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McGowan, Conor P.; Runge, Michael C.; and Larson, Michael A., "Incorporating parametric uncertainty into population viability analysis models" (2011). *USGS Staff -- Published Research*. 554.

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Incorporating parametric uncertainty into population viability analysis models

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ARTICLE INFO

Article history:

Received 18 May 2010

Received in revised form 23 December 2010

Accepted 10 January 2011

Available online 11 February 2011

Keywords:

Charadriusmelodus

Endangered species

Piping plover

Population modeling

Population viability analysis

Parametric uncertainty

Structured decision making

ABSTRACT

Uncertainty in parameter estimates from sampling variation or expert judgment can introduce substantial uncertainty into ecological predictions based on those estimates. However, in standard population viability analyses, one of the most widely used tools for managing plant, fish and wildlife populations, parametric uncertainty is often ignored in or discarded from model projections. We present a method for explicitly incorporating this source of uncertainty into population models to fully account for risk in management and decision contexts. Our method involves a two-step simulation process where parametric uncertainty is incorporated into the replication loop of the model and temporal variance is incorporated into the loop for time steps in the model. Using the piping plover, a federally threatened shorebird in the USA and Canada, as an example, we compare abundance projections and extinction probabilities from simulations that exclude and include parametric uncertainty. Although final abundance was very low for all sets of simulations, estimated extinction risk was much greater for the simulation that incorporated parametric uncertainty in the replication loop. Decisions about species conservation (e.g., listing, delisting, and jeopardy) might differ greatly depending on the treatment of parametric uncertainty in population models.

Published by Elsevier Ltd.

1. Introduction

Wildlife and fisheries management decisions are best made with a complete understanding of and accounting for all relevant uncertainties in the system of interest (Gregory and Keeney, 2002; Berkson et al., 2002; Williams et al., 2007). Uncertainty about system function affects predictions about how the system will respond to management actions. Failure to account for the effects of uncertainty on predictions of the effects of management actions can lead to a misunderstanding of the pertinent risks and could lead to poor decision making. Structured decision making, an emerging application of decision analysis in the ecological and environmental management fields, calls for explicit inclusion of uncertainty into decision problems to enhance decision making and subsequent learning about the managed system (Gregory and Keeney, 2002; Hammond et al., 2002; Martin et al., 2009). Models of population or ecosystem dynamics are often used to inform decisions about wildlife or environmental management because they make predictions based on data and assumptions that can be examined; that is, they are explicit (Morris and Doak,

2002; Akçakaya et al., 2004). Models are often used in endangered species management and decision making, where listing, delisting and other decisions are framed in terms of extinction probability (Mace and Lande, 1991; Goldwasser et al., 2000; Goodman, 2002a). As Goldwasser et al. (2000) note, extinction probability is essentially an expression of uncertainty regarding population abundance predictions. Explicit system models enable managers to fully incorporate uncertainty into predictions about the system of interest (Beissinger and McCullough, 2002; Possingham et al., 2002), thus accounting for uncertainty in model-based decision making.

Uncertainty in the results of population projections originates from several sources, including structural uncertainty, temporal variance, demographic stochasticity, and parametric uncertainty (Goodman, 2002a,b; Williams et al., 2002). Structural uncertainty arises from competing hypotheses about system dynamics (e.g., inclusion or exclusion of density dependence) that can be incorporated into a decision analysis as competing models (Nichols et al., 2007). Stochastic (or aleatory) variation is irreducible variance in the system, and comes in two forms. Temporal variance (also called environmental stochasticity or process variance) is the variation in the demographic parameters over time caused by uncontrollable fluctuations in the environment. Demographic stochasticity is the temporal change in the system state that is caused by chance fluctuations in the demographic make-up of the population of interest (Morris and Doak, 2002; Lande et al.,

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2003). Extensive research has been published on incorporating both types of stochastic variation into population models for wild-life management (Caswell, 2001; Morris and Doak, 2002; Lande et al., 2003).

Parametric uncertainty—uncertainty in the estimates of model parameters—arises from a number of sources (Goodman, 2002a; Williams et al., 2002; Calder et al., 2003). In an empirical setting, parametric uncertainty can arise from limitations in the data due to sampling variation, observer bias, and sampling error. In settings where parameter estimation is not based directly on empirical observation, parametric uncertainty can arise from errors in expert judgment. Parametric uncertainty can, in principle, be reduced through data collection, but the effects of parametric uncertainty on projections in wildlife population models are often ignored, especially in matrix population models and viability analyses (Goodman, 2002a,b; Calder et al., 2003). Ignoring or excluding parametric uncertainty from these types of models can greatly affect model prediction, model-based decision making, and risk assessment.

Some scientists have utilized Bayes Nets (sometimes called Bayesian Belief Networks) to evaluate the effects of structural and parametric uncertainty on inferences from models (Calder et al., 2003; Uusitalo, 2007; Biggs et al., 2009); often these uncertainties are estimated through expert elicitation, at least initially. A main strength of these models is the ability to examine uncertainty and how it propagates through the system of interest. However, temporal dynamics are often not incorporated into Bayes Nets because it is fairly cumbersome to implement in existing software (Calder et al., 2003; Uusitalo, 2007). Matrix projection models, or algebraic projection models, are useful tools for evaluating temporal dynamics (Caswell, 2001; Morris and Doak, 2002). There has been extensive research and theoretical development for incorporating the effects of demographic stochasticity and temporal variance into model predictions (e.g., Lande et al., 2003) and these approaches have been widely used in population modeling (Morris and Doak, 2002). Methods to address parametric uncertainty effects on model predictions in matrix models have not been widely adopted. In population viability analysis models to assess the conservation status and needs of rare or endangered species, parametric uncertainty is rarely addressed (e.g., Carrete et al., 2009; Peery and Henery, 2010; Grivet, 2010; Wittmer et al., 2010). Popular population viability modeling tools, such as VORTEX (Lacy et al., 1995), do not provide the capacity for inputting parametric uncertainty into model projections.

Several scientists have developed statistical methods for decomposing empirical parametric variance estimates into temporal variance and sampling variance (Link and Nichols, 1994; Gould and Nichols, 1998; White, 2000; Morris and Doak, 2002). Temporal variance is the expected variation in a parameter over time due to issues like environmental variability, and sampling variance represents lack of perfect knowledge about true parameter values due to population sampling (Williams et al., 2002). Gould and Nichols (1998), White (2000) and Morris and Doak (2002) emphasized the importance of decomposing variance estimates because of the effects that parametric uncertainty might have on projecting population growth. However, other than White (2000), they did not make any recommendations for incorporating parametric uncertainty into a simulation model. Although there has been extensive research done into partitioning sources of variance (Link and Nichols, 1994; Gould and Nichols, 1998; White, 2000), and some theoretical advances for incorporating parametric uncertainty in population modeling (White, 2000; Goldwasser et al., 2000; Goodman, 2002b; Calder et al., 2003), few population viability analyses account for parametric uncertainty in simulation models (e.g., Larson et al., 2002; Zabel et al., 2006; Millspaugh et al., 2008; Martin et al., 2008; Carrete et al., 2009; Peery and Henery,

2010; Grivet, 2010; Wittmer et al., 2010). Some scientists have recommended discarding the sampling variance component of parameter estimates in population viability analyses (Brook, 2000), thus ignoring the effects of parametric uncertainty on simulation model predictions. Goldwasser et al. (2002) and Goodman (2002b) present methods for addressing parametric uncertainty in population models. Goldwasser et al. (2002) explore the effects of parametric uncertainty on extinction risk assessments for a population of spotted owls (*Strix occidentalis*) by uniformly lowering or raising demographic parameter point estimates by one standard error, and showed great differences in extinction probability across scenarios. Calder et al. (2003) demonstrated that incorporating parametric uncertainty improved inferences from Bayesian statistical models fit to time series of population census data. Given the findings of these studies, especially with respect to population risk assessment, it is important for models intended to inform management decision making to incorporate parametric uncertainty and to develop methods for doing so.

This paper describes in detail a hierarchical process for incorporating parametric uncertainty in simulation models typically used in population viability analyses. The model we present (i.e., the discrete-time aspects, the sampling distributions) is an example of commonly used approaches with modifications to incorporate parametric uncertainty; different species and contexts may require alternative approaches. First, we describe the process for modeling life-history parameters for stage- or age-based matrix population models that project a population into the future. Second, we compare the uncertainty in model predictions when parametric uncertainty is or is not incorporated into the model, using a model developed to assess the population viability of piping plovers (*Charadrius melodus*) in the Great Plains (Ryan et al., 1993). The approach presented here should be used in any population simulation effort that endeavors to fully account for uncertainty in model predictions and could be particularly important for population viability analysis in endangered species management and decision making.

2. Modeling theory

2.1. Incorporating parametric uncertainty in population models

Discrete-time, stochastic simulation models of population dynamics often contain three important loops: an outer loop (the replication loop) that replicates the temporal simulation a specified number of times, restarting the simulation at time (t) = 0 for each replicate; a middle loop (the time-step loop) that simulates the dynamics of the system over a specified period of time, using discrete-time intervals appropriate to the life-history of the organism, within each replicate; and an inner loop (the individual loop) that simulates the fates of individual organisms within a particular time step and replicate. Each loop inherits state variables and parameter values from the loop outside it.

Demographic stochasticity can be modeled in an individual loop. It inherits the size of each population class and the life-history parameters from the time-step loop, and samples from the appropriate probability distribution to determine the fate (survival or death, success in reproduction, etc.) of the individuals. Temporal variance is modeled in the time-step loop. It inherits the size of each population class from the results of the previous time step, and the parameters that govern temporal variance from the replication loop.

Parametric uncertainty should be included in the replication loop of a population simulation model (White, 2000). Stochastic population models typically replicate the simulated population many thousands or millions of times to produce frequency-based

probability distributions that characterize the uncertainty in resulting population metrics such as growth rate, abundance, and extinction probability (Caswell, 2001; Morris and Doak, 2002). At the beginning of each replicate of the simulated population, the model should first sample a random value for each parameter from the probability distribution that represents parametric uncertainty (Appendix A).

As an example, consider the various types of uncertainty associated with survival of individual animals that should be incorporated in a simulation model (ignoring age or sex classes and temporal correlations for simplicity). At the beginning of year t in replicate i , there are $N_{i,t}$ animals alive, and the annual survival rate is $S_{i,t}$. The individual loop samples the Bernoulli fate of each individual in $N_{i,t}$ which is one approach to modeling demographic variability in a population. Thus, the number of animals that survive to the next year in a discrete-time step model, a commonly used approach in population viability analyses (Morris and Doak 2002; Akçakaya et al., 2004), might take a binomial distribution,

$$N_{i,t+1} \sim \text{binomial}(N_{i,t}, S_{i,t}). \quad (1)$$

The annual survival rate needs to vary to reflect temporal variance. A beta distribution is often used to model temporal variation in a survival rate because the distribution is bounded between zero and one and because the shape of the distribution can be modified to meet the specific needs of the problem at hand (Caswell, 2001; Morris and Doak, 2002) (For fecundity parameters, quantitative ecologists often use log-normal distributions or stretched-beta distributions; Morris and Doak, 2002.). Thus, for year t in replicate i , the survival rate $S_{i,t}$ could be sampled from a beta distribution that captures the temporal variance, σ_i , around a mean survival rate, μ_i ,

$$S_{i,t} \sim \text{beta}(\alpha_i, \beta_i) \quad (2)$$

where α_i and β_i are such that $\mu_i = \alpha_i / (\alpha_i + \beta_i)$ and $\sigma_i = \mu_i(1 - \mu_i) / (\alpha_i + \beta_i + 1)$. Temporal correlation of demographic parameters (i.e., $S_{i,t+1}$ is not independent of $S_{i,t}$) could be incorporated here when appropriate for the species and system being modeled.

Finally, parametric uncertainty appears in the replication loop (Appendix A) and represents the uncertainty in the underlying mean survival rate and temporal variance. At the beginning of replicate i , these two parameters are sampled from appropriate distributions given the species and system being modeled. As an example, the mean survival rate, μ_i , might be sampled from a beta distribution with parameters a and b (Morris and Doak 2002),

$$\mu_i \sim \text{beta}(a, b), \quad (3)$$

and the temporal variance, σ_i , might be sampled from an inverse Gaussian distribution with mean m and shape parameter λ (Royle and Dorazio 2008),

$$\sigma_i \sim \text{IG}(m, \lambda). \quad (4)$$

Thus, the mean survival rate and temporal variance are the same for all years within a replicate, but differ between replicates to represent the uncertainty about the underlying parameters that results from the fact that they were estimated. In the model of annual survival described above, there are only four parameters that need to be specified: a , b , m , and λ ; in hierarchical models, especially in Bayesian statistical settings, these are often referred to as hyper-parameters. Models for productivity or fecundity should use a similar hierarchy, but will likely use different probability distributions, such as a log-normal or stretched-beta distribution in place of the beta distribution (Morris and Doak, 2002; Appendix A), and a multinomial or Poisson distribution in place of the binomial (Fox and Kendall, 2002; Appendix A).

2.2. Estimating parametric uncertainty

The methods for estimating parametric uncertainty, specifically sampling variance, are well established. In a frequentist context, there are a number of published methods available for calculating and separating sampling variance and temporal variance for demographic parameters (Link and Nichols, 1994; Gould and Nichols, 1998; White, 2000). Recently, it has become more common to estimate the sampling distributions for demographic parameters and temporal variance using Bayesian methods (Calder et al., 2003; Biggs et al., 2009). Furthermore, expert elicitation, relying on experts in the field to estimate parameters when data are not available, is also growing in importance (Martin et al., 2005; Lele and Allen, 2006). Parametric uncertainty within and among experts can be used to create a distribution to be inserted into the replication loop of a population model.

Parametric covariance may also be an important consideration for population projection models predicting extinction risk (Morris and Doak, 2002). Uncertainty about the magnitude of parametric covariance could result in highly uncertain model predictions and therefore inadequate assessments of population risk and ill-informed management decision making. Empirical estimation of parametric covariance is challenging and likely requires many years of demographic data (Morris and Doak, 2002). We are not aware of methods to partition covariance into sampling variance and temporal co-variation, although it is quite possible they exist; we assume they would resemble the existing decomposition methods.

3. Example simulations

3.1. Piping plover population model

We used a piping plover population model developed by Ryan et al. (1993) to investigate the effects of different methods of incorporating parametric uncertainty on the results of simulation models. Piping plovers are small migratory shorebirds that range widely across North America, from Atlantic coast beaches through the Great Lakes and at rivers and alkali wetlands throughout the Northern Great Plains. They are listed as threatened under United States endangered species law and endangered in Canada. McGowan and Ryan (2009) extended this model to assess the effect of incidental take of piping plover eggs and chicks in the Missouri River on population viability in the Great Plains. Their model (McGowan and Ryan, 2009) included some parametric uncertainty as we have described here and the results showed high variation in model predictions.

For the purposes of this paper we used the basic Ryan et al. (1993) formulation of the Great Plains piping plover population model, but we added demographic stochasticity and parametric uncertainty (Appendix A). The model has two explicit loops, a replication loop and a time-step loop, with an implicit individual loop embedded in the time-step loop by using the binomial distribution for survival rates and the Poisson distribution for fecundity (Morris and Doak, 2002; Fox and Kendall, 2002; Appendix A). For each replicate i , the replication loop selects parameter values for mean adult survival (S_i^a ; where the superscript a indicates the adult age class) from a beta distribution with mean 0.737 and variance 0.00226 (the alpha and beta shape parameters are calculated using the method of moments, see Morris and Doak 2002) to represent parametric uncertainty in adult survival. To introduce parametric uncertainty in other parameter means it also selects mean juvenile survival (S_i^j ; where the superscript j indicates the juvenile age class) from a beta distribution with mean 0.48 and variance 0.00226 and mean fecundity (F_i) from a log-normal distribution

with mean 0.42 and variance 0.021. In the replication loop, the model also selected mean annual variation for each parameter from a normal distribution to allow for uncertainty in variance estimates. This process used the estimated temporal variance as the mean ($s_t^{ss} = 0.00198$ (adult survival temporal variance), $s_t^{sj} = 0.00198$ (juvenile survival temporal variance), $s_t^f = 0.21$ (fecundity temporal variance)) and values for sampling variance in those mean values based on a 5% coefficient of variation. The time-step loop inherited mean demographic parameter values and temporal variance values from the replication loop (subscript i), and used that inheritance to create probability distributions for selecting annual parameter values (subscript t) (Appendix A). For example, annual adult survival for replicate i in year t equaled:

$$S_{i,t}^a = \text{beta}(\alpha_i^{sa}, \beta_i^{sa}),$$

where

$$\alpha_i^{sa} = S_i^a \left(\left(\frac{S_i^a(1 - S_i^a)}{s_t^{ss}} \right) - 1 \right),$$

and

$$\beta_i^{sa} = (1 - S_i^a) \left(\left(\frac{S_i^a(1 - S_i^a)}{s_t^{ss}} \right) - 1 \right).$$

Those annual parameter values incorporate temporal variance; they were then passed into a projection equation that used binomial and Poisson distributions to account for demographic stochasticity. The projection equation for the model was as follows:

$$N_{i,t+1} = \left(\text{binomial}(N_{i,t}, S_{i,t}^a) + \text{binomial} \left(\sum (\text{Poisson}(N_{i,t}, F_{i,t})), S_{i,t}^j \right) \right), \quad (5)$$

where N was the female population size, t was the annual time step, $S_{i,t}^a$ was annual survival of breeding adult birds in replicate i and year t , $F_{i,t}$ was fecundity in replicate i in year t (average number of females fledged per breeding female), and $S_{i,t}^j$ was annual survival of hatch-year birds (juveniles) in replicate i and year t . This projection equation used a pre-breeding census. These steps closely followed the process described in Eqs. (1)–(4) above.

This was a female-only model, started with a population size of 2300 females, and incorporated ceiling-type density dependence with the maximum population size set at 8000 females. In the model, we used the adult survival values, sampling variance and temporal variance estimated by Larson et al. (2000). Juvenile survival was modeled following the method of Larson et al. (2002) and McGowan and Ryan (2009). All partitioned variance values in these parameters were calculated according to the methods described by White (2000) and the simulations include all non-process variation from those calculations into the model as parametric uncertainty and all process variance as temporal variance. We used fecundity values and associated variances that were appropriate for a shorebird species of this size, but not based on empirical data or specific published values (Evans and Pienkowski, 1984). We ran the simulation model with 10,000 replications for 50 years into the future. Any replicate population that declined to <1 individual was considered extinct and N_{t+1} for that replicate was set to zero to ensure that extinction was a permanent state.

We ran three sets of simulations, or scenarios. In one scenario (A) we separated and discarded parametric uncertainty and accounted for only the temporal variation for adult and hatch-year survival and annual fecundity in the annual loop using only Eqs. (1) and (2), an approach recommended by Brook (2000), Morris and Doak (2002) and widely used in current practice. In the second scenario (B) we did not decompose the estimated variance and included the total variance (e.g., for adult survival

$S_{i,t}^2 = 0.00226 + 0.00198 = 0.00424$; see values from above) in the annual loop, as if it were temporal variation using only Eqs. (1) and (2). Scenarios A and B did not have the hierarchical structure described above, but embedded all variability within the time-step loop. In the third scenario (C) we decomposed the total estimated variance into the sampling variance and temporal variance, and incorporated them in the model as described above using Eqs. (1)–(4). From these simulations, we compare extinction probabilities, median abundances, and the 2.5 and 97.5 percentiles of abundance over time.

3.2. Results

The median piping plover population declined under all three scenarios (Table 1; Fig. 1). The median trajectories did not differ across the three scenarios (Table 1; Fig. 1) with all three declining to approximately 20–30 individuals after 50 years. The primary differences across these scenarios were in the 2.5 and 97.5 percentiles (Table 1) and in the probability of extinction (Fig. 1). The scenario that separated and excluded parametric uncertainty (scenario A, Fig. 1A) and the scenario where both temporal variance and parametric uncertainty were lumped together as a single value in the annual loop (scenario B, Fig. 1B) predicted a near 0% chance that the population would go extinct within 50 years. The simulations that decomposed variance to include parametric uncertainty in the replication loop and temporal variance in the time-step loop (scenario C) predicted great variability in population trajectories and predicted a 0.22 probability of extinction within 50 years (Fig. 1C).

4. Discussion

The simulations of the Great Plains piping plover populations with differing variance structures were quite instructive regarding the consequences of failing to incorporate parametric uncertainty into population viability analyses. Approach A, with parametric uncertainty partitioned and excluded from the simulations, which was used by Larson et al. (2002, 2003), may greatly underestimate extinction risk for this population, a surprising and concerning result considering these are the most widely used approaches in population viability analyses (Brook, 2000; Morris and Doak, 2002). Scenario C, with parametric uncertainty explicitly incorporated into the replication loop, had replicates in which mean adult survival was as low as 0.60, and those replicates went extinct quickly, whereas other replicates had mean adult survival as high as 0.85, leading to rapid and sustained population growth for those replicates. We do not actually know the true mean values of the

Table 1

The median abundance (2.5th percentile–97.5th percentile) projections at 10, 20, 30, 40, and 50 years from three sets of simulations of piping plovers in the Great Plains of North America (initial population size = 2300).

| Year | No parametric uncertainty ^a | Combined variance ^b | Separated variance ^c |
|------|--|--------------------------------|---------------------------------|
| 10 | 976 (753–1291) | 955 (550–1619) | 1069 (216–5729) |
| 20 | 376 (246–571) | 356 (157–781) | 447 (17–7595) |
| 30 | 145 (81–249) | 133 (44–348) | 189 (1–7842) |
| 40 | 56 (23–110) | 49 (11–156) | 78 (0–7923) |
| 50 | 21 (5–51) | 18 (1–71) | 33 (0–7943) |

^a No parametric uncertainty = total variance was decomposed, and sampling variance was excluded from the model.

^b Combined variance = total variance (i.e., sampling and process variances) were included as a single value in the time-step loop of the model.

^c Separated variance = total variance was decomposed, and sampling variance and process variance were included in the model as parametric uncertainty and temporal variance, respectively.

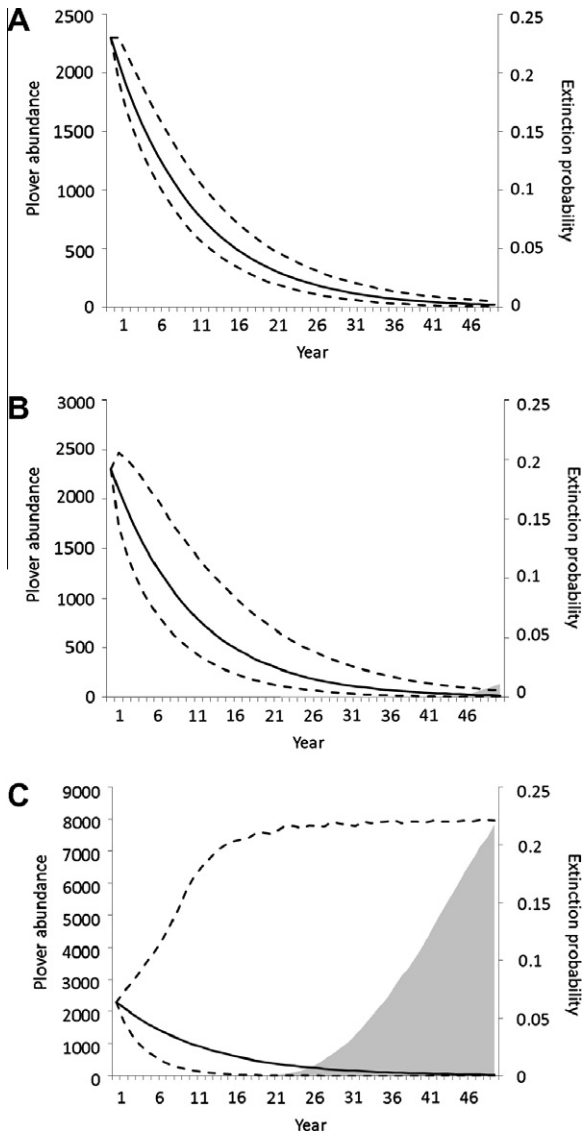


Fig. 1. Median Piping Plover abundance (solid line) with 2.5th and 97.5th percentiles (dashed lines; primary y-axis) and the projected probabilities of extinction (shaded area; secondary y-axis) from models that (A) decomposed total variance and excluded sampling variance from the population model, (B) did not decompose total variance and included all variance in the annual loop as process variance, and (C) decomposed total variance and included sampling variance in the replication loop of the population model.

annual demographic parameters in the model and sampling variance is a measure of our uncertainty in the parameters means. Incorporating this parametric uncertainty into the replication loop of the model, as we did, is one method for incorporating that parametric uncertainty into a simulation model. Scenario A restricts annual parameter estimates to a much smaller range of values. Approach C more accurately reflects the wide range of uncertainty and possible trajectories for the Piping Plover population. Under scenario C, some of the replicates went extinct due to low average annual survival or fecundity but some replicates fared quite well, reaching carrying capacity and remaining there, due to high average survival or fecundity. Incorporating this parametric uncertainty can account for recent unexpected large increases in abundance counts of Piping Plovers in the Great Plains from ~2300 individuals counted in 2001 to ~4600 in 2006 (Plissner and Haig, 2000; USFWS, 2009).

Including all forms of uncertainty—structural uncertainty, temporal variance, demographic stochasticity and, as we have dis-

cussed here, parametric uncertainty—results in better model predictions for making management decisions. Species management decisions, based on model predictions, evaluate the probable outcome of some management action and the risks associated with those actions and outcomes, especially in endangered species management (Possingham et al., 2002). Extinction risk predictions from population viability analyses are essentially expressions of uncertainty about abundance predictions (Goldwasser et al., 2002). Therefore, failing to account for parametric uncertainty in population models likely alters risk assessments based on model predictions.

In a conservation or management context, we argue that it is most appropriate to include parametric uncertainty in the replication loop of a simulation model (Scenario C). We make this argument primarily on philosophical, not empirical, grounds. Parametric uncertainty is a form of epistemic uncertainty (Regan et al., 2002), and represents what we do not know about how the system in question works. The replicates performed in a simulation model are meant to represent trajectories the system might take. We do not know the true values for the mean and variance of survival, for example, but whatever those values are, we assume they do not change over time. So, it is appropriate then to fix those values for the course of one replicate, and let the many replicates capture the epistemic uncertainty.

There are also theoretical and empirical reasons for incorporating parametric uncertainty in the way we have shown. First, in the theory on products of random matrices (a projection model can be viewed as a product of random matrices), the effects of variance that is sampled for each matrix (i.e., temporal variance) are very different than the effects of variance that is sampled for an initial matrix that then remains fixed (Tuljapurkar, 1989). Second, in an optimization setting for management decision making (Possingham et al., 2002), including parametric uncertainty can have a large influence on the decision. Third, our results here showed dramatic differences in extinction risk predictions and demonstrated the stark consequences of the method of incorporating parametric uncertainty. Thus, we argue that of three treatments of uncertainty presented here, only the method embodied in scenario C offers a full account of uncertainty, and therefore risk, in the population projections. Even though scenario B incorporates more variation into the simulations, it still does a poor job of accounting for uncertainty compared to scenario C. Including all variation (parametric uncertainty as well as temporal variance) in the time-step loop of the model should not be considered a reasonable compromise. We believe that scenario B is not an appropriate approach for incorporating sampling variation into population simulation models because the initial matrix in the model is still fixed, albeit with larger annual variance than scenario A (Tuljapurkar, 1989).

Parametric uncertainty can arise from a number of sources, including true sampling variance, observer error, observer bias, and expert judgment, some of which are estimable and some of which are not. Our approach does not treat these different sources of parametric uncertainty differently, as they are all types of epistemic uncertainty that give rise to errors in estimates of the true, unknown value of the parameters. We are not aware of mathematical methods to separate these sources of parametric uncertainty. Link and Nichols (1994), Gould and Nichols (1998) and White (2000) present methodologies for partitioning temporal variance from total variance and we included all non-temporal variance in our simulations as parametric uncertainty. Bias, whether from sampling, observers, or experts, perhaps represents the most unique challenge. Known bias is presumably removed from, or corrected for, during parameter estimation. How should *unknown* bias be incorporated into simulation models? A difficult question in its very nature. We think the best way is the traditional way—sensitivity analysis, whereby the investigator asks how much the

results might change in the face of systematic bias in one or more parameters.

Goodman (2002b) noted that endangerment is often defined in terms of a species' or population's probability of extinction exceeding some threshold within some specified time. Decisions regarding listing, delisting, jeopardy, or even management strategies can be thought of in terms of 'What is this species' probability of extinction within some time frame?' and 'How does this action affect this species' probability of extinction within some time frame?' (Goodman, 2002b; Possingham et al., 2002). In the piping plover example in this paper, including parametric uncertainty in the simulations dramatically changed the estimated probability of extinction and thus would likely change considerations regarding listing, delisting, jeopardy or management actions. When models are used to inform management decisions, fully accounting for parametric uncertainty and including that uncertainty in the models can have substantial impacts on the results of the assessment. The issues relating to population management and decision making extend far beyond the endangered species example presented herein. Wildlife harvest regulation decisions would benefit greatly from a more thorough accounting of parametric uncertainty (Berkson et al., 2002). Risk assessment analyses with regard to the cost of overharvesting would likely underestimate risks if parametric uncertainty were excluded.

Granted, the magnitude of parametric uncertainty can lead to greater variability in model predictions. Parametric uncertainty, different from temporal variance, can be reduced with increased knowledge, whether that is through further field work, increased sample sizes in empirical datasets, or more thorough expert elicitation. Analysis of epistemic uncertainty can inform decision-makers about the value of further work to refine parameter estimates and reduce parametric uncertainty, specifically whether such reduction of epistemic uncertainty will improve decision making (Runge et al., 2011).

Parametric uncertainty makes us uncertain about model predictions of abundance, extinction probability, or whatever the model is meant to predict. Although uncertainty in model outcomes due to parametric uncertainty does not reflect biological processes, parametric uncertainty is an epistemological issue that should not be excluded from population models because our ignorance about a system needs to be as much a part of our decision making as our knowledge. Despite recent methodological advancements in the treatment of parametric uncertainty in population models (e.g., White, 2000; Calder et al., 2003), these methods are seldom employed in population viability analyses. As our simulations have

shown, the effects of excluding parametric uncertainty on model predictions can be consequential. Many of the available population modeling packages do not have the capability or flexibility to incorporate parametric uncertainty; if they are used, they should be used with caution.

Acknowledgments

This work was supported by the USGS Patuxent Wildlife Research Center and the Minnesota Department of Natural Resources. We thank M.R. Ryan, J.D. Nichols, M. Eaton, and J. Martin for reviewing earlier drafts of this manuscript. We also thank the editors and anonymous reviews for helping us to improve this manuscript.

Appendix A

Template population model for projecting population abundance in the face of parametric uncertainty, temporal variance, and demographic stochasticity. The population model incorporates parametric uncertainty into the iteration loop for all survival and fecundity parameters in the model, temporal variance into the annual loop of the model, and demographic stochasticity into the population dynamics equations. The code provided in this appendix is intended to provide an example and guidance on using the parametric uncertainty methodology; The R code presented below is available on the web: www.auburn.edu/~cpm0014/parametric-uncertainty.htm (accessed 26 January, 2011).

```
#####
# Sample R code to generate values of piping plover adult and
# juvenile survival
# from beta distributions, and fecundity from log-normal
# distributions, incorporating
# sampling, temporal, and demographic variance. The program
# executes some
# simple population dynamics using the generated survival and
# fecundity values.
# Parametric uncertainty is incorporated in the iteration loop of
# the simulation based on the
# method described in this paper. The code for this example
# simulation was written by
# Conor P. McGowan and Michael C. Runge.
#####
```

```
#Declare variables
it = 10000
yrs = 50
aSait = 62.5
bSait = 22.3

aSjit = 42.5
bSjit = 56.9

ilnFm = -0.80
ilnFsd = 0.3
SaVar<- matrix(0, it,1)
SaVarm = 0.00198
SaVars = 0.0001
SjVar<- matrix(0,it,1)
SjVarm= 0.00198
SjVars = 0.0001
Fsd<- matrix(0,it,1)
Fsdm = 0.21
```

```
# No. iterations in simulation.
# No. years in simulation.
# Alpha and beta shape parameters derived from
# estimated mean adult survival and
# estimated sampling variance (Larson et al., 2000).
# Alpha and beta shape parameters derived from estimated mean
#juvenile survival
#and estimated temporal variance (Larson et al., 2000).
# Shape parameters for the log-normal distribution for
# generating iteration-level fecundity values.
# Vector for adult survival variance values.
# Estimated temporal variance of adult survival
# (Larson et al., 2000).
# Vector for Juvenile survival variance values.
# Estimated temporal variance on juvenile
# survival (Larson et al., 2000).
# Vector for annual fecundity variance values.
# mean temporal variance for fecundity.
```

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```

FsdS = 0.01 # variance on mean variance
Sai<- matrix(0, it, 1) # Vector for the iteration-level adult Survival values
aSayr<- matrix(0, it, 1) # Vector for the iteration-level alpha shape
# parameter for each iteration for adult survival.
bSayr<- matrix(0, it, 1) # Vector for the iteration-level beta shape
# parameter for each iteration for adult survival.
Sji<- matrix(0, it, 1) # Vector for the iteration-level juvenile
# survival values
aSjyr<- matrix(0, it, 1) # Vector for the iteration-level alpha shape.
# parameter for each iteration for juvenile survival.
bSjyr<- matrix(0, it, 1) # Vector for the iteration-level beta shape.
# parameter for each iteration for juvenile survival.
Fi <- matrix(0, it, 1) # Vector for the iteration-level Fecundity
# values.
lnFm<- matrix(0, it, 1) # Vector for the iteration-level shape
# parameters for each iteration for fecundity.
lnFsd<- matrix(0, it, 1) # Vector for the iteration-level shape
# parameter for each iteration for fecundity.
Sa <- matrix(0, it, yrs) # Vector for the annual adult survival values
# for each year.
Sj<- matrix(0, it, yrs) # Vector for the annual juvenile survival
# values for each year.
F <- matrix(0, it, yrs) # Vector for the annual fecundity values for
# each year.
yy<-matrix(0,it,yrs) # Vector for young of the year produced.
yy[i,1]=500 # initial young of the year.
P <- matrix(0, it, yrs) # Vector for population size.
P[1:it,0] = 2300 # sets initial population size.
e <- matrix(0,it,yrs) # Vectors to track extinction.
ep<- matrix(0,1,yrs)

```

```

# initiates iteration loop
for(i in 1:it)
{
  # select adult survival value and variance for each iteration from a beta
  # distribution, replace with 0.737 to eliminate sampling variation
  Sai[i] <- rbeta(1, aSait, bSait)
  SaVar[i] <- rnorm(1,SaVarm, SaVars)
  ***Here we used a normal distribution because the rinvgauss function is not a
  # standard function in R, but must be installed in a separate package.
  # calculate alpha shape parameter for each iteration
  aSayr[i] = Sai[i]*((Sai[i]*(1-Sai[i])/SaVar[i])-1)
  # Calculate beta shape parameter for each iteration
  bSayr[i] = (1-Sai[i])*((Sai[i]*(1-Sai[i])/SaVar[i])-1)
  # select juvenile survival value for each iteration from a beta distribution, replace
  # with 0.45 to eliminate sampling variance
  Sji[i] <- rbeta(1, aSjit, bSjit)
  SjVar[i] <-rnorm(1, SjVarm, SjVars)
  # calculate alpha shape parameter for each iteration
  aSjyr[i] = Sji[i]*((Sji[i]*(1-Sji[i])/SjVar[i])-1)
  # Calculate beta shape parameter for each iteration
  bSjyr[i] = (1-Sji[i])*((Sji[i]*(1-Sji[i])/SjVar[i])-1)
  # select fecundity value for each iteration from a log-normal distribution, replace
  # with 0.42 to eliminate sampling variance
  Fi[i] <- rlnorm(1,ilnFm, ilnFsd)
  Fsd[i] <- rnorm(1, Fsdm, FsdS)
  # Calculate the log-normal shape parameters for the annual selection of fecundity values
  lnFsd[i] = log((Fsd[i]^2)/(Fi[i]^2) + 1)
  lnFm[i] = log(Fi[i])-1/2*lnFsd[i]

```

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```

# initiate annual loop
for(j in 1:(yrs))
{
  # select adult survival value for each year in each iteration from a beta distribution
  Sa[i,j] <- rbeta(1, aSayr[i], bSayr[i])
  # select juvenile survival value for each year in each iteration from a beta distribution
  Sj[i,j] <- rbeta(1, aSjyr[i], bSjyr[i])
  #selects annual fecundity value from a log-normal distribution
  F[i,j] <- rlnorm(1,lnFm[i],lnFsd[i])
  # Demographic Stochasticity for fecundity, Poisson distributed no. of female chicks produced per female
  yy[i,j-1]=sum(rpois(P[i,j-1],F[i,j-1]))
  ##### Combining Temporal variance and Demographic Stochasticity in Pop.
  # dynamics. Binomially distributed survival of adults (P[i,j-1]) with
  # probability Sa[i,j-1] plus the binomially distributed survival of young of
  # the year (yy[i,j-1]) with probability Sj[i,j-1]
  if (j == 1) P[i,j] = 2300
  else P[i,j] = (rbinom(1,P[i,j-1],Sa[i,j-1])) + (rbinom(1,yy[i,j-1],Sj[i,j-1]))
  # Set density-dependent population ceiling
  if (P[i,j] >= 8000) F[i,j] = 0.0
  # count the number of replicates that go extinct
  if (P[i,j] < 1) e[i,j]=1
} # Close the annual loop
} # Close the iteration loop

# Summarize simulation data and create plots of population trajectories
# Calculate the proportion of simulations that went extinct
se = apply(e,2,sum)
pe = se/it
pe
# calculate median population size
mP = apply(P,2,median)
mP
# Calculate the upper and lower 2.5 percentiles
lb = apply(P, 2, quantile, probs = c(0.025))
ub = apply(P,2,quantile, probs = c(0.975))
# Create plots of abundance
plot(mP,main = "", xlab = "years", ylab = "abundance", ylim=c(0,9000))
lines(mP)
lines(lb)
lines(ub)
# Create an output file to store simulation data.
data<-data.frame(mP,lb,ub,pe)
write.table(data,file="samp-var.csv",sep=",")

```

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