SENSITIVITY ANALYSIS FOR MODELS OF POPULATION VIABILITY

Michael A. McCarthy*
Forestry Section, University of Melbourne, Parkville, Victoria 3052, Australia

Mark A. Burgman
Forestry Section, University of Melbourne, Creswick, Victoria 3363, Australia

&

Scott Ferson
Applied Biomathematics, 100 North Country Road, Setauket, NY 11733, USA

(Received 4 November 1993; accepted 8 March 1994)

Abstract
A method of sensitivity analysis for population viability models is presented that uses logistic regression to evaluate the importance of model parameters that influence the risks of extinction. This approach is used to evaluate the importance of fecundity parameters and the initial number of non-breeding birds in a stochastic stage-structured model of helmeted honeyeater Lichenostomus melanops cassidix population dynamics. The regression analysis indicates which model parameters have the greatest impact on the risk of population decline. The results demonstrate that a simple expression containing the parameters of the model can encapsulate predictions of risk. This technique is proposed as an efficient alternative method of sensitivity analysis for population viability models. Of four fecundity parameters, the mean fecundity of intact pairs had the greatest influence on the risks faced by the helmeted honeyeater population. Mean fecundity of split pairs and the sex ratio of offspring were also important parameters. Over the range of parameters considered in this paper, environmental variation in fecundity and the initial number of non-breeding birds had little influence on the risks of decline. The importance of interactions between parameters was analyzed.

Keywords: sensitivity analysis, population viability, extinction, logistic regression.

INTRODUCTION
Sensitivity analysis is an important component of modelling. It provides practical information for model builders and users by highlighting the parameters that have the greatest influence on the results of the model. Sensitivity analysis can highlight model parameters that ought to be most accurately measured so as to maximise the precision of the model, give a general indication of the reliability of the model predictions, and highlight parameters and interactions that have the largest influence on the population to help determine effective management strategies.

Models of natural populations may become complex, particularly when individuals are modelled, and understanding the relative importance of different parameters and interactions between parameters may become computationally difficult. However, sensitivity analysis is employed only occasionally in population viability analysis (PVA), despite its benefits and the importance of using it when assessing management options (Possingham et al., 1993). Usually, sensitivity analysis is measured by varying a parameter by a small amount around its estimated value. The resulting change in the state variable provides an index of sensitivity of the model to that parameter (e.g. Burgman et al., 1993). Applications of PVA to biological conservation would be improved with the use of sensitivity analysis.

The sensitivity and elasticity of the deterministic growth rate of matrix models can be determined analytically by eigen analysis (Caswell, 1978; de Kroon et al., 1986). However, extension of these techniques to models of population viability is not appropriate for at least three reasons: (1) population viability models tend to be nonlinear so obtaining analytical solutions is often complex if not impossible; (2) in PVA the result of interest is the risk of population decline rather than the deterministic growth rate (Burgman et al., 1993); and (3) these analytical methods cannot determine if there are any significant interactions between parameters.

There is no single, universally accepted procedure for the sensitivity analysis of stochastic models, but Swartzman and Kaluzny (1987) recommend characteristics that should be evident in such a method. The method should be clearly defined, interactions between parameters should be distinguishable from single
parameter effects, and the method should account for the variability associated with parameter estimates, and allow interpretation of several output variables.

The sensitivity of PVA models is best expressed in terms of the change in the risk of quasextinction (defined as the risk of decline to any specified threshold, Ginzburg et al., 1982). For the majority of recently published PVA models, only limited, if any, sensitivity analysis of the risk of population decline has been conducted (e.g. Beudels et al., 1992; Burgman & Lamont, 1992; Durant & Harwood, 1992; Haig et al., 1993; McCarthy et al., 1994) although there are exceptions (e.g. Beier, 1993).

The lack of sensitivity analysis for most PVA models is likely to be due to practical difficulties. For example, one method of sensitivity analysis would be to determine quasextinction risk for an exhaustive array of model parameters. If there are 10 parameters and three levels for each parameter then 21 different parameter combinations would be necessary to assess each parameter independently. However, $3^{21} = 59049$ different combinations are required to allow for all possible interactions. Such a large number of combinations causes numerous practical problems, not the least of which includes large computational time and difficulty in interpreting the vast array of results. A factorial design may be used to reduce the number of simulations (Henderson-Sellers & Henderson-Sellers, 1993), but this means that not all interactions may be assessed. The purpose of this paper is to describe, with an example, a potentially more efficient approach to sensitivity analysis that reduces the computational effort required and which serves to summarise the effects of different parameters and interactions.

METHODS

The exhaustive approach to sensitivity analysis described above attempts to describe the form of the relationship between the model parameters and the risk of population decline. Logistic regression can be used to perform a similar task. The difference is that logistic regression determines a 'line' (actually a multi-dimensional plane) of best fit for the relationship rather than providing exact values for specified points in the parameter space.

Logistic regression is useful to describe a binary response (e.g. extinction or persistence) as a function of one or more explanatory variables (Hosmer & Lemeshow, 1989). The dependent variable of the analysis is whether or not the outcome of interest occurs. Logistic regression is based on a generalised linear model of the form

$$\logit(p) = \ln \left( \frac{p}{1-p} \right) = \beta_0 + \beta_1 X_1 + \ldots + \beta_n X_n,$$

where $p$ is the probability of an event occurring, $X_i$ is the $i$th independent variable and $\beta_i$ is the regression coefficient (Hosmer & Lemeshow, 1989). An interaction may be included in the regression by using the product of the interaction variables as an additional variable in eqn 1.

In standard linear regression and analysis of covariance, it is assumed that the dependent variable is normally distributed, which will be invalid when the result is binary. In contrast, logistic regression specifically accounts for binary dependent variables. Logistic regression may be used to predict the probability of a binary event occurring as a function of a set of independent variables.

Logistic regression has a wide utility. For example, Griffith et al. (1989) used it to determine factors that influence the chance of successfully releasing animals from captivity, Austin et al. (1990) to characterise the realised niche of species of Eucalyptus, and Lindenmayer et al. (1990) to predict from particular forest characteristics the probability of occupancy of hollow-bearing trees by arboreal marsupials.

Given that extinction is a binary outcome, it seems reasonable to use logistic regression to predict the risk of population decline from the parameters of a model of population viability. Logistic regression can be used to approximate the complex function that relates the model parameters to quasextinction risk. When scaled against the parameter uncertainty, the value of regression coefficients will indicate the relative contribution of the parameter to the risk of quasextinction. The importance of interactions between parameters can be investigated. The usefulness of this method can be assessed by the accuracy of the approximation, i.e. the agreement between the predictions of quasextinction risks obtained from the logistic regression equations and those estimated directly from the population model.

Logistic regression was used to conduct sensitivity analysis of a model of the last remaining population of the helmeted honeyeater Lichenostomus melanops casidix. Backhouse (1987), Smales et al. (1990) and Menkhorst and Middleton (1991) have reviewed its conservation status. In September 1992 the single remaining wild population of 67 birds was restricted to localities within and adjacent to the Yellingbo State Nature Reserve in south-central Victoria, Australia. This paper presents results of the sensitivity analysis and an assessment of its accuracy.

The population model

A brief description of the helmeted honeyeater population model used in this paper is presented below. It is related to models presented by McCarthy et al. (1994), but also incorporates aspects of spatial structure and environmental variation. The model was developed through consultation with members of the Helmeted Honeyeater Recovery Team. Menkhorst and Middleton (1991) described the collection of the behavioural and ecological information upon which the model is based.

The helmeted honeyeater population at Yellingbo is composed of several separate breeding groups of between one and 11 pairs that are up to 4 km apart. Non-breeding birds or floaters may establish temporary territories on the periphery of the breeding territories,
but also may remain undetected for several months. The population model accounts for this spatial structure by modelling groups separately and determining the level of dispersal between them.

The model accounts for males and females separately and distinguishes between breeding and non-breeding birds. Opportunities to breed are restricted by the age of the bird, the availability of mates of the appropriate age and sex, and by access to a limited amount of suitable habitat. Territoriality and natal dispersal are controlled by a peck order that is based on sex, age and breeding status. The model was analysed by individual-based computer simulation at 6-month time steps since this is the time scale of reproduction of the helmeted honeyeater.

Helmeted honeyeater pairs that remain intact throughout their 6-month breeding season produce more offspring than pairs in which one or both of the birds die (McCarthy et al., 1994). The mean fecundity per pair was varied each year by generating a random normal variate with a specified mean and coefficient of variation. This coefficient of variation in fecundity reflected annual variation in the environment that may be attributed to unpredictable events such as the loss of nests to predation and floods. The actual number of young raised by each breeding pair was sampled from a Poisson distribution. The sex of each offspring was determined randomly. Thus, four parameters control reproduction in the model: mean fecundity of split pairs, mean fecundity of intact pairs, sex ratio, and coefficient of variation in mean fecundity. Uncertainty about the estimation of these four parameters was considered in the sensitivity analysis. Methods of parameter estimation and estimated parameter values are described in McCarthy et al. (1994).

Regression analysis
The stage-structured model was used to generate data for the logistic sensitivity analysis using a random sampling procedure (Swartzman & Kaluzny, 1987). This analysis related the fecundity parameters of the model to the risk of population decline to zero and 30. The procedure involved the random generation of the four fecundity parameters independently of each other from uniform distributions. The range of variation of each parameter reflected the scale of uncertainty in its estimation. Therefore, the two mean fecundity rates, annual coefficient of variation of these rates and sex ratio, were changed randomly for each set of parameters. Each set of parameters was recorded and the model was run 10 times. For each of these runs, the minimum population size within the first 50 years was recorded. A total of 500 different sets of parameters was used, giving a total of 5000 replicates of the model.

Uncertainty about the initial stage distribution of the population is another potential source of uncertainty associated with population forecasts. Burgman et al. 1995 have shown that risks of decline may be sensitive to the initial proportion of individuals in the stage classes of a population model. Therefore, the influence of uncertainty about the initial distribution of helmeted honeyeaters was investigated. The sex of territorial birds can be determined by behavioural characteristics associated with breeding, and their numbers are known with a high degree of accuracy (McCarthy et al., 1994). In contrast, determining the sex of non-breeding birds is less reliable. Morphological differences between the sexes of the helmeted honeyeater are small, so if breeding behaviour is not observed then sex remains unknown or is based on subjective assessment. Also, these floaters are observed less frequently, so there is some uncertainty about the actual number in the population (D. C. Franklin and I. J. Smales, pers. comm.).

In this analysis the dependent variable was whether or not the population fell below a specified threshold for a particular combination of parameters. The independent variables of the regression were the model parameters. For logistic regression it is assumed that changes in the parameters cause a linear change in the logit of the dependent variable. Therefore, it was necessary to be sure that this assumption was satisfied. Hosmer and Lemeshow (1989) discussed various methods for checking that the logit of the probability is linear with respect to the independent variables. One of the simplest of these methods is to plot the independent variables versus the logit of the probability of decline. The data were grouped into 10 evenly spaced categories to smooth the plots. For each category the proportion of runs in which the population fell below the specified threshold was determined. This proportion was transformed to the logit (eqn 1) and plotted against the category value. Visual inspection indicated that the number of young per pair and the coefficient of variation in fecundity were roughly linear in the logit, while the sex ratio appeared nonlinear so a quadratic term was included (Fig. 1).

The regression coefficients were obtained by maximum likelihood estimation using iterative reweighted least-squares regression (Hosmer & Lemeshow, 1989). After selection of the logistic regression equations, quasiextinction risks were estimated directly from the population model to assess the accuracy of the regression predictions. Each variable was analysed at five levels over the range used in the logistic regression analysis. All 625 (=5^5) combinations were investigated by conducting 1000 simulations for each combination. This method of direct estimation of risks over a range of parameter values can be regarded as the traditional, exhaustive approach to sensitivity analysis of population viability models. It required a total of 625,000 simulations while the logistic regression method required only 5000 simulations.

Helmeted honeyeaters breed monogamously and the number of males and females in the population appears to be equal. However, as noted above, these estimates may be unreliable because it is difficult to determine the sex of these non-breeding birds and even if the equilibrium sex ratio was 1, random perturbations may change the actual number. Furthermore, the number of floaters is not known precisely but in the previous sim-
Fig. 1. Plots of the logit of the probability of decline versus fecundity parameters for decline to 30 individuals (C) and complete extinction of the helmeted honeyeater (D). The data were grouped into 10 categories to smooth the curves. The plots indicate that fecundity of split pairs, fecundity of intact pairs and coefficient of variation in fecundity are approximately linear with respect to the logit. Sex ratio appears to be nonlinear.

ulations it was assumed that there were 12 female and 11 male floaters. To investigate the importance of these sources of uncertainty, the initial number of floaters was included in a logistic sensitivity analysis. The initial number of female floaters was varied between 6 and 18, around a mean of 12, and the number of male floaters was varied independently of the females between 5 and 17, around a mean of 11.

In this example, we have ignored the possibility that fire might destroy the population. Fires are relatively common in south-east Australia and have caused the ultimate extinction of two of the last three populations of helmeted honeyeaters (Menkhorst & Middleton, 1991). Akçakaya et al. (this issue) demonstrate that fire may have an important impact on the risk of decline of the helmeted honeyeater and it may affect the preferred spatial structure of the metapopulation. Although fire will change the risks of extinction, it is likely to have little or no effect on the relative sensitivity of the model to the fecundity parameters and the initial number of floaters. Therefore, the chance of fire was ignored in this study.

RESULTS

Backward stepwise variable selection indicated that the coefficient of variation in fecundity was the only unimportant fecundity parameter. For a quasixtinction threshold of 30, interaction between the fecundity of split pairs and the fecundity of intact pairs was impor-

tant. Other interactions, including three-way terms, were not important. The results of the logistic regression analysis lead to the following two equations for predicting the risk of population decline

$$\logit[q(0)] = 22.538 - 2.655F_s - 5.578F_i - 60.186S - 57.519S^2,$$

and

$$\logit[q(30)] = 30.458 - 9.058F_s - 8.260F_i + 4.649F_sF_i - 68.325S + 66.562S^2,$$

where $q(T)$ is the risk that the population will decline to $T$ individuals or fewer at least once within 50 years. $F_s$ is the mean fecundity of split pairs, $F_i$ is the mean fecundity of intact pairs and $S$ is the sex ratio.

Graphs of predicted risk of decline versus each of the fecundity parameters are given in Fig. 2. Quasixtinction risk versus sex ratio is shown in Fig. 3 for five levels of fecundity of intact pairs. For comparison, estimates of risks obtained directly from the model are also shown in Figs 2 and 3. The regression predictions were also plotted against the direct estimates for all 625 different parameter combinations (Fig. 4). Figures 2, 3 and 4 indicate that the logistic regression predictions and the direct estimation method generate similar results. Within the parameter range considered, the logistic regression predictions are reasonable approximations for risks of decline estimated directly from the helmeted honeyeater population model.

Of the fecundity parameters, uncertainty in the number of young raised per intact pair has the greatest

Fig. 2. Quasixtinction risk of the helmeted honeyeater versus fecundity parameters as predicted by the logistic regression equations. For each relationship the other parameters in the logistic regression equations were held constant at their mean value. For each case the dashed line is the risk that the population will decline to 30 and the solid line is the risk of extinction. The circles represent risks that were calculated from 1000 simulations of the population model to test the accuracy of the regression equations.
Fig. 3. Risk of decline to 30 individuals (a) and risk of complete extinction (b) versus sex ratio for the helmeted honeyeater as predicted by the logistic regression equations. For each case, the risk of decline is shown for five levels of fecundity of intact pairs (F = 1.08, 1.26, 1.44, 1.62, 1.80). The symbols represent risks that were calculated from 1000 simulations of the population model to test the accuracy of the regression equations.

Fig. 4. Comparison of the risk of population decline predicted by the regression equations and that estimated directly from 1000 simulations of the population model, for decline to 30 individuals (a), (c) and complete extinction (b), (d) of the helmeted honeyeater. Residual plots (c), (d) show the difference between the risks obtained from the two methods versus the risks estimated directly from the model. The risks were determined for the 625 parameter sets that represent all combinations of five levels of fecundity parameter.

impact on the risks of population decline (Fig. 2). Over most of its range, variation in fecundity of intact pairs causes important changes in the risk of decline. In comparison, when the sex ratio varies between 0.45 and 0.55, the risk of population decline changes only slightly. However, a sex ratio lower than 0.4 can increase the risk of population decline. The model is relatively insensitive to uncertainty in the fecundity of split pairs. Over the range considered in this paper, uncertainty about the coefficient of variation in mean fecundity of pairs is unimportant in the helmeted honeyeater model. Other simulations suggest that even quite large annual variation in fecundity (30%) causes the risks of population decline to increase only slightly (=5%).

Logistic regression analysis indicated that, over the range considered, neither the number of male floaters nor the number of female floaters contributed to the risk of population decline to 30 individuals. The regression suggested that the number of male floaters had an important effect on the risk of extinction, but the change in the risk is only small given various numbers of birds (Fig. 5) because of the small regression coefficient. The equation describing the effect of the initial number of floaters on extinction risks is

\[ \log(\theta(0)) = -2.5318 - 0.0551MF, \]

where \( MF \) is the number of male floaters.

**DISCUSSION**

The method proposed in this paper involves fitting a multiple regression equation to data generated by a population model over a specified range of parameters. The resulting equation approximates the complex function that relates the parameters of the population model to the predicted risks of decline. Essentially, any form of regression analysis could be used to obtain an
approximation of this function. However, standard least squares regression requires that the dependent variable be normally distributed, which is an invalid assumption when the result of interest is expressed as a probability. Logistic regression is particularly suitable because it specifically accounts for the dependent variable being a probability and the required data are easily generated from the model. However, the accuracy of the method relies on ensuring that the logit is linear with respect to the variables in the equation. In the above example it was necessary to add a quadratic term to account properly for the nonlinear effect of the sex ratio. Hosmer and Lemeshow (1989) discussed methods for detecting and accounting for nonlinearity in logistic regression.

The importance of regression parameters is normally assessed by statistical measures of their significance (p-values). In the proposed sensitivity analysis the significance of the parameters is a function of the somewhat arbitrary sample size. Therefore, statistical significance is a rather meaningless measure of the importance of a parameter. However, parameters that have a large influence on extinction risks will be more significant than less important variables. In this analysis main effects were included in the regression equations when their p-values were less than 0.05. The fecundity parameters that were included in the equations had p-values less than 0.001. Coefficient of variation in fecundity, which was eliminated from the regression equation, had a p-value greater than 0.4. It is worth noting that the importance of a variable is reflected in the magnitude of the coefficient. To that end, the relative importance of a parameter is reflected in the relative magnitude of its standardised regression coefficient, i.e. the value of the regression coefficient when scaled against the uncertainty. Even though the initial number of male floaters had a low p-value (p = 0.03) its small regression coefficient indicates that, over the range considered in this paper, it has little effect on risks of decline.

An apparent tenet of population viability analysis is that, in general, environmental stochasticity has a greater impact on extinction risks than demographic stochasticity (Burgman et al., 1988; Simberloff, 1988; Boyce, 1992). However, this belief is often based on models that may underestimate the importance of demographic stochasticity (Gilpin, 1992; McCarthy et al., 1994). This study suggests that environmental variation in fecundity, reflected in the coefficient of variation, has little impact on the risks faced by the helmeted honeyeater. The risks due to demographic stochasticity (McCarthy et al., 1994) may be substantially greater than those due to environmental variation in fecundity. The likely reason that the risks of decline are relatively insensitive to annual variation in fecundity is that reproduction is averaged over a number of years, so a few bad reproductive years can be compensated for by a few good years. In comparison, variation in the survival of breeding birds would cause an immediate impact on population size and its future productivity. Therefore, it is likely that environmental variation in survival will have an important effect on extinction risks. It is important to remember that previous attempts to assess the importance of environmental stochasticity have used unstructured models (e.g. Goodman, 1987), and it was not possible to compare the effect of variation in fecundity with that of variation in survival. In general, as the number of breeding opportunities of individuals increases, environmental variation in fecundity may become less important because periodic variation in fecundity will have a less direct impact on variation in population size. Various studies have considered the evolutionary significance of such risk-spreading strategies (Schaffer, 1974; Goodman, 1984). Perhaps a more useful measure of variation in fecundity would be variation in lifetime reproductive success.

Over the range considered in this paper, the total number of floaters has little impact on the risks of extinction, so uncertainty about the sex ratio of floaters appears unimportant. The insensitivity of the model to the number of floaters indicates that changing the population size will have little impact on the risks of extinction. The likely reason for this is that an apparent lack of available breeding habitat (Pearce et al., 1994) is currently one of the greatest threats to the population, and once the population fills the available habitat, further increases in the number of birds may have little benefit (McCarthy, 1995). Increasing the amount of available habitat, perhaps through translocation to other areas or by vegetation management at Yellingbo, will decrease the risks faced by the helmeted honeyeater.

The removal of a few floaters from the current population will lead to a relatively small increase in the risk of decline of the Yellingbo population. However, the use of these birds for translocation to form another colony may not reduce the overall risk to the species in the wild (Akçakaya et al., this issue; McCarthy, 1995). This is because small isolated populations of helmeted honeyeaters, such as those that may result from translocation, are particularly vulnerable to extinction (Smale et al., 1990; Menkhors & Middleton, 1991; McCarthy, 1995). On the other hand, translocation to areas in and around Yellingbo State Nature Reserve would increase the size of the breeding population and may be more effective for reducing risks of decline.

In the future, it may be desirable to decrease the level of monitoring of the helmeted honeyeater population. Territorial birds tend to move only short distances and during the breeding season they rarely leave their territory. In comparison, floaters are highly mobile and may remain unsighted for up to several months. In less thorough monitoring programmes it is likely that the floaters will be sighted less often and the population size will be underestimated. However, risk of decline is relatively insensitive to the number of floaters, so it is likely that the number of territorial birds will provide a good indication of the population's viability. Therefore,
monitoring programmes that do not count floaters may still provide useful information for management. The important impact on quasixtinction risk of the interaction between fecundity of split pairs and fecundity of intact pairs is probably due to the influence of pair survival on fecundity. As the two fecundity rates diverge, annual variation in population fecundity and correlation between fecundity and survival will increase. This increased variation and correlation will amplify fluctuations in population size and increase the risk of decline. McCarthy et al. (1994) discuss the importance of these and other demographic characteristics in population modelling of the helmeted honeyeater.

Changes in the level of environmental variation in fecundity and the number and sex ratio of floaters have little impact on predicted extinction risks. Therefore, uncertainty associated with the estimation of these values is relatively unimportant and predictions of the model can be regarded with greater confidence. As with any model, the predicted risks may not necessarily reflect the risks faced by the population because important aspects of the bird’s ecology may be overlooked. However, changes in predicted risks, due to changes in parameters or initial conditions, are likely to reflect the actual costs and benefits to the populations. Logistic regression can be used to provide information about the relative magnitude of these costs and benefits in an efficient manner. It is these relative risks that are most useful for ranking management options (Possingham et al., 1993).

The logistic regression equations are good summaries of the results obtained from the helmeted honeyeater population model. Over a specified range of parameter values, these equations can provide estimates of the risk of population decline more efficiently than standard PVA simulation. The regression analysis highlights the most important model parameters and their relative importance in an efficient and easily interpretable manner. This method of sensitivity analysis can be applied to models of population viability to help direct the efficient allocation of resources for conservation.

ACKNOWLEDGEMENTS

The members of the Helmeted Honeyeater Recovery Team, coordinated by Peter Menkhorst, provided essential information required during the development of the population model. Don Franklin and Ian Smales have been particularly helpful. We have benefited from discussions with Jennie Pearce and Debbie McDonald. This work was conducted in part while M. McCarthy was visiting the Department of Ecology and Evolution at the State University of New York at Stony Brook from the University of Melbourne. He thanks the faculty, staff and students at E&E, particularly Lev Ginzburg who facilitated his visit. We are grateful to Tony Norton and an anonymous reviewer for comments that improved this manuscript.

REFERENCES


