1-2.32>

How to cite this article: Riecke TV, Sedinger BS, Williams PJ, Leach AG, Sedinger JS. Estimating correlations among demographic parameters in population models. *Ecol Evol*. 2019;9:13521–13531. <https://doi.org/10.1002/ece3.5809>