

EVALUATING PREDICTION PERFORMANCE OF POPULATION VIABILITY ANALYSIS
WHEN POPULATION PARAMETERS ARE ESTIMATED

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ABSTRACT

Population viability analysis (PVA) is a widely used tool in conservation biology to predict population size or assess extinction risk. The reliability and usefulness of PVA has been debated. In particular, PVA predictions may be suspect when uncertainty about parameters used in a the PVA is ignored. I used a simulation study to evaluate bias in predictions of final population sizes and prediction interval coverage of true final population sizes when parameter uncertainty was or was not included in a 50-year prospective PVA. Coverage was nearly nominal when uncertainty was propagated through the PVA, but was far less than nominal when uncertainty was ignored. Point estimates of final population size were negatively biased when true values were large, but bias was less evident when point estimates were compared to expected theoretical final population sizes generated from a true PVA using known true parameter values. Deviations of point estimates from expected theoretical values were large when expected values were large. Point estimates of final population sizes are misleading representations of PVA predictions, and decision-making process relying on PVA results should account for the entire distribution of possible outcomes.

INTRODUCTION

Population viability analysis (PVA) is widely used in conservation biology to predict extinction risk or future population size, evaluate potential population implications of alternative management options, inform conservation policy of rare species, or establish recovery criteria for endangered species (Lindenmayer *et al.* 1993; Morris *et al.* 2002; Schultz & Hammond 2003; e.g., Schtickzelle *et al.* 2005; Peery & Henry 2010). Several recent studies seem to validate short-term predictions of population trajectories (Brook *et al.* 2000; Holmes & Fagan 2002), but others, citing concerns about precision, data quality, and the effects of estimation error, have questioned the usefulness of absolute PVA predictions (Mangel & Tier 1994; Taylor 1995; Ludwig 1996; 1999; Fieberg & Ellner 2000; Coulson *et al.* 2001; Ellner *et al.* 2002). Some authors have suggested that relative predictions (e.g., comparative implications of various management options) are more useful than absolute predictions (Hamilton & Moller 1995; Coulson *et al.* 2001; Reed *et al.* 2002; McCarthy, Andelman, & Possingham 2003).

PVA uses stochastic computer simulation of population trajectories to generate a distribution of final population sizes at some specified time horizon (Boyce 1992; Akçakaya & Sjögren-Gulve 2000). The proportion of trajectories that declines through some defined population threshold (i.e., the threshold where a shift to small-population dynamics fundamentally different from large-population dynamics might occur) constitutes the probability of “quasi-extinction” for the specific population under investigation. The stochastic projection model is parameterized with information about population vital rates, mechanisms of population dynamics, and/or population genetic information.

In conservation biology, the probability of quasi-extinction or predicted population size at some long time horizons (50-100 years) often is of interest. However, studies that claim to

validate PVA predictive accuracy have used time horizons of only 7-20 years (Brook *et al.* 2000; Holmes & Fagan 2002). PVA predictions at such long time horizons should be considerably more uncertain because stochastic error is compounded, the effect of rare catastrophes not encountered in the parameterization of the PVA adds additional uncertainty, and the environment in which the population live may change in unpredictable ways.

A PVA should incorporate all sources of uncertainty and propagate them throughout the simulation (Goodman 2002). Types of possible uncertainty include environmental stochasticity, demographic stochasticity, model uncertainty, and parameter uncertainty owing to observation error and sampling variation. Environmental and demographic stochasticity typically are incorporated into prospective PVAs by sampling parameters from appropriate distributions with specified means and variances that are usually are treated as known. However, the means and variances of these distributions often are derived from retrospective analyses of population count data or encounter histories of marked individuals which consequently have associated uncertainty. This uncertainty can have a major influence on the reliability or usefulness of PVA predictions (Taylor 1995; McLoughlin & Messier 2004). Uncertainty about the population dynamics model also seldom is incorporated into PVA (but see Patterson & Murray 2008).

The goal of this study was to evaluate PVA predictions when parameter uncertainty was or was not propagated through the PVA, but assuming no change in environmental variation. Using a modified diffusion model and a biologically reasonable distribution of intrinsic finite rates of population increase (λ), but without density-dependence or demographic stochasticity, I generated 100 known population time series of 75 years. Time series of population sizes over the first 25 years, assuming no observation error, were used for Bayesian retrospective analyses to estimate λ s for subsequent prospective PVAs. Based on the retrospective analysis I then

projected forward 50 years, either incorporating or not incorporating the uncertainty of the lambda estimates, and compared the predictions of the PVAs to 1) the known outcomes for each time series, and 2) PVA predictions from a true PVA, i.e., one parameterized with the true values for lambda and its variation. The first comparison is common in assessments of PVA accuracy (e.g., Brook *et al.* 2000; Holmes & Fagan 2002) but does not account for the fact that the true time series is itself a stochastic outcome from a distribution of possible outcomes and may in fact be an extreme outcome. Thus, using a single true value or a small sample of true values to evaluate PVA predictive accuracy may itself constitute a biased test. Therefore I also compared PVA predictions to results from a true PVA (Ellner *et al.* 2002) which does properly account for all possible time series arising from the true parameter values and thus does represent the true expectation for those parameter values. Obviously, such a comparison is possible only in simulation studies where the true parameter values are known.

METHODS

Simulating population trajectories

I created an ensemble of populations, each with an initial population size of 150 and a true $\bar{\lambda}$ and $\sigma_{\bar{\lambda}}$ drawn from a lognormal distribution with a biologically reasonable mean (i.e., mean of means) and standard deviation (Table 1) based roughly on estimates reported for red deer (Brook *et al.* 2000). Populations did not have any age-structure, density dependence, demographic stochasticity, or genetic influences (e.g., inbreeding depression at small population size) on λ_t . For each simulated time series, I randomly selected one population (with its associated $\bar{\lambda}$ and $\sigma_{\bar{\lambda}}$) and projected it forward for 75 time steps, where for each time step environmental

variation in λ_t was represented by random draws from a lognormal distribution represented by that population's $\bar{\lambda}$ and σ_λ .

Retrospective analysis and prospective PVA

I used observations of the first 25 years of each time series to conduct a Bayesian retrospective analysis to estimate $\bar{\lambda}$ and σ_λ for that time series. Perfect observations and knowledge of the correct projection model were assumed, and conventional vague priors on the log-space parameter distributions (i.e., uniform for $\bar{\lambda}$, and $p(\sigma_\lambda^2)$ proportional to the reciprocal of σ_λ^2) were assumed. The prospective PVA was parameterized as follows. The initial population size, n_0 , was specified as the population count in the final (25th) year of the retrospective analysis. Parameter uncertainty was incorporated by sampling the Bayesian posterior distribution of $\bar{\lambda}$ and σ_λ to obtain a different $\bar{\lambda}$ and σ_λ for each iterated trajectory in the prospective PVA. Each realization of $\bar{\lambda}$ and σ_λ was retained for the entire trajectory, and in each time step, a λ_t was randomly chosen from the distribution specified by that $\bar{\lambda}$ and σ_λ . Thus, $\bar{\lambda}$ and σ_λ represented a constant distribution of environmental stochasticity applied to each time step but were different for each trajectory because of uncertainty about their true value. For the PVA that did not incorporate parameter uncertainty, the posterior modes of $\bar{\lambda}$ and σ_λ were taken to represent the “best” estimates for $\bar{\lambda}$ and σ_λ . These values of $\bar{\lambda}$ and σ_λ thus specified a constant distribution for environmental stochasticity at each time step and were identical for *all* trajectories. Density dependence was not included in the PVA except for a hard population ceiling of 100,000. The number of trajectories simulated for each PVA was 3 million. The time horizon was 50 years.

Evaluating PVA performance

The output of each PVA was a histogram of final population sizes with 500 bins. I evaluated both types of PVA by quantifying prediction interval coverage and absolute bias in predicted population sizes at the time horizon as compared to 1) true final population size and 2) population sizes predicted by the true PVA. I also compared extinction probabilities predicted by both PVA types with those predicted by the true PVA.

To evaluate coverage, I calculated the proportion of prediction intervals from all the PVAs that included the actual population size at the end of the time series. For each histogram I interpolated tail probabilities to find the 2.5th, 5th, 12.5th, 25th, 37.5th, 62.5th, 75th, 87.5th, 95th, and 97.5th percentiles. Pairing the percentiles provided 95%, 90%, 75%, 50%, and 25% prediction intervals with equal tail probabilities.

Final predicted population sizes were compared with true final population size in two ways. I compared the proportion of predicted populations that were less than or equal to x times the true starting population at the beginning of the PVA projection to the proportion of true final population sizes that were less than or equal to the same population threshold (sensu Brook *et al.* 2000; Holmes & Fagan 2002). In essence, this is a test applied to the ensemble that evaluates directional bias but is not informative about precision or magnitude of bias (Ellner *et al.* 2002). I also evaluated precision and the magnitude of deviations by subtracting the true final population size from the predicted final population size. The distribution of final population sizes was expected to be approximately lognormal, and sometimes highly asymmetric. Therefore I evaluated deviations of three possible point estimate – posterior mode, mean, and median – to represent predicted final population size.

The true final population size represents only a single outcome, possibly extreme, of many possible stochastic outcomes given the true parameter values, and this does not necessarily represent the expected true final population size. Therefore I also compared the distribution of final population sizes to a distribution from a true PVA which was parameterized with the known values of $\bar{\lambda}$ and $\sigma_{\bar{\lambda}}$ used to generate the time series for each population. This distribution does represent the true expectation given the true parameter values. I compared the overall probability of extinction, and population sizes at the 2.5th, 5th, 12.5th, 25th, 37.5th, 50th, 62.5th, 75th, 87.5th, 95th, and 97.5th percentiles, and at the posterior mean and mode.

RESULTS

The mean final population size of the true trajectories was 311, two populations declined to 0, three other populations declines to <20, and four populations increased to >1000. Most populations had a final population size of <500 (Fig. 1).

Coverage

Coverage of true final population size by prediction intervals estimated from the PVA was near nominal to slightly greater than nominal when parameter uncertainty was incorporated into the PVA. Coverage also was close to nominal for the true PVA. Conversely, coverage was far below nominal when parameter uncertainty was ignored (Table 2).

Comparisons to true final population size

The proportion of final predicted population sizes that were less than or equal to x times the true initial size seemed to fairly closely track the proportion of final true population sizes that were less than or equal to the same threshold, especially when parameter uncertainty was ignored (Fig 2). However, many of the posterior distributions were highly asymmetric (had long upper tails), and it is clear that for all levels of x the mode was usually lower than the true population.

In contrast, posterior means and medians were more often greater than the specified threshold when x was small, especially for PVAs that included parameter uncertainty (posterior distributions more asymmetric than when uncertainty was ignored), but when x was large, the proportion of posterior means and medians that was less than or equal to the threshold was always greater than the comparable proportion of true populations (Fig 3).

As expected, the deviations between predicted population sizes for both types of PVA and true final population increased in magnitude with increasing true final population size (Fig. 3). Additionally, there appears to be a large, negative bias in PVA predictions when true final population sizes were very large (>1000). Posterior distributions were more asymmetric when parameter uncertainty was included; consequently, posterior modes tended to be lower, and means greater, than in the case where uncertainty was ignored (Fig 3). Posterior medians were similar for both types of PVA. Overall, posterior modes and medians were negatively biased, most notably the mode, and most severely when the posterior distribution included parameter uncertainty, whereas the posterior mean had a slight positive bias (Table 3).

Comparisons to true PVA

When evaluated as the differences in predictions from the test PVA and predictions from the true PVA, deviations also increased dramatically with increasing population size, but deviations were generally smaller than deviations from the observed final population sizes, and there was no distinct negative bias at very large population sizes (Fig. 4). Although both types of PVA sometimes resulted in either positive or negative deviations, PVAs that included parameter uncertainty clearly predicted smaller population sizes when evaluated at lower percentiles and at the posterior mode than did PVAs that ignored parameter uncertainty (Fig. 4, Table 4). The deviations of both types of PVA were very similar at the 50th percentile (median), and at larger

percentiles, predictions were larger when uncertainty was included than when it was ignored. Posterior means also were greater when parameter uncertainty was included than when it was ignored (Fig. 4). For both types of PVA, there was also a tendency to overestimate extinction probability (Fig. 4).

DISCUSSION

Prediction intervals from PVAs that ignored parameter uncertainty clearly were too narrow. An implication is that probability of extinction should be underestimated. I was not able to evaluate this prediction because so few actual populations went extinct. In fact, based on a comparison with a true PVA, incorporating parameter uncertainty or using “best estimates” both resulted in *overestimating* extinction probability. However, the true extinction probability was very low, so any uncertainty about $\bar{\lambda}$ or use of any “best estimate” lower than the true $\bar{\lambda}$ would result in a greater occurrence of predicted than observed extinctions, i.e., extinction probability could scarcely be underestimated.

Real population trajectories are only one realization of a theoretical distribution defined by the true (but unknown) parameters for that population, and the distribution’s parameters are unknown. In this study, the negative bias when final population sizes were large, resulted from the fact that the theoretical distribution of final population sizes was asymmetric, and particularly large observed final population sizes came from the long upper tail. This can be seen by the fact that the mode, mean, and median from the true PVA (which represent the true theoretical values) also were negatively biased relative to the observed final value (Fig. 3). The observed population size could be from an entirely different region of the theoretical distribution than the region of the predicted posterior that contains the PVA point estimate under consideration. Therefore, it does not seem possible that accuracy of PVA, in general, can be assessed with real population

time series, beyond the simple proportional tests used by Brook *et al.* (2000 , see Fig. 1) and Holmes and Fagan (2002 , see Fig. 3). These tests evaluate the performance of a PVA over an ensemble of populations, and although it may be encouraging that there appears to be concordance between the predicted and observed proportion of the ensemble that reaches a particular threshold, it is somewhat misleading to interpret such concordance as evidence for accuracy of PVA in general (Ellner *et al.* 2002). Such an assessment can be made only when true population parameters are known, i.e., in a simulation study.

Systematic bias at large final population sizes did not exist when evaluated as the predicted population sizes compared to the theoretical sizes (from the true PVA) because comparisons were being made from like regions of the distributions. This allowed case by case evaluation of the magnitude of deviations from the theoretical values. As expected, large values of $\bar{\lambda}$ resulted in large final population sizes, and it is not surprising that prediction intervals were large and deviations of predictions from true values were large. Large prediction intervals emphasize the point that for any given PVA, point estimates of final population sizes at a distant time horizon (50 years in this case) can be very wrong.

Interestingly, deviations for PVAs that included parameter uncertainty switched from negative to positive for increasing predicted posterior percentiles (Table 4). This indicates that uncertainty about the parameter values shifted greater weight in the posterior tails relative to a true posterior, which may reflect a “flattening” effect of a uniform prior on the posterior distribution of $\bar{\lambda}$. Using a true empirical prior may shift more probability density out of the tails. Deviations for both PVA types are most similar at the posterior modes, which is not surprising, given that the posterior modes from the retrospective analysis, ignoring the rest of the distribution, were used to parameterize the prospective PVA.

Median deviations of the predicted posterior point estimates from the true posterior point statistics were less variable when parameter uncertainty was ignored than when uncertainty was incorporated into the PVA (Table 4). Although this might seem to suggest that ignoring uncertainty results in more reliable predictions than does accounting for uncertainty, two important points should be considered. First, it seems clear that none of the possible point estimates (mode, mean, median) adequately predict final population size – usually all of them were wrong, especially when final population sizes were large. Therefore, the metric of interest in a PVA result should be the entire posterior distribution, which theoretically represents all the possibilities. For any given population, it is highly misleading to present a point estimate and say it is “the” predicted final population size. Second, when parameter uncertainty was ignored, confidence intervals calculated from the posterior distribution of final populations sized excluded the true population size too frequently. Thus, even though median (and mean) absolute deviations were smaller than when parameter uncertainty was included, the posterior distribution often failed to include the correct fraction of trajectory outcomes, sometimes by a wide margin.

In summary, I draw four main conclusions from my analyses. First, PVAs that use “best” estimates for forward projection produce confidence intervals that are too narrow, whereas confidence intervals are correct when parameter uncertainty is appropriately incorporated into the PVA. Second, accuracy of PVA predictions is best assessed when population trajectories are simulated and true parameter values are known. Real population trajectories conceivably could come from improbable parts of the theoretical distribution and thus assessments of bias based on such theoretically improbable trajectories could be greatly distorted. Third, regardless of whether “best” estimates are used to parameterize a PVA or parameter uncertainty is properly accounted, predictive intervals at long time horizons are broad, especially for growing populations, or where

there is considerable environmental variation in the populations' growth rates. Fourth, use of point estimates to describe final population sizes predicted by a PVA ignore all uncertainty and thus are highly misleading. Any decision-making process using results of a PVA should account for the entire distribution of possible outcomes.

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Table 1. Ensemble parameters defining lognormal distributions of parameters that in turn define lognormal distributions specifying means and environmental variation for each of the populations in the ensemble.

Parameter	mean	std dev
$\bar{\lambda}$	1.005	0.01
$\sigma_{\bar{\lambda}}$	0.05	0.05

Table 2. Percent of true final population sizes (n=100) that were included in the predicted confidence intervals from PVAs that did or did not include uncertainty about the mean and standard deviation of lambda, and for a PVA that included true values used to simulate population trajectories.

Interval (%)	Actual coverage (%)		
	Parameter uncertainty	“Best” estimates	True parameters
95	96	77	93
90	92	70	89
75	77	49	80
50	51	34	55
25	30	14	22

Table 3. Mean, sd, and median of deviations in predicted final population sizes (n=100) relative to true final population sizes, where predicted size was represent by either the mode, mean or median of the posterior distribution of final population size from two types of PVA: one that did, and on that did not include uncertainty about $\bar{\lambda}$ and $\sigma_{\bar{\lambda}}$. Time horizon for the projection was 50 years.

Posterior statistic	Parameter uncertainty		“Best” estimates	
	Mean (sd) of deviations	Median of deviations	Mean (sd) of deviations	Median of deviations
Mode	-89.2 (269.6)	-32.5	-50.4 (248.8)	-14.5
Mean	38.3 (260.2)	11.0	-14.4 (240.6)	3.0
Median	-32.0 (241.4)	-7.0	-29.0 (241.9)	-3.0

Table 4. Mean and sd of bias of probability of extinction, and final population sizes (n=100) predicted from two types of PVA: one that did, and one that did not include uncertainty about $\bar{\lambda}$ and σ_{λ} , when compared to probability of extinction and population sizes predicted from a true PVA (parameterized with true values used to simulate the population trajectories that parameterized the test PVAs). Time horizon for the projection was 50 years.

Posterior statistic	Parameter uncertainty		“Best” estimates	
	Mean (sd) of deviations	Median of deviations	Mean (sd) of deviations	Median of deviations
p(extinction)	0.0097 (0.054)	0.0	0.0075 (0.050)	0.0
N(t), 2.5th percentile	-45.6 (62.2)	-34.0	9.4 (76.3)	-2.5
N(t), 5th percentile	-41.6 (66.0)	-31.5	9.8 (81.6)	-3.0
N(t), 12.5th percentile	-32.9 (73.9)	-27.0	10.5 (91.8)	-5.0
N(t), 25th percentile	-21.0 (87.9)	-24.0	10.7 (104.6)	-6.5
N(t), 37.5th percentile	-8.5 (105.6)	-15.0	10.3 (117.0)	-7.5
Median (N(t))	6.6 (129.4)	-13.5	9.6 (130.0)	-9.0
N(t), 62.7th percentile	27.4 (164.2)	-1.5	8.4 (145.5)	-9.0
N(t), 75th percentile	59.5 (223.4)	5.5	5.9 (166.5)	-11.0
N(t), 87.5th percentile	129.0 (355.6)	27.5	0.2 (202.3)	-15.0
N(t), 95th percentile	236.6 (610.0)	75.0	-12.5 (254.0)	-16.5
N(t), 97.5th percentile	421.2 (895.9)	110.0	-27.7 (302.2)	-25.5
Mean (N(t))	57.2 (193.2)	5.5	4.5 (141.2)	-9.0
Mode (N(t))	-26.2 (102.0)	-16.5	12.6 (115.2)	-5.0

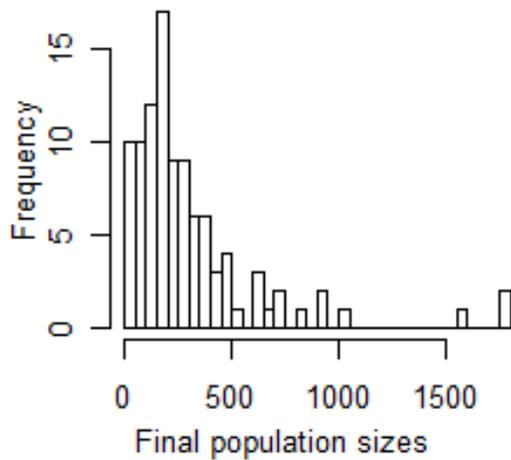


Figure 1. Distribution of true final population sizes for 100 simulated population trajectories.

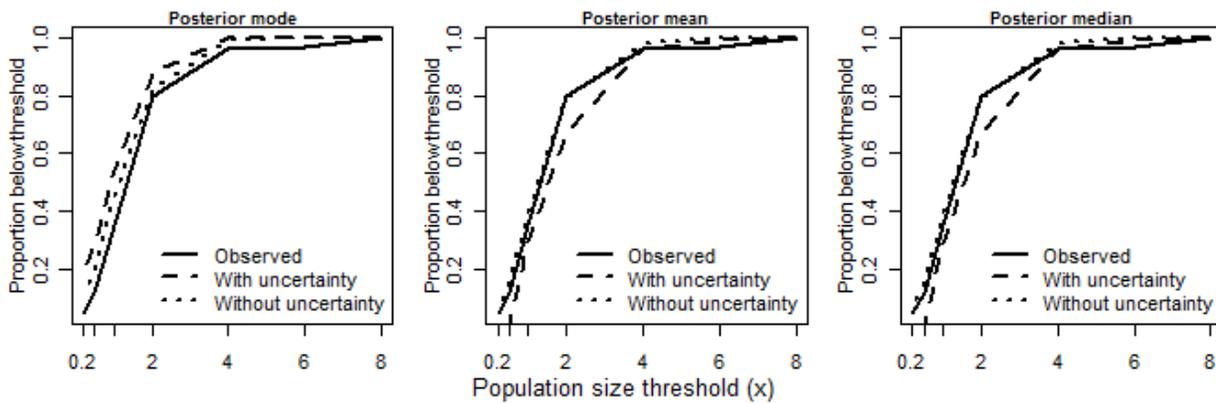


Figure 2. Proportion of predicted and true final population sizes that were less than or equal to x times the true population size at the beginning of the PVA projection when predicted population size is represented by either the mode, mean, or median of the PVA posterior distribution of final population sizes. Two types of PVA are represented: one that incorporates uncertainty about the true value of $\bar{\lambda}$ and σ_{λ} (by sampling the retrospective posteriors for each parameter in PVA iteration), and one that ignores parameter uncertainty and instead considers the retrospective posterior modes as the “best” parameter estimates. Note that proportions greater than the solid line indicated that final population sizes were less than or equal to the threshold more often than expected, and thus imply negative bias in predicted final population sizes.

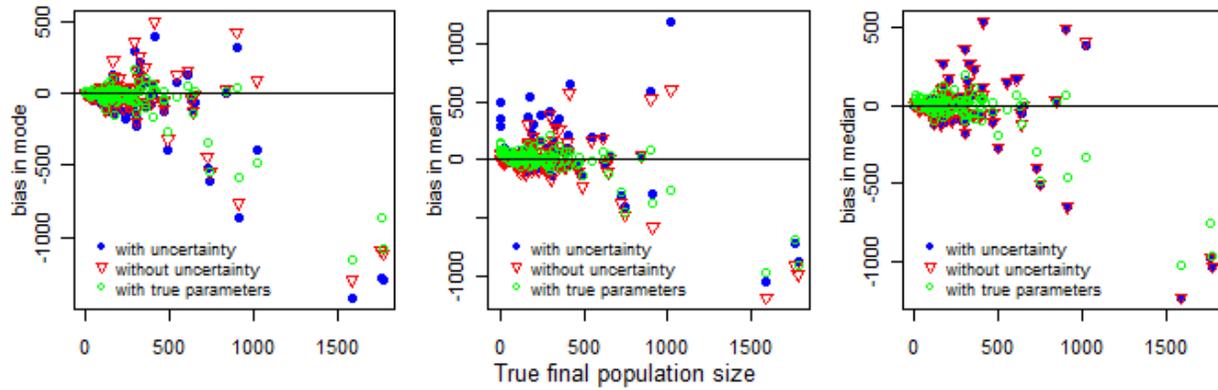


Figure 3. Bias in predicted final population sizes represented by either the mode, mean, or median of the PVA posterior distribution of final population sizes. Two types of PVA are represented: one that incorporates uncertainty about the true value of $\bar{\lambda}$ and σ_{λ} (by sampling the retrospective posteriors for each parameter in PVA iteration), and one that ignores parameter uncertainty and instead considers the retrospective posterior modes as the “best” parameter estimates.

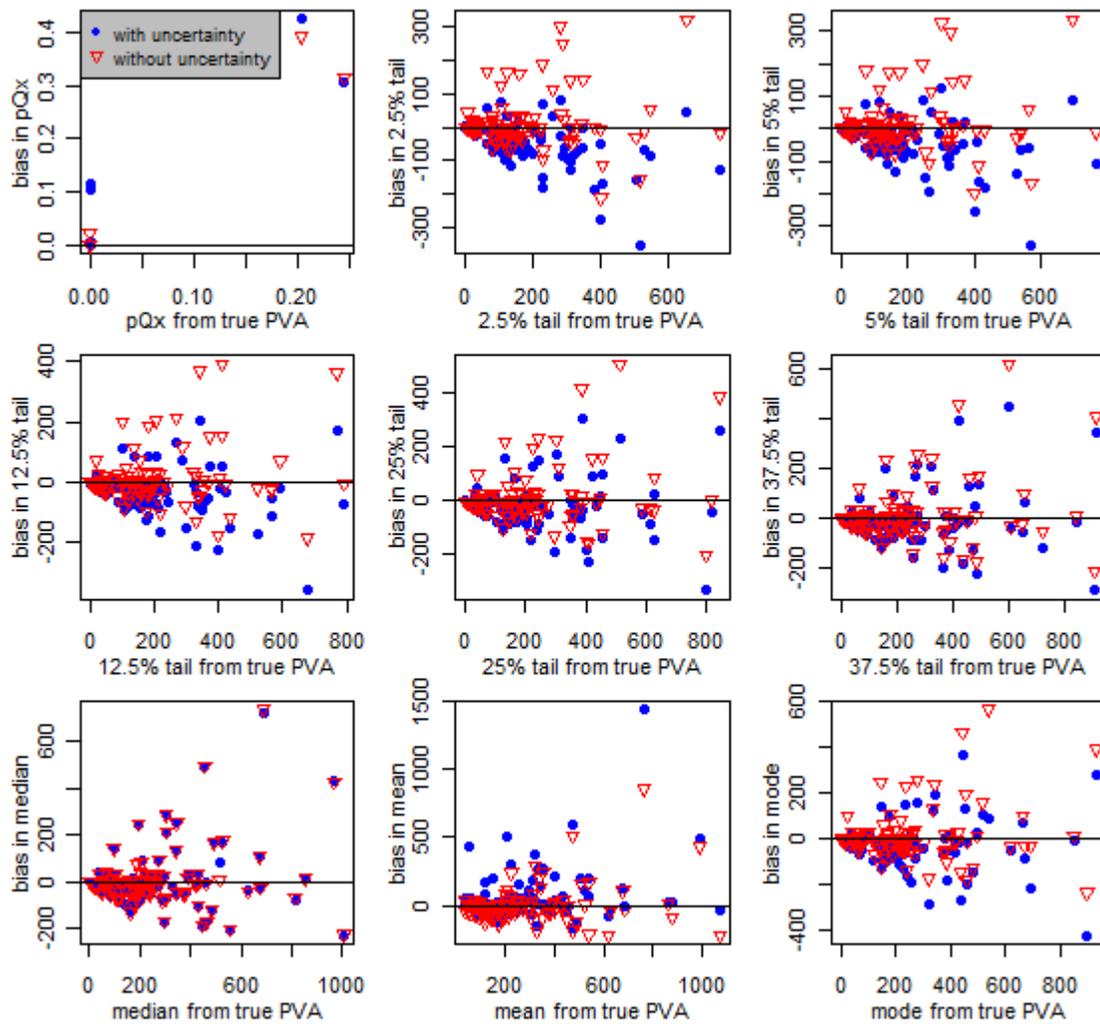


Figure 4. Bias of probability of extinction and final population sizes ($n=100$) predicted from two types of PVA: one that did, and one that did not include uncertainty about $\bar{\lambda}$ and σ_{λ} , when compared to probability of extinction and population sizes predicted from a true PVA (parameterized with true values used to simulate the population trajectories that parameterized the test PVAs).