

The Sensitivity of Population Viability Analysis to Uncertainty about Habitat Requirements: Implications for the Management of the Endangered Southern Brown Bandicoot

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Abstract: *Whenever population viability analysis (PVA) models are built to help guide decisions about the management of rare and threatened species, an important component of model building is the specification of a habitat model describing how a species is related to landscape or bioclimatic variables. Model-selection uncertainty may arise because there is often a great deal of ambiguity about which habitat model structure best approximates the true underlying biological processes. The standard approach to incorporate habitat models into PVA is to assume the best habitat model is correct, ignoring habitat-model uncertainty and alternative model structures that may lead to quantitatively different conclusions and management recommendations. Here we provide the first detailed examination of the influence of habitat-model uncertainty on the ranking of management scenarios from a PVA model. We evaluated and ranked 6 management scenarios for the endangered southern brown bandicoot (*Isodon obesulus*) with PVA models, each derived from plausible competing habitat models developed with logistic regression. The ranking of management scenarios was sensitive to the choice of the habitat model used in PVA predictions. Our results demonstrate the need to incorporate methods into PVA that better account for model uncertainty and highlight the sensitivity of PVA to decisions made during model building. We recommend that researchers search for and consider a range of habitat models when undertaking model-based decision making and suggest that routine sensitivity analyses should be expanded to include an analysis of the impact of habitat-model uncertainty and assumptions.*

Keywords: decision-theoretic approach, dynamic landscape metapopulation modeling, habitat modeling, *Isodon obesulus*, logistic regression, model uncertainty, population viability analysis, sensitivity analysis, southern brown bandicoot

La Sensibilidad del Análisis de Viabilidad Poblacional a la Incertidumbre sobre Requerimientos de Hábitat: Implicaciones para el Manejo de *Isodon obesulus*

Resumen: *Cuando los modelos de análisis de viabilidad poblacional (AVP) son construidos para ayudar a la toma de decisiones sobre el manejo de especies raras y amenazadas, un componente importante del modelo es la especificación del modelo de hábitat que describa cómo se relaciona una especie con las variables bioclimáticas o del paisaje. La incertidumbre de selección del modelo puede surgir porque a menudo hay mucha ambigüedad sobre la estructura de modelo de hábitat que mejor se aproxima a los procesos biológicos reales subyacentes. El método estándar para la incorporación de modelos de hábitat en los AVP es asumir que el mejor modelo de hábitat es correcto, ignorando la incertidumbre del modelo de hábitat y modelos*

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alternativos que pueden llevar a conclusiones y recomendaciones de manejo cuantitativamente diferentes. Aquí, proporcionamos el primer examen detallado de la influencia de la incertidumbre de modelo de hábitat sobre la clasificación de escenarios de manejo de un modelo de AVP. Evaluamos y clasificamos 5 escenarios de manejo para *Isoodon obesulus* con modelos de AVP, cada uno derivado de modelos de hábitat verosímiles desarrollados mediante regresión logística. La clasificación de escenarios de manejo fue sensible a la selección del modelo de hábitat utilizado en las predicciones del AVP. Nuestros resultados demuestran la necesidad de incorporar métodos a los AVP que expliquen la incertidumbre del modelo y resalten a sensibilidad de los AVP a las decisiones tomadas durante la construcción del modelo. Recomendamos que los investigadores busquen y consideren un rango de modelos de hábitat cuando se involucren en la toma de decisiones basadas en modelos y sugerimos que los análisis de sensibilidad rutinarios se expandan para incluir un análisis del impacto de la incertidumbre del modelo de hábitat y sus supuestos.

Palabras Clave: análisis de sensibilidad, análisis de viabilidad poblacional, incertidumbre del modelo, *Isoodon obesulus*, método de decisión teórica, modelado del hábitat, modelado de metapoblación en un paisaje dinámico, regresión logística

Introduction

Population viability analysis (PVA) is often used in conservation biology to help guide management decisions in the recovery of rare and threatened species (Lindemayer & Possingham 1996). Whenever PVA models are built, numerous decisions must be made with respect to parameter values and model structures (Pascual et al. 1997). Model builders usually justify decisions through a mix of ecological knowledge, parsimony, and statistical best-fit criteria, but in most cases there will be a variety of parameter values or a range of distinct model structures that appear to work equally well, making it problematic to choose one model over another (Conroy et al. 1995; Burnham & Anderson 1998; Wintle et al. 2003). Despite widespread recognition of the importance of incorporating these uncertainties into inference, many model-building decisions remain largely unaccounted for in PVA predictions, making the uncertainty associated with those decisions difficult to communicate to model users.

An important step in PVA is specification of a habitat model that describes how a species is related to a landscape or bioclimatic variables. A habitat model may take various forms—a regression model (Buckland & Elston 1993), a habitat suitability index (Burgman et al. 2002), a classification tree (Bell 1996), or a machine-learning algorithm—but in the majority of applications defines a mathematical relationship between faunal survey data and mapped environmental variables, such as vegetation type and age (A detailed review of habitat-modeling methods is beyond the scope of our study but can be found elsewhere [Guisan & Thuiller 2005]). A commonly used method for developing habitat models from biological-survey data when presence-absence data are available is logistic regression (McCullagh & Nelder 1989). Logistic regression may be used to predict the probability of species occupancy according to

$$\begin{aligned}\text{logit}(p_i) &= \log[p_i/(1 - p_i)] \\ &= \beta_0 + \beta_1 x_{i1} + \dots + \beta_j x_{ij},\end{aligned}$$

where p_i is the probability that the species is present at site i , β_0 is the intercept coefficient, and β_j represents the influence of the j th independent predictor variable, x_{ij} , on the probability the species is present at site i .

Habitat-model uncertainty may arise because there is often a great deal of ambiguity about which habitat model structure best approximates the true underlying biological processes (Buckland et al. 1997). The structure of the habitat model is defined by the choice of habitat variables, choice of link function, and interactions between habitat variables. A set of alternative habitat models comprising different combinations of habitat variables may fit the observed data almost equally well (Reichert & Omlin 1997), making it difficult for model builders to choose a single-best habitat model. The standard approach to incorporating habitat models into PVA is to use various variable selection methods to select the best (most parsimonious) model from a set of alternatives and assume the best model is correct. Under this assumption, habitat-model uncertainty is ignored and there may be considerable risk in basing inference and predictions on a single habitat model alone (Wintle et al. 2003).

Although some studies explicitly consider the impact of population-model uncertainty on management recommendations (McCarthy et al. 1994; Pascual et al. 1997), we could find no examples in the literature in which the influence of habitat-model uncertainty on PVA-model predictions and management-scenario rankings was measured. The absence of studies measuring the effect of this source of uncertainty on PVA predictions is surprising, given the broad recognition of the uncertainty of model selection (Buckland et al. 1997; Burnham & Anderson 1998) and its potential impacts on inference and prediction. Habitat-model uncertainty has probably been

ignored in PVA predictions because the input of habitat-model uncertainty on management scenario rankings will be context-specific.

Our objective was to test the influence of habitat-model uncertainty in a PVA model framework. We developed a case study for the endangered southern brown bandicoot (*Isoodon obesulus*) on the basis of data availability and uncertainty surrounding the species' habitat requirements. An evaluation of management strategies is needed for this species because increased predation threats and habitat loss have resulted in severe population declines (Paull 1995). We used PVA models to evaluate and rank 6 management options for the species. We based each model on plausible competing assumptions about the species' habitat requirements. The degree to which habitat-model uncertainty affected the ranking of management scenarios provided a practical measure of its importance.

Methods

Study Region and Species

Our study area (1769 km²) was located approximately 50 km southeast of Melbourne, Australia. Many fragmented patches of native forest are present in both private and public tenures, the most significant being the Botanic Gardens, the Langwarrin Reserve, and the Pines Reserve.

The region supports declining populations of *I. obesulus*, a medium-sized (0.4–1.6 kg) terrestrial marsupial and member of the family Peramelidae (Braithwaite 1995). Despite historical records indicating *I. obesulus* once occupied most of the study region, its current distribution has been reduced substantially. The only remaining productive populations protected from fox and cat predation are thought to be located in the Botanic Gardens (T. Coates, personal communication).

The most critical habitat requirement for the species within the study region appears to be the presence of a dense layer of ground and shrub vegetation (Menkhorst & Seebeck 1990; Paull 1995), although it is unclear how this requirement changes in the presence or absence of predators. Theories about the role of fire in mediating habitat availability remain somewhat contradictory (Stoddart & Braithwaite 1979; Lobert 1990).

Data Collation and Fieldwork

We developed competing habitat models for *I. obesulus* by compiling existing presence-absence data and by conducting a species survey within the study region. Existing presence-absence data were obtained from Parks Victoria for 53 plots (40 × 10 m) in the Botanic Gardens and 34 plots (40 × 10 m) in the Pines Reserve. Additional fieldwork was conducted to augment this existing data

and ensure sampling across the range of environmental predictor variables thought to influence *I. obesulus* occupancy.

We used a GIS-based algorithm (Landcare Research Sampling; J. Overton, personal communication, 2006) to randomly select 27 additional plots stratified across broad vegetation types and geographic space, which provided a geographically and environmentally stratified sample of the region when combined with the existing data (Edwards et al. 2006). We located plots with a geographical positioning system and visited each plot once. Although the size of the plot searched should ideally approximate the home-range of the species (Wintle et al. 2005b), we surveyed a plot size slightly smaller (0.25 ha, 50 × 50 m) than existing home-range studies estimate (0.5–6.0 ha; Lobert 1990) to allow for a sufficient number of plots to be surveyed within the limited time available. There was concern over detecting occupancy if the size of the plot was too small, although searching a plot substantially larger than the home range also presents detectability problems (Wintle et al. 2005c).

I. obesulus was assumed present if its characteristic diggings (conical in shape and approximately 15 cm deep) were found within each plot (Catling et al. 2002; Shan et al. 2006). We chose this method of detection over alternative methods such as hair tubing and trapping because of concern over the ability of these methods to detect individuals at low densities (T. Coates, personal communication, 2006). A precautionary approach to positive identification of diggings was used, whereby *I. obesulus* was recorded as absent if doubt surrounded the source of a digging. This may have served to slightly inflate the false-negative observation rate (Wintle et al. 2005c), although a companion study aimed at estimating false-negative observation rates indicated that these rates were negligible (<5%) in our study (D.M.S., unpublished data).

We measured and recorded habitat variables at each plot with the same methods used in the collection of existing survey data. Soil was categorized into 2 classes: sandy or other. The age of vegetation was inferred from fire-history maps and categorized into 3 classes (0–10 years, 11–20 years, >20 years). Whether or not each plot was within vegetation surrounded by fox-proof fencing was recorded, as was the proximity of each plot to the vegetation edge. We also recorded the percentage of litter cover, ground cover, and shrub cover in each plot following methods described by Catling et al. (2002).

Developing and Comparing Candidate Habitat Models

Using available survey data, we modeled variation in the probability of *I. obesulus* occupancy at survey locations as a function of measured habitat-predictor variables with logistic regression (McCullagh & Nelder 1989).

Regression modeling was conducted in the statistical free-ware R (R Development Core Team 2006).

Preliminary analysis of the response shapes of continuous variables was undertaken by fitting smoothing splines according to methods described by Franklin (1998), Austin (2002), and Wintle et al. (2005b). On inspection of preliminary spline fits, it was apparent that nonlinear relationships between *I. obesulus* occupancy and some of the habitat-predictor variables were likely within the range of available survey data. Two ecological interactions between habitat variables were considered plausible after consultations with experts in bandicoot ecology (T. Coates, personal communication): interaction between ground cover and the presence or absence of fox-proof fencing, and the interaction between shrub cover and the presence or absence of fox-proof fencing. Spline terms were used for preliminary investigations into nonlinear response shapes and not in the set of competing habitat models.

All ecologically realistic combinations of habitat-predictor variables and interaction terms made up a set of 240 candidate habitat models. The number of habitat-predictor variables in any given candidate habitat model were constrained to be in suitable proportion to the number of samples in the survey data set. A rough rule of thumb suggests the ratio between the number of samples and the number of habitat variables should be at least 10 (Harrell 2001).

We measured the relative performance of each candidate habitat model with Akaike's information criterion (AIC) (Akaike 1973). The AIC measures the trade-off between model fit and complexity. The model with the lowest AIC is considered most likely to be "best" in terms of this compromise. The model with the lowest AIC is often referred to as the AIC_{best} model (Burnham & Anderson 1998). Change in AIC is a measure of the relative utility of each competing model relative to the best model ($\Delta AIC_i = AIC_{\text{best}} - AIC_i$). The Akaike weight (w_i) of model i ($w_i = \Delta AIC_i / \sum \Delta AIC_i$) provides an indication of the support for model i relative to the other candidate models in the set. Akaike weights approximate the probability that the habitat model is the best among the set of candidate models (Burnham & Anderson 1998).

We did not measure the out-of-sample predictive performance (commonly undertaken with cross-validated receiver operating characteristics [ROC] analysis; Pearce & Ferrier 2000; Wintle et al. 2005b) because the AIC analysis provided a satisfactory characterization of model-selection uncertainty necessary for this study. It is plausible that ROC analysis could be used to characterize model-selection uncertainty by using ROC scores to weight models in a similar way to AIC. Nevertheless, the AIC analysis has the benefit of broadly accepted rules of thumb for competing model comparison (Burnham & Anderson 1998) and a sound theoretical foundation for use in analysis of model uncer-

tainty. An ROC equivalent would be a relatively ad hoc approach to dealing with the issue of model-selection uncertainty.

Dynamic Landscape Metapopulation Model for *I. Obesulus*

To model and evaluate the population consequences of management scenarios for *I. obesulus*, we developed a particular form of PVA model known as a dynamic landscape meta-population (DLMP) model with the software package RAMAS Landscape (Akçakaya et al. 2004; Wintle et al. 2005a). A DLMP model is particularly useful tool for evaluating the relative impacts or benefits of management options in terms of predicted future population size for a range of species (Akçakaya et al. 2004, 2005; Wintle et al. 2005a).

We developed a dynamic landscape model. We estimated a fire-return interval of 30 years on the basis of fire-history data for the region. The model simulated landscape change under assumptions about future management and generated predictions about the amount and spatial arrangement of suitable habitat for *I. obesulus* at 10 yearly intervals for 100 years. The connection between the habitat model and population demographic model was that the carrying capacity of each population was derived from the total amount of suitable habitat for each population. The number of individuals potentially occupying each patch of suitable habitat was assumed to be a linear function of habitat suitability, although the results of some studies show that this is not always the case (Van Horne 1983; Joseph et al. 2006). These predictions were then used, in combination with a metapopulation model describing *I. obesulus* survival rates, fecundity rates, and dispersal distances, to predict the future population size of *I. obesulus* as a result of management actions (see Supplementary Material for details on DLMP model development).

Although the DLMP framework is well equipped to model various forms of uncertainty associated with population parameters (by specifying an expression of uncertainty in terms of standard deviations and upper and lower bounds around a best estimates of model parameters), there is no formal method for routinely incorporating competing habitat models into predictions. We developed separate DLMP model scenarios for a set of competitive habitat models. For the sake of illustration, we define *competitive habitat models* as those with $\Delta AIC < 2$, indicating that they receive almost as much support from survey data as the AIC_{best} model (Burnham & Anderson 1998). A more generous threshold of, say $\Delta AIC < 4$, could be used and would expand the model set considered. Another alternative would be to consider all competing models, weighted by their model weight. This would require substantial computing effort for relatively little gain (in this instance) and is beyond the scope of our investigation.

The DLMP model allowed for relative survivorship to be modeled at various locations within the study region. Relative survivorship is the probability of *I. obesulus* surviving at particular locations in the landscape due to threats from humans and other species at those locations. After consultation with local experts, we assumed *I. obesulus* mortality increased in areas without fox-proof fencing by 80% because of fox predation, increased by 4% within 800 m of urban zones because of cat predation, and increased by 6% within 200 m of roads because of vehicle mortality (A. Lechner, unpublished data).

Defining and Modeling Management Scenarios

Beyond fox-proof fencing at the Botanic Gardens, no specific management actions have been undertaken within the study region with the goal of improving the persistence of *I. obesulus*. We modeled 6 possible management scenarios for the species by altering parameter values in the landscape and metapopulation model to represent how the landscape and population may behave under altered conditions. A greater range of management options, including combinations of various scenarios, could have been considered. An exhaustive analysis of all management options was beyond the scope of our study.

Scenario 1 evaluated the likely population trajectory of *I. obesulus* without management. Scenario 2 involved fence development and maintenance at the Pines Reserve. We simulated the removal of predation threats through fox and cat control on this reserve and implemented a fire regime that maximized the most suitable vegetation for *I. obesulus*. This scenario increased the carrying capacity of the reserve and decreased *I. obesulus* mortality rates in proportion to fox control. Scenario 3 assumed fox baiting conducted over the entire study region could halve widespread fox threats. We modeled this scenario by increasing the survivorship of *I. obesulus* in areas without fox-proof fencing. Scenario 4 simulated the development of a vegetation corridor between the Pines Reserve and the Langwarrin Reserve to facilitate the dispersal of individuals between these habitat patches. Scenario 5 simulated regular burning of the entire landscape to maximize the most suitable vegetation age for *I. obesulus* occupancy. Scenario 6 assumed that appropriate management could eliminate cat predation

from the region, thereby increasing the relative survivorship of *I. obesulus* at locations within 800 m of urban zones.

Simulations and Ranking of Management Scenarios

A total of 24 management-scenario and habitat-model combinations (6 management scenarios each under 4 competing habitat models) were generated for *I. obesulus* within the landscape. The DLMP model generated predictions of vegetation composition and structure for each scenario as a time series of raster maps (0.25-ha cell size) at 10 yearly intervals for a duration of 100 years. RAMAS Landscape used the landscape simulations to predict the average population size and expected minimum population size for *I. obesulus* for each scenario over the forecast period.

The performance of competing management scenarios was primarily evaluated in terms of the expected minimum population (EMP) size. The EMP is defined as the mean of the predicted minimum population sizes from all simulations of a given model over the simulation period (McCarthy & Thompson 2001). The EMP for each scenario was estimated with 50 landscape replications (because landscape dynamics are modeled stochastically in DLMP) and 100 population replicates on each landscape.

Results

Habitat Models

Substantial uncertainty surrounded the choice of a single-best habitat model, with 4 candidate habitat models having a $\Delta AIC < 2$. The approximately even spread of Akaike weights across the top 4 models provided further indication of the considerable uncertainty surrounding the choice of a single-best habitat model for *I. obesulus* (Table 1). The top 4 habitat models included the habitat variables shrub cover, soil type, and fox-proof fencing. The habitat variables litter cover, ground cover, distance to vegetation edge, and interaction between ground cover and fox-proof fencing were rejected from these habitat models. Nonlinear relationships between *I. obesulus* occupancy and some habitat variables were rejected.

Table 1. Rank of 4 predictive habitat models for *I. obesulus* from available survey data.*

Model ranking	Variables selected	AIC	ΔAIC	w_i	Residual deviance
1	soil + shrub + fence + shrub:fence	110.95	0.00	0.34	100.95
2	soil + shrub + fence + age + shrub:fence	111.02	0.07	0.33	97.02
3	soil + shrub + fence	112.10	1.25	0.18	104.12
4	soil + shrub + fence + age	112.73	1.78	0.14	100.73

*Habitat model 1 is considered the best habitat model according to Akaike information criterion (AIC), ΔAIC , and Akaike weights (w_i) developed for each habitat model in a candidate set. All habitat models with a ΔAIC value of < 2 were considered in PVA predictions.

A deviance reduction of approximately 36% ($100 \times [(\text{null deviance} - \text{residual deviance})/\text{null deviance}]$) was achieved by the best 4 models.

The best habitat model (i.e., lowest AIC value: 110.95; $w_i = 0.34$) predicted that the probability of occurrence of *I. obesulus* diggings would increase linearly with shrub cover, be higher on sandy soils than on other soils, be higher in the presence of fox-proof fencing, and included the interaction between shrub cover and the presence or absence of fox-proof fencing. The habitat model with the second-lowest AIC value (111.02; $w_i = 0.33$) predicted that probability of presence of a digging would increase linearly with shrub cover, be higher on sandy soils than on other soils, be higher when enclosed by fox-proof fencing, be higher in vegetation of 10–20 years of age, and included the interaction between shrub cover and presence or absence of fox-proof fencing. The structure of habitat model 3 (AIC = 112.10; $w_i = 0.18$) and habitat model 4 (AIC = 112.73; $w_i = 0.14$) was identical to the top 2 habitat models, except without the interaction term between shrub cover and the presence or absence of fox-proof fencing (Table 1).

Effect of Model Uncertainty on Scenario Evaluation

On the basis of average densities of *I. obesulus* for the region (Lobert 1990), the AIC_{best} habitat model predicted a starting population of 2143 individuals. Without management intervention the base PVA model predicted that 1276 individuals would remain within the study region after 100 years (Fig. 1) with a 95% risk of decline to <887 individuals (Fig. 2) and an EMP of 740 individuals over that period.

When the AIC_{best} habitat model was incorporated into PVA predictions, fencing the Pines Reserve resulted in the greatest increase in EMP (31%), with 1521 individuals predicted to occupy the landscape at the end of the simulation period. Halving widespread fox threats ranked second, increasing EMP over the base scenario by 28%, and improving the average population size to 1370 individuals after 100 years. Developing a vegetation corridor between the Pines Reserve and the Langwarrin Reserve ranked third under AIC_{best} habitat model, increasing EMP over the base scenario by 8% and predicting 1378 individuals to occupy the landscape in 100 years. Implementing a widespread fire regime and eliminating cat predation did not improve EMP or increase the number of individuals over the base PVA model (Fig. 1).

The ranking of scenarios under the second-best habitat model was identical to when the AIC_{best} habitat model was assumed correct. Developing a fox-proof fence around the Pines Reserve was the best, with a 30% increase in EMP. Halving widespread fox threats ranked second, increasing EMP by 23%, whereas an 18% increase in EMP resulted from the vegetation corridor between the Pines Reserve and the Langwarrin Reserve. Implementing

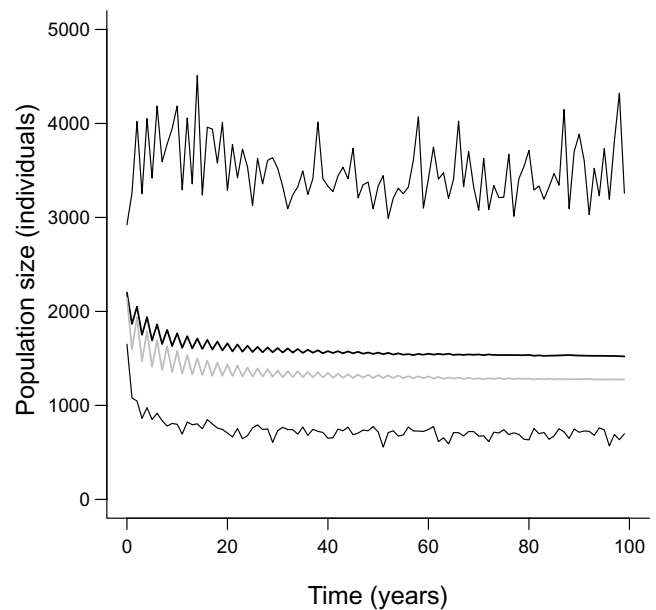


Figure 1. Predicted average population size of *I. obesulus* without management (gray line) and when the Pines Reserve was fenced under the AIC_{best} habitat model (uppermost line). The line above and below the gray line are 95% CIs on the expected minimum population (EMP) size.

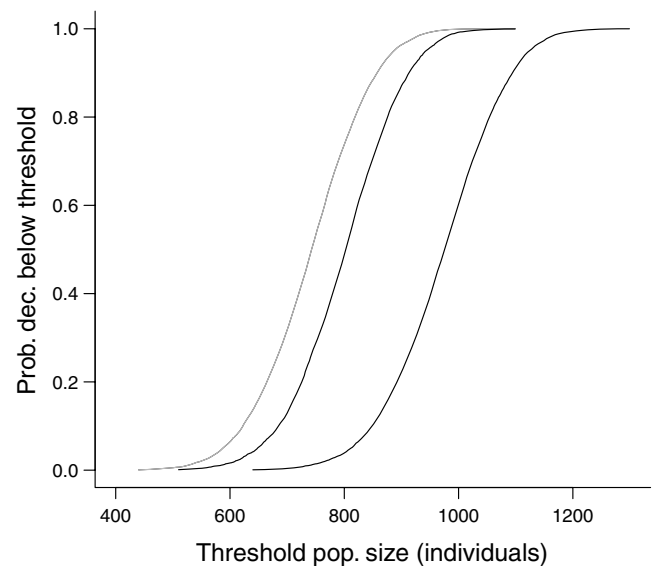


Figure 2. Interval-extinction risk curves for *I. obesulus* represent the probability (prob.) of populations (pop.) decreasing (dec.) below a specified threshold over the course of the simulation for a selection of management options: left-hand line, risk without management; middle line, risk with development of a vegetation corridor between the Pines Reserve and the Botanic Gardens; right-hand line, risk when the Pines Reserve is fenced.

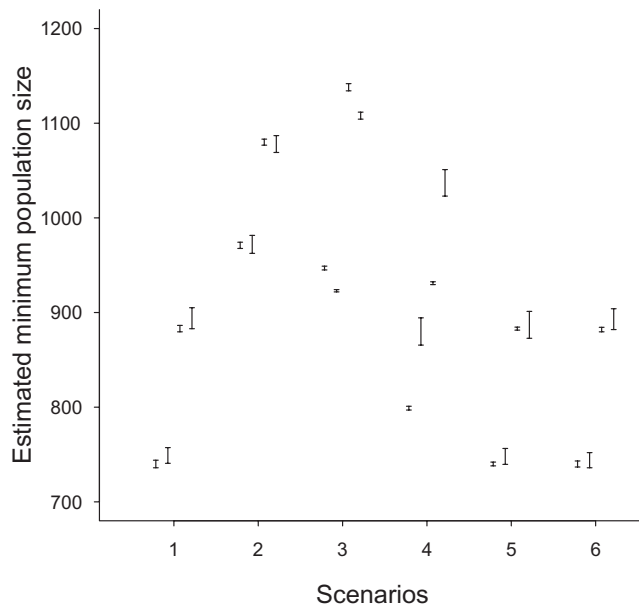


Figure 3. Sensitivity of the estimated minimum population size (EMP) of *I. obesulus* to habitat-model uncertainty under each of the 6 management scenarios. For each scenario (the x-axis), vertical error bars represent the 95% CI of EMP for each of the 4 competitive habitat models. Habitat model 1 is given as the left-most interval of the 4 intervals for each scenario, with model 4 the right most and models 2 and 3, respectively, in between. The intervals are 95% CIs for the mean of the minimum population size for a set of simulations and do not represent the full range of variation in population size across all population simulations.

an optimal fire regime and eliminating cat predation under the second-best habitat model did not improve EMP over the base scenario.

When the third- and fourth-best habitat models were used to generate PVA predictions, the rankings of management scenarios were different than when the best 2 habitat models were assumed correct. Halving widespread fox threats provided the greatest increase in EMP (29% under model 3 and 24% under model 4). Fencing the Pines Reserve ranked second. Developing a vegetation corridor and eliminating cat predation under the third- and fourth-best habitat models did not improve EMP over the base scenario (Fig. 3).

Discussion

Uncertainty and Inference about *I. obesulus* Habitat Requirements

The competing set of habitat models developed for *I. obesulus* provide some indication of the degree of habitat-

model uncertainty and the relative contribution and roles of the different habitat variables in determining occupancy. The variables soil type, shrub cover, and the presence of fox-proof fencing were consistently represented in the top-ranked habitat models (Table 1), which supports previous research that identified these habitat variables as important requirements for the species (Claridge & Barry 2000; Shan et al. 2006). Considerable uncertainty surrounded the inclusion of the variable vegetation age and the interaction between shrub cover and the presence or absence of fox-proof fencing. Incorporating or rejecting these habitat variables from the habitat model implies a qualitatively different interpretation or belief about what constitutes *I. obesulus* habitat. By rejecting the variable vegetation age from the habitat model, it was assumed that seral vegetation stages following disturbances does not affect occupancy. Habitat models without the interaction between shrub cover and fox-proof fencing implied that the relationship between shrub cover and occupancy was the same for all levels of predation.

Sensitivity of the PVA Model to Habitat-Model Uncertainty

Results of the PVA modeling under a range of habitat assumptions provides insight into the relative efficiency of population enhancement strategies with the caveat that such insights are somewhat sensitive to the parameterization of the PVA model and in particular to the habitat component. The PVA model predictions and subsequent ranking of management scenarios on the basis of one habitat model alone was naïve to the uncertainty inherent in the analysis. When the AIC_{best} habitat model was assumed correct and other alternatives that were almost as good were ignored for the purpose of inference, the PVA model overconfidently predicted the benefits of fencing the Pines Reserve and underestimated the value of halving widespread fox threats. Decision makers unaware of the influence of alternative habitat models may choose to fence the Pines Reserve without full knowledge of the uncertainty associated with such a decision.

The sensitivity of scenario rankings to alternative habitat models created ambiguity about which management strategy is in fact best for the species. The switching in scenario rankings was due to the apparent subtle differences in habitat-model structures, in particular, the interaction between shrub cover and the presence or absence of fox-proof fencing. When this interaction was included in the habitat model, the suitability of occupied habitat outside the Botanic Gardens was reduced, resulting in fewer individuals occupying the bulk of the landscape. This in turn reduced the apparent value of the management activities that altered the distribution and quality of habitat outside the Botanic Gardens. The PVA model predictions and scenario rankings were much less

sensitive to the variable vegetation age, indicating that finite conservation funding may be better spent on reducing predation threats than on costly fire-management activities with uncertain benefits to the species.

Habitat-model (and other sources of) PVA uncertainty may be incorporated in decision making in a variety of ways. The performance of fencing the Pines Reserve was relatively insensitive to the choice of habitat model. Decision makers wishing to implement the most reliable management strategy for *I. obesulus* may decide on this management option. Explicitly representing uncertainty in model predictions enables a precautionary approach to management. Choosing the management option that offers the best worst-case prediction across all plausible habitat models may be considered precautionary with respect to habitat-model uncertainty.

Other Forms of Uncertainty That Influence PVA Predictions

Despite incorporating habitat-model uncertainty and some aspects of population-model uncertainty into PVA predictions, our methods did not account for all forms of uncertainty inherent in the PVA model (Wintle et al. 2005a). The assumption that mapped variables were accurate (Elith et al. 2002; Van Niel & Austin 2007), fire-behavior characteristics for the landscape were correctly specified, and false-positive observations were absent from the survey data (Wintle et al. 2005a) likely contributed to the underestimation of prediction uncertainty. Lack of knowledge about mortality rates of *I. obesulus* under the range of predation control strategies also made defining relative survivorship at different locations across the landscape difficult. Accounting for as much uncertainty as possible in the decision process may complicate decision making; however, it does help avoid nasty surprises.

Although we developed competing habitat models with logistic regression, a number of alternative techniques can be used to describe species-habitat relationships. Methods such as neural networks, regression trees, machine learning algorithms, or even expertly derived habitat suitability indices may have produced competing habitat models consisting of different model structures, potentially resulting in qualitatively different PVA model predictions. It is also worth noting some models do not explicitly use a habitat model to determine population carrying capacities. Models that directly estimate carrying capacities without considering how carrying capacity varies with environment and habitat quality do not “escape” habitat-model uncertainty; rather, they ignore it, introducing an unacknowledged form of uncertainty to the analysis. Our method explicitly recognizes and quantifies the uncertainty about the relationship between environment, habitat, and carrying capacity in terms of EMP.

Incorporating Habitat-Model Uncertainty into DLMP Predictions and Decision Making

It is well known that no matter how much ecological data are collected, there will always be a limit to the ability of model builders to interpret the relative value and contribution of competing models (Burnham & Anderson 1998; Wintle et al. 2003). Even when empirical data are not available, model builders will often be confronted with a number of conflicting expertly derived habitat models. Our results demonstrate the magnitude and practical implications of habitat-model uncertainty that may go unnoticed if model builders ignore alternative model structures and assume the single-best habitat model is correct for the purpose of inference.

Despite our results, habitat-model uncertainty may not exist in all circumstances, and if present, may not always affect PVA conclusions and management-scenario rankings. When the habitat requirements of a species are well defined, well understood, and measurable, habitat-model uncertainty and its effects on PVA will be reduced. The sensitivity of PVA results depends on the habitat variables incorporated or rejected from the competing habitat models and on the relationship between these variables and the management scenarios evaluated, making the specification of the model set and the choice of the ΔAIC threshold value important.

Because the influence of habitat-model uncertainty on PVA predictions will not be known unless multiple habitat models are tested during model building, we suggest model builders search for and consider alternative model structures when developing PVA models. The procedure we used to search for and evaluate multiple habitat models under alternative scenarios provides a relatively straightforward treatment of habitat-model uncertainty that can be easily incorporated into PVA frameworks when species-habitat relationships are derived from logistic regression.

Although we incorporated model uncertainty into predictions, we did not aggregate habitat models to represent habitat-model uncertainty with one bound. This would require a model-averaging approach to be integrated into the PVA framework, whereby PVA model predictions are weighted by habitat-model AIC weights. Prediction uncertainty would be averaged across all competing habitat models. Such aggregation methods may be useful if a single representation of overall uncertainty is sought and would avoid the need to specify a ΔAIC threshold value. The computation demands of such an approach would be higher than the approach we adopted here.

A formal decision-theoretic approach for determining the most robust management option from spatially explicit PVA could not be found in the literature. Methods such as info-gap decision theory provide a framework for incorporating model uncertainty into decisions and

identifying management options that are most robust to that uncertainty (Ben-Haim 2001). Incorporating PVA in an explicit decision-theory framework would facilitate characterization of uncertainty during model building and provide a transparent, repeatable approach to model-based decision making (Nichols & Williams 2006). Developing methods that integrate PVA approaches with decision-making tools constitutes an important area of future research in conservation planning.

Conclusions

Our research provides one of the first attempts to explicitly measure the influence of habitat-model uncertainty on PVA predictions. The sensitivity of PVA predictions to habitat-model uncertainty highlights the importance of characterizing and accounting for sources of uncertainty in PVA model predictions. Model builders should be willing to search for and consider alternative models to represent the system and to improve the representation of uncertainty and the robustness of management decisions to identified sources of uncertainty. The procedure we used to search for and evaluate multiple habitat models under alternative scenarios provided a relatively straightforward treatment of habitat-model uncertainty that may be used to alert researchers to the potential impact of model uncertainty in their particular decision problem. Routine PVA sensitivity analysis should be expanded to include an analysis of habitat-model uncertainty.

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Supplementary Material

A description of the PVA model developed for *I. obesus* (including details of parameter estimates for population and landscape model modules of RAMAS Landscape) is available as part of the on-line article from <http://www.blackwell-synergy.com/> (Appendix S1). The author is responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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