

Using scalar models for precautionary assessments of threatened species

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Abstract

Scalar population models, commonly referred to as count-based models, are based on time-series data of population sizes and may be useful for screening-level ecological risk assessments when data for more complex models are not available. Appropriate use of such models for management purposes, however, requires understanding inherent biases that may exist in these models. Through a series of simulations, which compared predictions of decline risk of scalar and matrix-based models we examined whether discrepancies may arise from different dynamics displayed due to age structure and generation time. We also examined scalar and matrix-based population models of 18 real populations for potential patterns of bias in population viability estimates. In the simulation study, precautionary bias (i.e., overestimating risks of decline) of scalar models increased as a function of generation time. Models of real populations showed poor fit between scalar and matrix-based models, with scalar-models predicting significantly higher risks of decline on average. The strength of this bias was not correlated with generation time, suggesting that additional sources of bias may be masking this relationship. Scalar models can be useful for screening-level assessments, which should in general be precautionary, but the potential shortfalls of these models should be considered before using them as a basis for management decisions.

Introduction

Population viability analysis (PVA) has become an increasingly common tool for the conservation and management of threatened species. A PVA involves the development of quantitative population models based on parameters extracted from demographic and ecological data (Boyce 1992). These models are used to predict future size and extinction risks of populations and are useful for assessing the efficacy of management strategies. Results are also used as criterion for listing and classifying threatened species by the World Conservation Union (IUCN 2001).

There are several methods for generating PVA models that incorporate various spatial and temporal scales and employ different mathematical bases. The required data and output of results varies depending on model specification (Burgman et al. 1993; Reed

et al. 2002). The two basic model types commonly used for PVA are scalar models and matrix-based models, which differ in their degree of complexity. The simple scalar models are based on time-series data of population sizes, without including details of population age or stage structure. Matrix-based models are more detailed in that they incorporate population structure by accounting for differences in demographic parameters of the various age or stage classes in a population.

Scalar models are appealing for managers and conservation biologists because, for most populations, detailed demographic data are unavailable or unreliable, whereas time and monetary constraints frequently preclude gathering sufficient data for developing detailed matrix models. When decisions involving natural-resource management must be made despite incomplete information, simple scalar models may be able to capture crucial attributes of an age-structured population with minimal data collection or model calibration (Lande and Orzak 1988, Dennis 1991, Ferson 2002). Morris et al. (2002) found that of the 136 recovery plans approved by the U.S. Fish and Wildlife Service, 78% propose collecting sufficient data for scalar models, whereas only 23% propose collection of adequate data to perform age- or stage-structured models. Given their ease and frequency of use, it is critical to identify inherent biases that may exist in scalar models so that appropriate interpretation of results can be applied to management actions or setting conservation priorities.

A possible cause of bias in scalar models of age-structured populations is that they inappropriately model fluctuations in population growth rates caused by unstable age structure. When stable age structure is perturbed in a real population or in an age-structured model, it will result in deterministic oscillations that dampen as the structure converges (Caswell 2001). Scalar models attribute all forms of variation in growth rate to environmental variability and thus model all fluctuations as stochastic variation. Thus, a scalar model will erroneously model deterministic oscillations due to unstable age structure as stochastic variation.

To illustrate, if the only variation in population size is oscillations driven by unstable age structure, the real population will have zero probability of declining below any threshold set under the lowest trough of the oscillations, and an age-structured model will correctly predict zero probability. However, a scalar model will erroneously predict there is a risk of declining below such thresholds because it inappropriately models the deterministic variation as stochastic.

In reality, environmental stochasticity may continually disrupt age distributions such that continued fluctuations persist, partially due to environmental effects and partially due to deterministic oscillations due to age structure. Even if a population initially had a stable age distribution, stochastic fluctuations would still frequently push the age structure away from a stable distribution. Thus, bias in scalar models should arise even if the initial structure of the real population is at the stable age distribution. Here we demonstrate how scalar models of age-structured populations will result in inflated predictions of decline risk due to erroneous representation of oscillatory variation derived from age structure, even under environmental stochasticity.

Bias in scalar models may also be due to demographic stochasticity. In matrix-based models, demographic stochasticity must be removed from the observed variance to estimate and incorporate the variance due to environmental stochasticity. Otherwise, the variances, and hence risks of decline and extinction, may be overestimated. While methods for removing demographic or sampling variance have been developed for data from marked individuals (Burnham et al. 1987; Gould and Nichols 1998; White et al. 2002) and from

detailed censuses (Kendall 1998; Akçakaya 2002a), there are no comparable methods for removing variance due to demographic stochasticity from the observed variance of a population growth rate used in scalar models (Morris & Doak 2002). Scalar models may therefore overestimate (or underestimate) variability if the simulated population size becomes much larger (or much smaller) than the range of population sizes at which the population growth rate and its variance were estimated.

The second reason a scalar model may have higher decline risks involves correlations among vital rates, which are often encountered in populations but not always incorporated into matrix-based models (Morris & Doak 2002). If positive correlations in vital rates are not included in the matrix-models, then the variance in growth rate will be lower than actual variance resulting in underestimated predictions of extinction risk (Doak et al. 1994). In scalar models this problem is avoided because estimates of growth rate variance are calculated directly from population numbers. In some cases negative correlations among vital rates may occur, Not accounting for these may result in inflated variance calculations for matrix models,.

A third possible reason that scalar models may predict higher risks than matrix models is the difference in sampling variation. Studies employing scalar models commonly use a time-series of the number of individuals in the age or stage class, that may be the easiest to survey. However, often, the variability measured in one age class will differ from the variability at the population level (Holmes 2001). This type of census may commonly result in inflated estimates of variation (Holmes 2004), even if there is no observation error. Sampling error may also differ because in an age-structured model, errors for parameters of different age classes may cancel each other out to some extent, whereas this is not possible in a scalar model. Each parameter of the age-structured model, however, is typically based on a smaller number of individuals (abundance of individuals in age classes) than the scalar parameters (based on total population size), which may increase the sampling error for each parameter.

We addressed the issue of bias due to age structure through a series of simulations in which we compared age-structured matrix-based models with scalar models of hypothetical populations with different generation times. Our design for these simulations controlled for the three factors discussed above, so that any bias in the results is likely to be caused by oscillations due to age structure. We also explored whether altering the time step that parameters are estimated will reduce these biases due to age structure by removing some of the variation in the growth rate caused by age structure fluctuations. For example, for a matrix-based model with an annual time step, the scalar model can have a 3-year time step, with growth rate (and its standard deviation) based on abundances with a 3-year lag (e.g., $N(4)/N(1)$, $N(5)/N(2)$, etc.). The correct census period of such a lag depends on the convergence time (or damping ratio) of the population trajectory. The longest lasting of the oscillatory components due to age structure approximately corresponds to generation time (Caswell 2001, p. 100), thus the bias in the scalar model may be reduced if one uses a census period or lag that is longer than the time step of the matrix-based model but shorter than the generation time.

We then look for discrepancies in scalar and matrix-based population models in a more general context by examining 18 real populations for potential patterns of bias in terms of the predicted viability of the population. We conclude by suggesting appropriate uses of both model types.

Methods

Simulations

We ran a series of simulations with stochastic age-structured, matrix-based models repeated with nine different generation times, and compared results with scalar models to test how generation time and census interval can affect biases in risk predictions. The age-structured models were created in a matrix-based software package, RAMAS Metapop (Akçakaya 2002). The models used the same finite rate of increase (eigenvalue=1.0), annual survival rate (0.5), and variation (CV for fecundity = 10%; CV for survival = 5%), but generation times varied from 2 to 10 years (determined by the age of first reproduction and fecundity). The age of first reproduction varied from 1 to 9 years, and the fecundity was adjusted so that each model had the same finite rate of increase. Lifespan was not truncated (the last age class was a composite age class with survival equal to the previous age class), and fecundity was the same for all age classes after the first age of reproduction. The survivals and fecundities were assumed to be fully correlated among age classes. To reduce variation due to sampling error and demographic stochasticity, we used a large initial population size (10000000) and did not model demographic stochasticity. Models were started at stable age distribution. We ran each of the nine models with 10,000 replications for 120 years. For each replication, we calculated the average and standard deviation of the population growth rate with six different sampling intervals (1, 2, ..., 6 years). We then built six scalar models with these parameters for each of the nine corresponding age-structured models (that vary only by generation time). To create a scalar model with no age or stage structure, this software package uses the equation $N_{t+1} = R_t N_t$, where R_t is a deviate taken from lognormal distribution with a mean and standard deviation estimated from the time series. We then ran the scalar models for 120, 60, ..., or 20 time steps, such that all models ran for 120 years. For example, for a census period of 3 years, 10,000 replications of the structured model are run for 120 years, and for each replication, the population size resulting from the structured model was used every 3 years to calculate the average and standard deviation of the 3-year growth rate. For each scenario, we compared the risk of a 50% decline in each matrix-based model with each of the corresponding scalar models. We also repeated the above with seven different initial age-distributions of the matrix-based model with a 10-year generation time. The initial age-structures were varied by altering the proportions of breeders (last 2 age classes) to non-breeders in the starting population from 0.16% to 0.64% in increments of 0.08%. At stable age-distribution, the proportion of breeders was approximately 0.4%.

Model Comparisons

For comparison of general biases in PVA models for real species, we chose populations based on the availability of age- or stage-structured models and corresponding time-series data of North American species. An extensive search of the literature resulted in the selection of 18 populations for which data were available: 10 bird, 3 mammal, 1 amphibian, 2 fish, and 2 plant populations (Table 1.). We limited our search to North American species because our primary funding source was interested in these populations and we felt the resulting 18 populations were sufficient. These were the only data sets identified from North America in which sufficient data were available for the analysis.

Quasi-extinction risks from the matrix-based models presented in the literature were compared with scalar models we created from time-series data of the same population with RAMAS Metapop (Akçakaya 2002). All matrix-based models corresponding to each species used were found in the literature (cited in Table 1). The PVA packages for matrix-based models varied for populations used in the analysis. However, when used appropriately, they are expected to give comparable results (Brook et al. 2000). For the peregrine falcon and two spotted owl populations (Table 1), quasi-extinction risks were not presented in the literature so we used RAMAS Metapop (Akçakaya 2002) to re-create a matrix-based model for each population from the given parameters.

To create the scalar models for comparison, we used census data from the same populations and time periods (citations in Table 1). We calculated the realized rate of population change between successive surveys in a continuous series as: $R_i = (N_i/N_{i-1})$, where N_i is the population size at year i , ($i = 0, 1, 2...q$). All census data had annual time steps. These population growth rates were then used to calculate the mean and standard deviation of R for the models created in RAMAS Metapop. We did not make any attempt to remove variance due to potential observation error in these time series, because the corresponding matrix-based models did not remove observation error, either. The same initial population sizes, threshold abundances, and time intervals used in the matrix-based models were also used for the scalar models. If density dependence or declining trends in either population size or carrying capacity were incorporated into the matrix-based model, we included these parameters in the corresponding scalar model in the same way (Table 1). All models used in the analysis that employed density dependence used ceiling-type density dependence that affected all stages.

Each scalar model was used to generate 10,000 replications. We used these results to calculate the quasi-extinction risk, defined here as the probability of falling below a critical threshold population size, N_{crit} , at some future time. A quasi-extinction risk curve is created from the cumulative probability distribution of the minimum abundances of model simulations (Akçakaya et al. 1999). We compared quasi-extinction results of scalar models to those of corresponding matrix-based models. The baseline risk estimate, or estimate based on the most likely scenario, was used for comparison when several estimates were given for a matrix-based PVA. To avoid mathematical biases, N_{crit} values and time intervals were chosen to avoid extreme quasi-extinction probabilities (0 or 1) when possible (see Table 1). The range of uncertainty is truncated for risks of either extreme; choosing threshold values or time intervals that lead to intermediate risk values will, therefore, give a better representation of differences between model types (McCarthy et al. 2003). Note that choosing a threshold does not change the model or its results, it only changes the way the results are summarized. Ideally, comparisons should be made using minimum expected population size because they have better numerical properties and are more stable; however these were not available in several of the model papers we used for our analysis.

Because the damping ratio of fluctuations due to age structure depends on generation time (Caswell 2001), we examined simulations of real populations for a relationship between model discrepancy and species' generation time. We hypothesized that if fluctuations due to age structure result in an inflated, non-dampening variance over time in scalar models, then longer generation times (relative to sampling interval) will be more likely to be associated with a stronger bias toward higher endangerment risk estimates in scalar models.

Results

Simulations

The bias in scalar models (in terms of the difference in risk of a 50% decline) increased as a function of generation time: the longer the generation time, the larger the overestimation of risk by the scalar models (the y-intercepts in Figure 1). This bias occurred even though scalar models incorporated 120 years of simulated data. This bias was reduced when longer time steps (sampling interval) were used to calculate the growth rate for creating the scalar model (Figure 1). For each matrix-based model, the bias in the corresponding scalar model was eliminated at a census period that was longer than the time step of the matrix model (1 year for all models, Figure 1) but shorter than the species' generation time. For census periods equal to or longer than generation length, the bias became negative (i.e., the risk of decline was underestimated by the scalar models). The maximum bias observed in our simulations was a 12% increase in decline risk. Deviation of initial age-distribution from stable distribution resulted in additional variability in the amount of bias (Figure 2), however, scalar models still predicted inflated risk of decline, even in cases where altering the age-structure resulted in an initial decline in population size

Model comparison

The results show a poor fit ($R^2 = 0.17$, $P = 0.462$, $N = 18$) between quasi-extinction results of age- or stage-structured matrix models and scalar models that were created from times-series data across 18 populations (Figure 3 a). Differences between resulting distributions were not significant under a Kolmogorov-Smirnov test ($Z = 1.167$, $p = 0.131$, $df = 17$). Scalar models appeared conservative overall (Figure 3 b), predicting risk levels that were, on average, 18% higher than their matrix-based counterparts. This bias was significant (Wilcoxon signed rank test, $Z = -2.025$, $p = 0.043$ $df = 17$). Risk predictions generated from scalar models for 13 of 18 species showed higher extinction risks than their matrix-based counterparts. The five scalar models that predicted lower quasi-extinction risks than the corresponding matrix-based models included those for the peregrine falcon, Florida scrub jay, black-capped vireo, snail kite, and gopher frog (see Table 1 for scientific names). When model discrepancy (scalar bias) was plotted against generation time or against length (duration) of the time series data, no relationships were found ($R^2 = 0.00$ in both cases).

Discussion

Our analysis has resulted in two main conclusions. First, our comparison of scalar and age-structured models of real populations showed that scalar models often have a precautionary bias (overestimating variability of population size, and hence the risk of decline). Second, our simulation study, in which we built and ran scalar models based on outputs of age-structured models, suggested that this bias may be caused, at least in part, by the damped oscillations due to age structure that are erroneously incorporated in scalar models as environmentally induced fluctuations. This bias was shown to be greater for species with longer generation times because of the longer dampening rate of the oscillations caused by unstable age structure.

The second conclusion is tentative because generation time did not show a positive relationship with level of discrepancy between models of real populations as predicted by

our hypothesis. However, this does not mean age structure fluctuations are not contributing to the observed bias. The magnitude of bias caused by age structure in the real data may be small enough that the effect was masked by other causes of bias. In addition, the models we compared incorporated different growth rates, number of yearly observations, and stochasticity levels, each of which are expected to interact with generation time to produce different risk predictions. Thus, we are not suggesting that the bias in scalar models observed here is exclusively the result of age structure, but it may be an important factor in this bias.

In our simulations that started with stable age distribution, the maximum bias in decline risk of scalar models we observed was only 12%. However, the magnitude of bias is expected to vary as a function of initial age structure of the population and the life history characteristics of the target species. This bias is also expected to be greater in populations where age- or stage-specific counts are used as a surrogate for total population counts (Holmes 2001).

Previous studies have also shown that age structure, observation error, and other factors contribute to bias in the estimation of variance in scalar models, and proposed methods for proper estimation of the variance (Holmes 2001, 2004, Holmes and Fagan 2002). Because it is difficult to judge the practical conservation importance of a bias in a variance estimate, we focused on the bias in risk of decline in this study. In addition, we demonstrated bias in models of several species, developed for conservation purposes. Further research is clearly needed to determine other factors that may be driving the observed bias and if it holds with a larger sample of species.

Our simulations controlled for the three other factors that may cause a scalar model to predict a higher risk than the corresponding age-structured model of the same population (see Introduction). Although we set survivals and fecundities to be fully correlated among age classes, correlations do not have an effect on our simulation results. This is because, in the simulations, we are comparing an age-structured model to a scalar model, which is based on the output of the age-structured model. If the age-structured model did not have correlation, both it and the scalar model based on its output would have lower variability; the difference between the two would not be affected. Sampling error and demographic stochasticity also do not affect the simulation results, because we used a large initial population size, a large number of time steps, and did not model demographic stochasticity. Further evidence that sampling error does not cause the observed bias comes from our comparison of the two types of models for real populations, in which there was no relationship between the magnitude of the observed bias and the length of time series data (which likely affects sampling error). Thus, the bias observed in simulations is very likely to be due to damped oscillations in age structure that are erroneously incorporated in scalar models as additional environmental variation.

Our simulations also demonstrated that the bias due to deterministic age structure oscillations could be minimized by estimating the parameters of the scalar model for a time step that is longer than that of the matrix-based model and shorter than the generation time. This approach is similar to the method proposed by Holmes (2001) to reduce bias in estimates of variance of scalar models from time series data. For most of our models, the correct time step was close to one-half of generation time. This is consistent with our hypothesis. The longest lasting oscillations caused by perturbed age structure are on the order of one generation. Thus, the bias is expected to be minimal between one time step and one generation. In most of our simulations, the period that minimized the bias was

around one-half of the generation time (Figure 1), but ranged from 20% to 100% of the generation time when the initial age distribution was altered (Figure 2).

In most cases, finding the correct census period would not be a practical solution because it requires full knowledge of the population structure (in which case, a scalar model would not be used anyway). Crude calculations based only on generation time may overcorrect and create a non-precautionary bias (underestimating risks of decline and extinction) (Figure 1). This is also a problem with the the generation-time smoothing recommended by Holmes (2001) for removing sampling (and other) variation from natural variability on scalar models, which is sensitive to the number of counts to be included in the running sum (Morris & Doak 2002).

The results of this study suggest the potential biases of the model types should be considered before using them as a basis for management decisions. The more appropriate model for PVA depends on the ability of the model to capture the details of mechanisms that determine population growth trends such that the most effective management solutions can be made (Grimm et al. 2005). If data are available for both scalar and matrix-based models, it might be preferable to build both types of models because model development is not costly if data are available. Otherwise, we propose that scalar models only be used to make preliminary and precautionary assessments of extinction risks in cases where age-structured data are unavailable.

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Table 1. Information about populations used in the model comparisons of decline risk between scalar and age- or stage-structured population models.

Scientific Name	Common Name	Code	N_{crit}	T	Density Dependence	Citation
<i>Falco peregrinus</i> *	Peregrine Falcon	FP	0	50	None	Wootton & Bell 1992
<i>Aphelaeoma coerulescens</i>	Florida Scrub Jay	AC	10	60	Ceiling	NASA 2003; Root 1998
<i>Charadrius alexandrinus</i> *	Snowy Plover	CA	1000	100	None	Nur et al. 2001; USFWS 2001
<i>Vireo atricapillus</i>	Black-Capped Vireo	VA	0	17	Ceiling	Parysow & Tazik 2002; Weinberg et al. 1998
<i>Dendroica chrysoparia</i> *	Golden-Cheeked Warbler	DC	200	100	Ceiling	Aldredge et al. 2004, in press; Jett et al. 1998
<i>Strix occidentalis lucida</i> *	Mexican Spotted Owl (a)	SOa	0	25	None	Seamans et al. 1999
<i>Strix occidentalis lucida</i> *	Mexican Spotted Owl (b)	SOB	0	25	None	Seamans et al. 1999
<i>Sterna antillarum browni</i> *	California Least Tern	SA	7035	50	Ceiling	Akçakaya et al. 2003
<i>Charadrius melodus</i> *	Piping Plover	CM	0	40	Ceiling	Plissner & Haig 2000; Ryan et al. 1993
<i>Rostrhamus sociabilis</i>	Snail Kite	RS	0	100	None	Beissinger 1995
<i>Martes americana</i> *	American Marten	MA	0	500	None	Lacy & Clark 1993
<i>Antilocapra americana</i> *	Sonoran Pronghorn	AA	0	50	Ceiling	Hosack et al. 2002; USFWS 1998
<i>Canis lupus</i> *	Wolf	CL	30	20	None	Brook et al. 2000; NERC 1999
<i>Rana servosa</i> *	Gopher Frog	RC	0	5	None	Richter et al. 2003
<i>Oncorhynchus tshawytscha</i> *	Chinook Salmon	OT	0	100	None	Ratner et al. 1997
<i>Oncorhynchus clarki pleuriticus</i>	Colorado Cutthroat Trout	OC	10	80	None	Hilderbrand 2003
<i>Asarum canadense</i>	Wild ginger	WG	0	100	None	Damman & Cain 1998
<i>Astragalus crennophylax</i>	Sentry Milk Vetch	AC	50	100	None	Maschinski et al. 1997

N_{crit} is the population threshold size used in estimating quasi-extinction risks. T is the time interval used to estimate quasi-extinction risks. * indicates generation time could be calculated from literature.

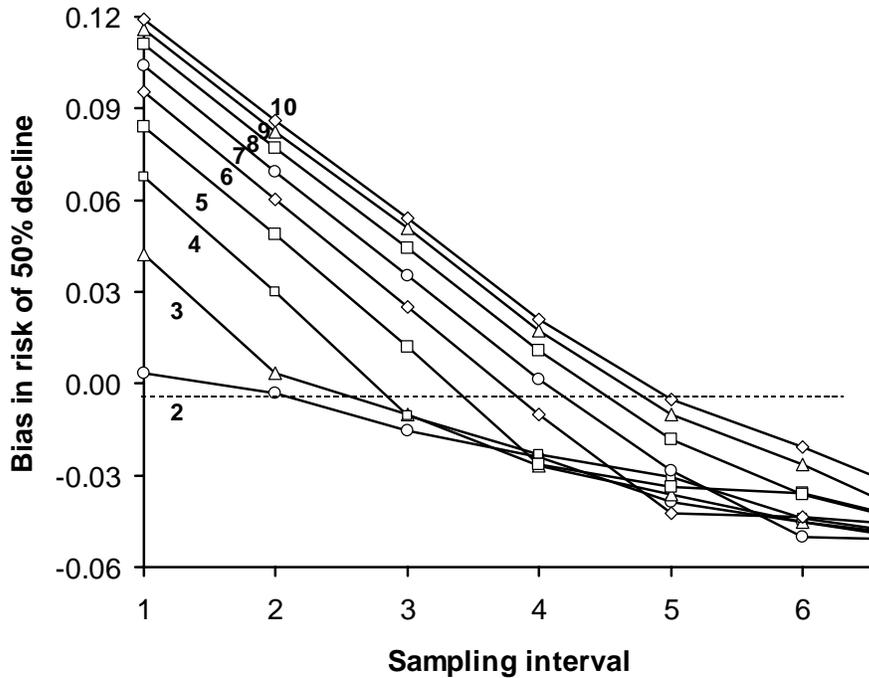


Figure 1. Simulation results. Bias in risk of 50% decline for scalar models relative to matrix-based models under different generation times (from 2 to 10 years as indicated for each curve) and as a function of the census period. The nine structured models have the same finite rate of increase (eigenvalue=1.0), annual survival rate (0.5), and variation (CV for fecundity=10%; CV for survival=5%), but varying generation times.

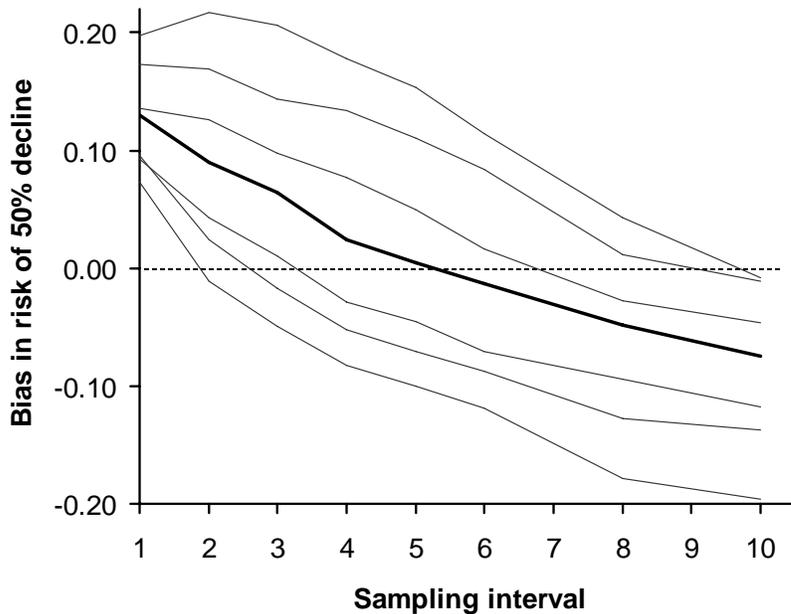


Figure 2. Effect of initial age structure on the bias in the prediction of scalar models. Bias and sampling interval are as in Figure 1. All age structured models had a generation time of 10 years. Initial age structure was varied by changing the proportion of individuals in the breeding (two oldest) age classes from 0.16% (lowest curve) to 0.64% (highest curve), in increments of 0.08%. At the stable age distribution, the percentage in breeding age classes is about 0.4% (the middle curve).

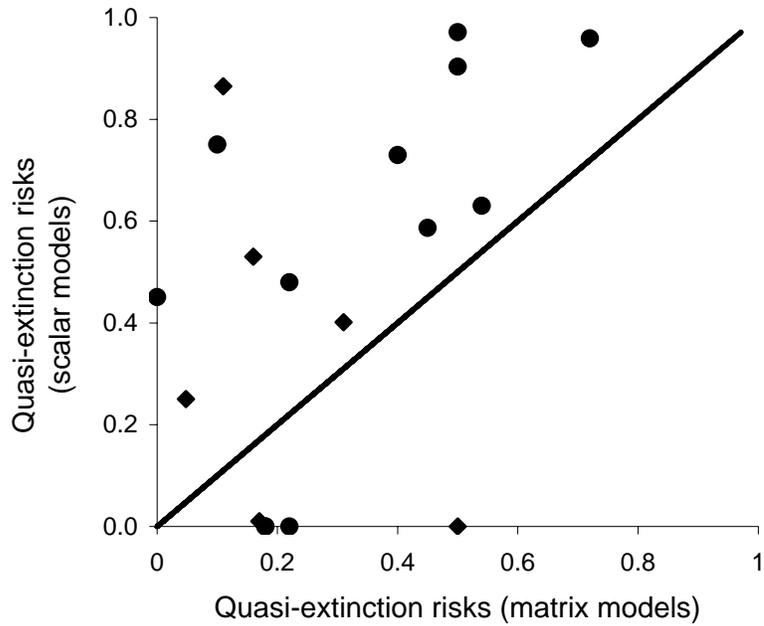


Figure 3. (a) Comparison of quasi-extinction results from scalar population models created with parameters estimated from time-series data, and structured models estimated from demographic data. Data points represent models from 18 species for which age-structured models were previously available (the x,y point 0.0, 0.18 is obscured by another with the same values). Diamonds represent pairs of models performed with ceiling-type density dependence. No density dependence was used for other models represented by circles. (b) Frequency of discrepancy between quasi-extinction risk predictions of scalar models relative to corresponding matrix-based models of 18 populations (x-axis represents percent difference of scalar results relative to matrix-based model results).