# Reliability of Relative Predictions in Population Viability Analysis

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**Abstract:** *Despite numerous claims that population viability analysis (PVA) makes reliable predictions of the relative risks of extinction, there is little evidence to support this assertion. To assess the veracity of the claim, we investigated uncertainty in the relative predictions of a PVA model with simulation experiments. We used a stochastic Ricker model to investigate the reliability of predicted changes in risks of decline in response to changes in parameters, the reliability of ranking species in terms of their relative threat, and the reliability of choosing the better of two management decisions. The predicted changes in risks of decline within 100 years were more reliable than absolute predictions. We made useful predictions of relative risks using only 10 years of data. Across 160 different parameter combinations, the rank correlation between the true risks of extinction within 100 years and predicted risks was 0.59 with 10 years of data, increasing to 0.89 with 100 years of data. We identified the better of two management strategies 67–74% of the time using 10 years of data, increasing to 92–93% of the time with 100 years of data. Our results demonstrate that, despite considerable uncertainty in the predicted risks of decline, PVA may reliably contribute to the management of threatened species.*

Confiabilidad de Predicciones Relativas en el Análisis de Viabilidad Poblacional

**Resumen:** *A pesar de que varios autores afirman que el análisis de viabilidad poblacional (AVP) permite hacer predicciones confiables de los riesgos relativos de extinción, hay escasas pruebas que apoyen tal aseveración. Para evaluar su veracidad, utilizamos experimentos simulados para investigar la incertidumbre de las predicciones relativas de un modelo de AVP. Utilizamos un modelo estocástico de Ricker para investigar la confiabilidad de cambios previstos en los riesgos de declinación en respuesta a cambios en los parámetros, la confiabilidad de jerarquizar a las especies en términos de su amenaza relativa y la confiabilidad de seleccionar la mejor de dos decisiones de manejo. Los cambios previstos en los riesgos de declinación en 100 años fueron más confiables que las predicciones absolutas. Se hicieron predicciones útiles de los riesgos relativos utilizando datos de solo 10 años. En 160 combinaciones diferentes de parámetros, la correlación de rangos entre riesgos de extinción verdaderos en 100 años y los riesgos previstos fue 0.59 con datos de 10 años, e incrementó a 0.89 con datos de 100 años. La mejor de las decisiones de manejo se identificó entre 67 y 74% de las veces utilizando datos de 10 años, y entre 92–93% de lasveres con datos de 100 años. Nuestros resultados demuestran que, a pesar de la considerable incertidumbre en los riesgos de declinación previstos, el AVP puede contribuir confiablemente al manejo de especies amenazadas.*

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## Introduction

Although population viability analysis (PVA) appears to provide unbiased predictions of extinction risk (Brook et al. 2000; Ellner et al. 2002), the predictions are typically subject to considerable uncertainty (Taylor 1995; McCarthy et al. 1996; Ludwig 1999; McCarthy et al. 1999). As a result, there is doubt about the usefulness of these predictions in individual cases (Possingham et al. 1993; Beissinger & Westphal 1998; Ludwig 1999). This concern is important because PVA is used extensively in conservation biology to predict both the risk of extinction faced by populations and species and the efficacy of management strategies that seek to mitigate these threats (Shaffer 1981; Gilpin & Soulé 1986; Boyce 1992; Burgman et al. 1993; Possingham et al. 1993). Despite this uncertainty, advocates of PVA argue that the relative predictions of these models are useful, even though the absolute predictions may be unreliable (Burgman et al. 1993; Possingham et al. 1993; Lindenmayer & Possingham 1995, 1996; Akçakaya & Raphael 1998; Beissinger & Westphal 1998; McCarthy et al. 2001). It is claimed that the use of PVA to assess relative risks is less prone to uncertainties about the structure of the model and parameter estimates than the absolute predictions. Although this argument seems plausible, the only evidence to support the claim is from two case studies (Lindenmayer & Possingham 1996; Akçakaya & Raphael 1998).

At least three types of relative predictions can be generated by PVA. First, relative predictions may be generated for a particular species or population by predicting how a particular management strategy will decrease or increase the risk of population decline (Akçakaya & Raphael 1998). Second, risks of population decline faced by different species or populations may be assessed, and the species may then be prioritized for management, protection, or recovery on the basis of the predicted risks of decline. This ranking of species relies at least to some extent on the precision of the absolute predictions (Taylor 1995). Third, relative predictions may be generated to determine the most effective management strategy from a range of different possibilities (Lindenmayer & Possingham 1995, 1996).

We sought to determine whether relative predictions are likely to be more reliable than absolute predictions and whether they remain reliable when the absolute predictions are subject to considerable uncertainty. In particular, we asked whether PVA could be used to (1) determine how risks will change in response to management, (2) rank species in terms of their level of threat, and (3) determine the best management strategy.

## Methods

Our study was based on simulations in which we used a stochasitc Ricker (1975) population model to generate data and then used these data for estimating parameters and making predictions. The code for the program used for simulation and parameter estimation is available at http://www.nceas.ucsb.edu/~mccarthy/research.html.

The simulations were based on 160 "species" that represented different parameter combinations. We followed three steps for each set of parameters:

(1) We generated through simulation a given number of years of data (10, 20, 50, or 100 yearly intervals) by using a stochastic Ricker population model.
(2) We obtained unbiased parameter estimates of the model based on the data from 10, 20, 50, or 100 years and made predictions of extinction risk within 100 years and of changes in this risk under two management strategies. These predictions were based on simulation of the model with 1000 iterations.
(3) We repeated steps 1 and 2 1000 times for a given set of parameters, generating 1000 different parameter estimates and associated predictions. We then calculated the uncertainty of the predictions by measuring the inner 90th percentile range of these 1000 predictions.

Details of each of the steps are given below.

We used a Ricker (1975) population model for all simulations:

$$N_{t+1} = N_t \exp(a - bN_t + \sigma\varepsilon_t), \tag{1}$$

where $N_t$ is population size at time $t$, $a$ and $b$ are parameters of the model controlling the nature of density dependence, $\sigma$ is the standard deviation in the population growth rate due to environmental stochasticity, and $\varepsilon_t$ is a random normal deviate with mean equal to 0 and variance equal to 1. Other population models are likely to produce results qualitatively similar to those reported here, but we used the Ricker model because it is capable of simulating both contest and scramble competition, thereby spanning a greater range of forms of population dynamics. It is also the same model used by Ludwig (1999), who demonstrated the large uncertainty often associated with predicted risks of extinction. The model does not include demographic stochasticity, but preliminary work with models including demographic stochasticity indicates qualitatively similar results to those we report here (M.A.M., unpublished data).

For each parameter combination, the predicted risks of extinction (as calculated in the steps above) were compared with the true risks. The true risk of extinction (chance of falling to 1 individual or fewer within 100 years) was determined by stochastic simulation of the original model with 1000 iterations. This risk is equivalent to the proportion of identical populations of a species that would be expected to become extinct.

### Data Generation

We generated data by simulating the dynamics of Eq. 1 for a range of parameter values: $a$ = 0.01, 0.02, 0.05, 0.1, 0.2, 0.5, 1.0, 2.0; $k = a/b$ = 100, 1,000, 10,000; 100,000, and $\sigma$ = 0.05, 0.1, 0.2, 0.4, 0.6. Thus, we examined 160 different parameter combinations, representing species with a wide range of population dynamics. Such parameter values reflect dynamics of species ranging from those that are short-lived with the potential for rapid growth rates through those with low (but positive) potential population growth rates. The initial population size was equal to the equilibrium population size in each simulation ($k$). Time series with 11, 21, 51, or 101 periods were simulated, yielding data sets with 10, 20, 50, or 100 observations of changes in population size. These latter numbers were used to refer to the length of the data set. The shorter time series were not a subset of the longer ones.

### Parameter Estimation

Parameter estimates for the Ricker model can be obtained by transforming Eq. 1 and using the following regression:

$$r_t = \ln(N_{t+1}/N_t) = a - bN_t. \quad (2)$$

However, because the population sizes and the errors about the regression line are not independent, standard linear regression leads to biased parameter estimates. The method of parameter estimation used by Ludwig (1999) retained considerable biases (especially for low values of $a$), so we used a different method of parameter estimation in which the bias was estimated by simulation (Walters 1985).

### Assessments of Predictive Accuracy

We conducted an initial analysis to confirm the work of Ludwig (1999) and demonstrated the considerable uncertainty associated with predicting the absolute risks of extinction. For each of the 160 different parameter combinations and lengths of data sets, we generated 1000 different time series. In each case, we obtained unbiased parameter estimates using the method of Walters (1985). For each time series, and thus each corresponding set of parameter estimates, we predicted the risk of extinction (chance of falling to one individual or fewer) within 100 years by stochastic simulation with 1000 iterations.

We assessed the uncertainty in the predicted risks of extinction for each parameter combination by calculating the range of the inner 90th percentile from the 1000 simulations. This involved sorting the 1000 predictions of risk in numerical order, finding the 50th and 950th result, and calculating the difference between these two numbers. This range would be close to 0 in cases where the predictions of the different time series were consistent for a given time period and parameter combination. If the different predictions were not consistent (e.g., varying between 0 and 1), the range would be close to 1.

Second, we predicted the change in the risk of extinction under two management scenarios: (1) an increase in the population growth rate of 5% at all population sizes (by multiplying $r_t$ [Eq. 2] by 1.05) and (2) an increase in the carrying capacity of 50% (by dividing parameter $b$ by 1.5). These changes reflect management actions that reduce mortality or increase fecundity rates or increase the amount of habitat available to the species. We chose the specific values for the changes (5% and 50%) by trial and error, so that for half of the 160 different parameter combinations the strategy of increasing the carrying capacity would be preferable to the strategy of increasing the growth rate (i.e., would lead to greater reductions in the true risks of decline). The same time series (i.e., the exact same sequence of population sizes) used to examine the variation in the predicted risk of extinction were used to examine the variation in these relative risks of extinction. As with the absolute risks, we assessed the precision of the relative predictions by measuring the range of the inner 90th percentile from the 1000 simulations of each parameter combination and time period.

We examined correlations between the predicted and true risks across the 160 different parameter combinations to indicate the ability of PVA to rank accurately the risks faced by different species. For each of the 160 parameter combinations, a single time series was generated and parameter estimates were obtained. These parameter estimates were used to predict the risk of extinction and the change in the risk of extinction under the two management scenarios through stochastic simulation of the model with 1000 iterations. We used a single time series to reflect the case that in reality we have only one set of data for each species.

Finally, we examined the ability to choose the best of the two possible management strategies. The best strategy—to increase growth rates or increase carrying capacity—for each of the 160 parameter combinations was the one that led to the greatest reduction in the risk of population decline. For each of the 160 data sets we predicted the best management strategy (using the parameter estimates and predictions based on a single data set for each parameter combination) by determining the one that produced the largest decrease in the predicted risk of extinction. We calculated the proportion of times this prediction was correct by comparing the choice to the management strategy that led to the greatest decrease in the true risk of extinction. This indicated the reliability of using PVA to decide between competing management strategies. We examined relationships between the accuracy of the predictions and the parameter values in an effort to determine the circumstances under

which the predictions were most likely to fail. This was done by examining plots of how the proportion of correct decisions varied with values of $a$, $k$, and $\sigma$.

In addition to extinction risk, we used the expected minimum population size to measure threat (McCarthy & Thompson 2001). Because of uncertainty about predicting population dynamics at small population sizes and concern about population decline, not just extinction, it is common in PVA to predict risks of decline to small population sizes (quasi extinction; Ginzburg et al. 1982). Plotting the risk of population decline versus the threshold population size produces a quasi-extinction risk curve (Burgman et al. 1993). These curves can be summarized by calculating the expected minimum population size (the mean of the smallest population size recorded in each iteration of a PVA; McCarthy 1996; McCarthy & Thompson 2001). The expected minimum population size indicates the average propensity of the population to decline at some time within the period being considered and may be expressed as a proportion of the initial population size. We used it in the current study (in addition to the extinction risk) to quantify the risk of population decline. The expected minimum population size has an advantage over the extinction risk for measuring threat because it gives a better indication of the propensity for decline when the extinction risk is small (McCarthy & Thompson 2001).

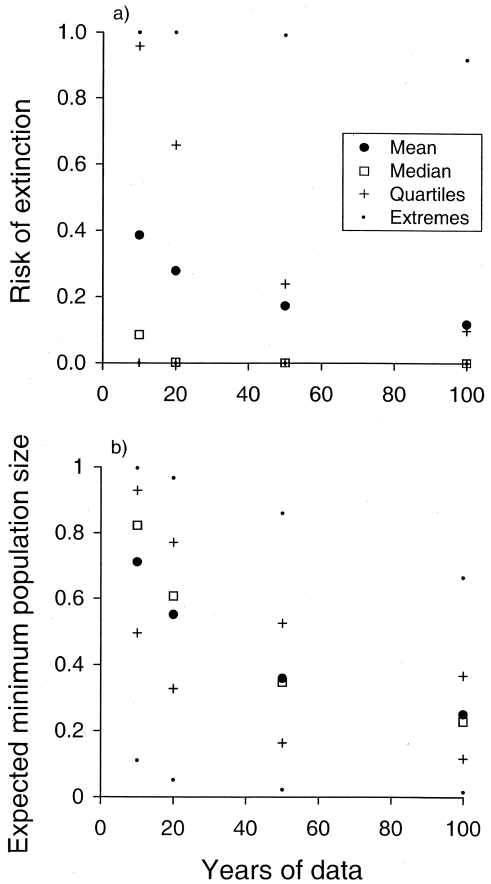


*Figure 1. (a) Inner 90th percentile range of the extinction risk and (b) expected minimum population size for the 1000 simulations versus the number of years of data. The results show the median, mean, quartiles, and extremes for the 160 different parameter combinations. The expected minimum population was scaled between 0 and 1 by dividing by the initial population size.*

## Results

The results of the simulations demonstrate the considerable uncertainty associated with predicting the risk of extinction. Despite this uncertainty in the absolute predictions of extinction risk, the relative predictions were less variable and were useful for ranking the level of threat faced by a species and deciding on the best management strategy. With 10 years of data, the mean of the ranges of the inner ninetieth percentile of extinction risk was 0.39, with a median of 0.09 (Fig. 1a). For 25% of the 160 parameter combinations, however, the inner 90th percentile range was >0.96 (Fig. 1a), indicating the considerable uncertainty that may occur in the absolute predictions. As the years of available data increased, the precision of the predictions increased, such that the inner 90th percentile range was reduced to approximately zero for more than 50% of the 160 parameter combinations when 100 years of data were available (Fig. 1a). When the simulations were assessed with the expected minimum population size, the range in the predictions was greater but had a similar pattern (Fig. 1b).

As expected, the predicted changes in the risks of extinction due to either increasing growth rates or increasing carrying capacity were more precise than the absolute predictions (Fig. 2). Even with only 10 years of data, the inner 90th percentile ranges of the change in the risk of extinction due to increases in the carrying capacity were <0.11 for all 160 parameter combinations. The median of the 160 different inner 90th percentile ranges was 0.00. This value was 0.05 when changes from increasing the population growth rate were considered. With 100 years of data, the inner 90th percentile ranges of the changes in the risks were all <0.075 (for increases in the carrying capacity) or <0.42 (for increases in the population growth rate). When the simulations were assessed with the change in the expected minimum population size, the range in the predictions was greater, although the pattern was similar to that for the risk of extinction (Fig. 2c & 2d).

When only one set of simulations for each of the 160 parameter combinations was used, the Spearman rank correlation between predicted risks of extinction and the true risks was 0.59 when predictions were based on

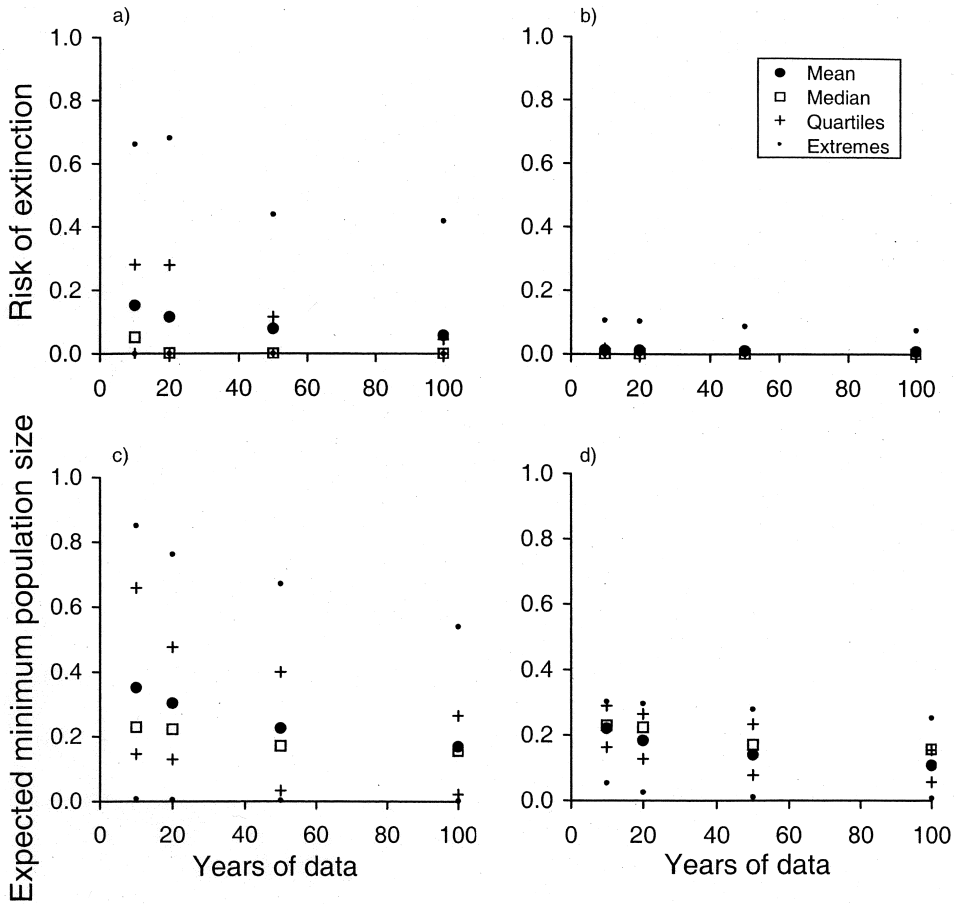


*Figure 2. (a & b) Inner 90th percentile range of the change in the extinction risk and (c & d) expected minimum population size for the 1000 simulations versus the number of years of data. Changes due to a 5% increase in the population growth rate (a & c) and a 50% increase in carrying capacity (b & d) are shown. The results show the median, mean, quartiles, and extremes for the 160 different parameter combinations. The change in the expected minimum population was scaled between 0 and 1 by dividing by the initial population size.*

10 years of data, increasing to 0.89 when 100 years of data were available. When the expected minimum population size was analyzed, the correlation between the predicted and true values was 0.90 with 10 years of data, increasing to 0.98 with 100 years of data (Fig. 3).

Finally, the simulations demonstrated that for 67% of the 160 different parameter combinations, 10 years of survey data were sufficient to identify the management strategy—to increase population growth rate or increase carrying capacity—that minimized the risk of extinction. The correct decision was made 74% of the time with 10 years of data, when analyzed in terms of the expected minimum population size (Fig. 4). The probability of making the correct decision increased to 0.92–0.93 (for extinction risk and expected minimum population size) when 100 years of data were available. There was no clear relationship between the chance of making a correct decision and the parameter values describing the population dynamics.

## Discussion

Previous tests of PVAs have assessed their predictive value (Ludwig 1999; Brook et al. 2000; McCarthy & Broome 2000; McCarthy et al. 2000), yet it is commonly believed that PVAs are most useful for their heuristic value and their ability to aid decision-making (Burgman et al. 1993; Possingham et al. 1993; Burgman & Possingham 2000). When PVA is used as a decision-support tool, it is important that predicted changes in the risks of extinction due to management are reliable, that the relative risks faced by different species are predicted accurately, and that the models can be used to help decide the most effective management strategy. The results of our study indicate that even when only 10 years of data are available, the models may be used to inform management decisions that involve making predictions 100 years into the future. This occurred because the predicted changes in the risks were considerably less vari-

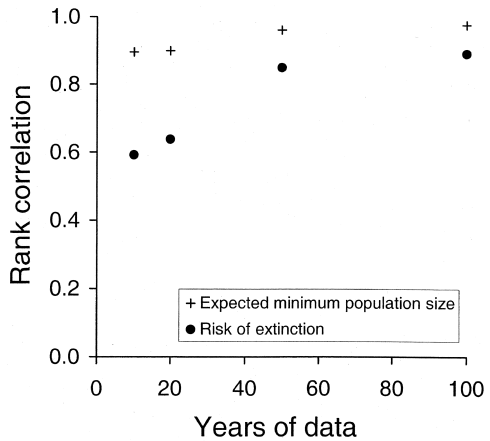


*Figure 3. Spearman rank correlation coefficient between the true risks of decline (extinction risk and expected minimum population size) and those predicted by a single data set (10, 20, 50, or 100 years of data) for each of the 160 different parameter combinations.*

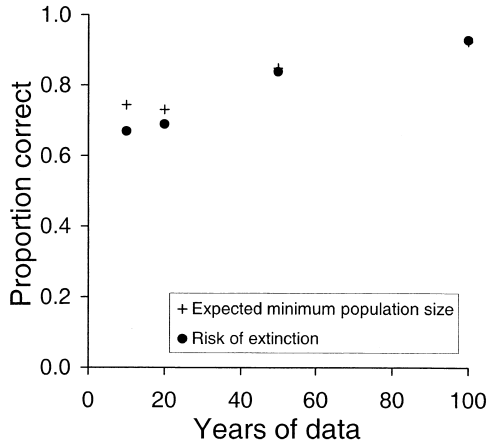


*Figure 4. Proportion of the 160 parameter combinations for which the correct management decision (50% increase in carrying capacity or 5% increase in population growth rate) was made when assessed by means of the change in the risk of extinction or in the expected minimum population size.*

able than the absolute risks. Also, when species were compared, the predicted risks faced by the different species were positively correlated with the actual risks. And—perhaps most important—the results indicated that the model could help identify the best of two competing management strategies, with rates of correct decision-making being better than random when only 10 years of data were available. This supports the assertion that, despite uncertainty in the predictions, PVA can be useful as a decision-support tool (Possingham et al. 1993; Akçakaya & Raphael 1998).

The predicted changes in the risks of decline due to increases in carrying capacity were considerably more reliable than the changes due to increases in the population growth rate. This is likely to occur because wide deterministic fluctuations (either limit cycles or chaos) were predicted for many of the data sets, such that increases in the population growth rate could increase rather than decrease the risk of decline. In these circumstances, it is more likely that management strategies favoring increases in carrying capacity would be chosen. This meant that in cases where an increase in the population growth rate was the best strategy, the correct decision was made less frequently than when an increase in the carrying capacity was the best strategy. For example, with 10 years of data, analyzed in terms of the expected minimum population size, the correct decision was made 84% of the time when increasing the carrying capacity was the best strategy but only 65% of the time when increasing the population growth rate was the best strategy.

For 68% of the parameter combinations, the true risk of extinction within 100 years was approximately 0. For risks close to 0 (or 1), the range of uncertainty can be somewhat truncated, meaning that there tends to be greater uncertainty when risks are close to 0.5. This is why we also assessed risks of decline in terms of the expected minimum population size: this value (as a proportion of the initial population size) had true values that were distributed relatively uniformly between 0.01 and 0.88. These results were less influenced by the possible truncation of values close to 0 or 1 and therefore provide a clearer representation of the uncertainty associated with the predictions.

Although we argue that the relative predictions of PVA are more important than the absolute predictions, tests of absolute predictions based on field data remain important (McCarthy et al. 2001). Such tests of absolute predictions should not focus on determining the truth of PVA models. As with any model, PVA should and always will be an imperfect description of reality, and it is misguided to use the model testing to indicate whether PVA is "right" or "wrong." Clearly, some models will make poor predictions and others will make better predictions. The role of model testing should be to identify the weakest aspects of the model so that its predictions can be improved. Although the results of our study suggest that PVA can assist such decisions even when the predictions remain uncertain, PVA predictions should be assessed with field data so that the models (and therefore the decisions based on them) can be improved further. The process of parameter estimation, model construction, prediction, and assessment should be viewed as a cycle rather than a one-way street (McCarthy et al. 2001; Lindenmayer et al. 2003).

In our simulation study, the only data available for estimating the parameters were the 10- to 100-year time se-

ries from a single population. Although 100 years of data may be a larger data set than is available for many endangered populations, we routinely have more data than just a single time series. For example, surveys of multiple populations for 15 years have produced almost 60 years of time-series data for mountain pygmy possums (*Burramys parvus*) in New South Wales and additional data on the population ecology of the species from other parts of its range in Australia (McCarthy & Broome 2000). In another example, McCarthy et al. (1999) used data from other raptors to help obtain an estimate of mortality rates for the Powerful Owl (*Ninox strenua*). When a real PVA is conducted, such information from other species or populations, additional life-history data (e.g., litter sizes), and ecological intuition all contribute to determining parameter estimates. Such additional data would be equivalent to increasing the length of the time series because it would help decrease the uncertainty associated with predictions of the risk of extinction.

Fieberg and Ellner (2000) investigated the precision of absolute risks and concluded that the length of the time series needed to be 5–10 times the time frame of the predictions for PVA to be reliable. So, to make reliable predictions of risk 100 years into the future, 500–1000 years of data would be required. In contrast, our results suggest that if relative risks are required, it may be possible to make useful predictions 100 years into the future based on only 10 years of data, which is a substantial improvement. When this result is evaluated, it should be kept in mind that our study ignored other sources of uncertainty, including imperfect knowledge of density dependence, imperfect knowledge of differences between individuals (e.g., differences that may relate to age structure and genetics), and imperfect survey methods leading to errors in the estimation of population size. The reliabilities of both the relative and absolute predictions of PVA in the face of such uncertainties remain to be determined. Nevertheless, our results suggest that there is some hope that the relative predictions of PVA will remain useful given realistic amounts of data.

Because of uncertainty about predictions of PVA, it has been suggested that levels of threat be determined by rule sets and similar methods (e.g., Millsap et al. 1990; World Conservation Union 1994) that do not rely on developing a population model (Beissinger & Westphal 1998). However, these alternatives may also be subject to considerable uncertainty (e.g., Burgman et al. 1999). When considering whether or not to use PVA, investigators need to bear in mind the other advantages of PVA. Population viability analysis can use more data, the level of detail in the model is flexible so that an appropriate level of complexity can be chosen, and there is an explicit relationship between the parameters of the model and the fate of the population. An additional advantage of PVA over the alternatives for classifying the conservation status of species is that the population models can be used to improve management strategies. The results of this study suggest that, despite uncertainty, PVA can contribute to the effective management of threatened species.

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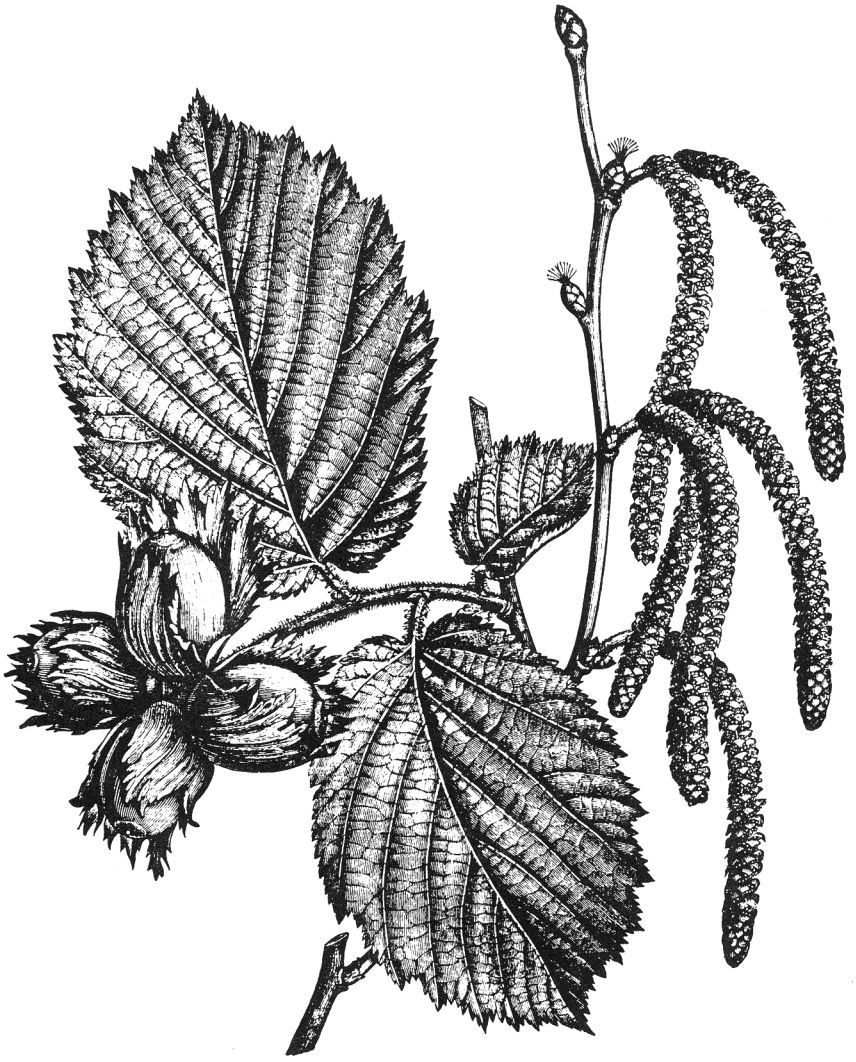
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