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Assessing spatial PVA models of arboreal marsupials using significance tests and Bayesian statistics

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Abstract

The predictions of stochastic metapopulation models of four species of arboreal marsupial were compared to field data on patch occupancy. The species examined were the greater glider *Petauroides volans*, the mountain brushtail possum *Trichosurus caninus*, the ringtail possum *Pseudocheirus peregrinus* and the yellow-bellied glider *Petaurus australis*. The models were developed for a system of 39 eucalypt patches in southeastern Australia, embedded within an exotic plantation of radiata pine *Pinus radiata*. Additionally, two alternative (null) models were developed for each species: one in which it was assumed that there was no impact of fragmentation; and a second that only modeled local population dynamics with no dispersal between patches. Congruence between the probability of occupancy of patches predicted by the metapopulation model and the actual occupancy observed in the field was assessed using tests of significance based on logistic regression. The relative performance of the three competing models was assessed for each species using Bayesian statistics. The results demonstrated that the metapopulation model made reasonable predictions for the greater glider and the yellow-bellied glider. However, none of the models predicted the observed increase in population density of mountain brushtail possums and ringtail possums in patches relative to continuous forests. Incorporating edge effects and inter-specific interactions would improve the predictions for these two species. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Extinction risk; Metapopulation; Patch occupancy; Population viability analysis; Validation

1. Introduction

Population viability analysis (PVA) is often regarded as a key component of conservation biology, but the predictions of PVA models are being increasingly questioned (Gilpin and Soulé, 1986; Boyce, 1992; Burgman et al., 1993; Possingham et al., 1993; Caughley, 1994; Taylor, 1995; McCarthy et al., 1996; Ludwig, 1999). Despite this uncertainty, population viability analysis is used to recommend management actions, assist reserve design and assess relative levels of threat faced by species (Burgman and Lamont, 1992; Burgman et al., 1993; Possingham et al., 1993; McCarthy and Lindenmayer, 1999). Uncertainty arises, in part, because many models are based on few data, and parameter estimates may be little more than educated guesses. Imperfect knowledge and the fact that no model could (or should) be a perfect description of reality mean that the predictions will be imperfect. In such circumstances, comparing the predictions of population models with real field data is important to help gauge their degree of accuracy and identify ways in which the models could be improved. While recognizing that it is difficult to obtain field data on the primary prediction of PVA (the risk of extinction), other predictions of PVA models can be scrutinized, including patterns of patch occupancy (Lindenmayer et al., 1999a), local extinction and colonization rates in metapopulations (Hanski, 1997), and the mean and variance of the population size or growth rate (Lacy, 1993; McCarthy and Broome, 2000). Assessing models

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by comparing their predictions to real data should be an intrinsic part of model development (Rykiel, 1996; Hilborn and Mangel, 1997).

The literature on assessing, testing and validating models is extensive (Rykiel, 1996). There appear to be two approaches to assessing models: one based on tests of significance (Rykiel, 1996); and the other based on Bayesian methods (Hilborn and Mangel, 1997). At the outset, it is important to note that, by definition, no model is a perfect description of reality, so testing or validating models is not an attempt to prove that a model is true or false (Rykiel, 1996). Instead, we regard model testing as a process that identifies the weakest aspects of a model so that it can be modified and the predictions improved. Model testing indicates the limits of accuracy of a model, and increases our understanding of the most important ecological processes in the system being studied. In this light, model testing is used to identify how, and possible reasons why, the predictions of a model differ from reality. With this approach, models are often evaluated with a significance test. However, in contrast to traditional hypothesis testing, if a model is shown to differ from reality (at a given significance level), it is not rejected outright, but modified if and where appropriate.

A complementary approach to assessing models is to use several competing models that are simultaneously compared to the available data with Bayesian statistics (Hilborn and Mangel, 1997). In this framework, various statistical methods, such as maximum likelihood estimation and Bayesian analysis may be used to fit parameters and analyze the relative confidence in the competing models (e.g. Moilanen, 1999; Wade, 2000). However, the use of simulation for PVA, the number of parameters required, the level of model complexity, and the incorporation of stochasticity in both the model structure and observations mean that such an approach may require an unrealistic computational burden. This is the case for the current study, but the Bayesian approach remains useful for choosing between different models with particular parameterizations.

In this paper, we develop metapopulation models of four species of arboreal marsupial in a system of remnant patches of native eucalypt forest embedded within an exotic plantation of radiata pine *Pinus radiata* in southeastern Australia. The models were parameterized with data obtained away from the patch system and tested with data on the occupancy of patches determined by field survey. The best metapopulation model that we could develop for each species (without prior knowledge of the field data on patch occupancy) was compared to two other competing models: one in which we assumed no effect of fragmentation; and a second model with no dispersal between patches. We determined the congruence between the predictions of the models and the field data with significance tests, and the relative level of confidence in the competing models using likelihood and Bayesian methods.

2. Methods

2.1. Study area

The Buccleuch State Forest (BSF), encompassing a total area of approximately 45,000 ha near Tumut, New South Wales, southeastern Australia, was chosen as our study area. Much of the original native eucalypt forest of the BSF was converted to an exotic plantation of radiata pine between the 1930s and the 1980s (Routley and Routley, 1975). A total of 192 remnant patches of native eucalypt forest (<1–>100 ha, total area of approximately 2600 ha) still exist within the landscape matrix of radiata pine. The forest type, size and location of the 192 patches were determined from repeated low-level aerial photography and field reconnaissance. This study was confined to a relatively isolated network of 39 patches in the BSF that ranged in area from 0.5 to 40 ha. The four forest types in these patches are characterized by the dominant eucalypt tree species: *Eucalyptus radiata*; *E. viminalis*; *E. camphora*; and *E. macrohyncha*. Continuous native forest borders this area of the plantation to the northeast and southeast, and agricultural land occurs on the northwest and southwest edges.

2.2. The arboreal marsupials

The four species of arboreal marsupial examined were the greater glider *Petauroides volans*, the common ringtail possum *Pseudocheirus peregrinus*, the mountain brushtail possum *Trichosurus caninus* and the yellow-bellied glider *Petaurus australis*. All these species are nocturnal, and shelter in nests or hollows during the day. Some notes relevant to this study on the biology and ecology of the four species are outlined below.

Greater gliders are specialist arboreal folivores with a diet that consists almost entirely of eucalypt leaves (Kavanagh and Lambert, 1990). The species weighs up to 1.3 kg and has a home range of approximately 1–2 ha (Comport et al., 1996). Greater gliders den and nest in hollows in eucalypt trees (Kehl and Borsboom, 1984). Because hollow development in eucalypt trees relies on fungal decay of the wood, such cavities take more than 100 years to develop and are absent from the pine plantation.

Common ringtail possums have a diverse diet that includes seeds, fruits, flowers and foliage from a range of plant species (How et al., 1984; Pahl, 1984). Adult animals weigh approximately 0.7–1.1 kg (McKay and Ong, 1995) and have a home range of 0.3–1 ha (Thomson and Owen, 1964; How, 1978). Animals may den in tree hollows or construct nests in dense vegetation using

materials such as grass, bark and leaves, and appear to live at low densities in radiata pine plantations (Friend, 1980).

Mountain brushtail possums are one of the largest species of arboreal marsupial in southeastern Australia, weighing up to 4.5 kg (Kerle, 1984; Lindenmayer et al., 1995). The diet of the species includes fungi and the foliage from a range of plant species (Seebeck et al., 1984). The home range of the species varies between habitats being approximately 2–6 ha (How, 1972; Lindenmayer et al., 1998; McCarthy and Lindenmayer, 1998). Mountain brushtail possums rely on tree hollows for denning and nesting (Lindenmayer et al., 1996), and, therefore, are largely absent from pine plantations.

Yellow-bellied gliders weigh between 0.45 and 0.7 kg, and feed extensively on plant and insect exudates such as sap, nectar, honeydew and manna. Eucalypt blossom is also consumed and protein is obtained from pollen and various arthropods (Craig, 1985). During the day, yellow-bellied gliders den in hollows in eucalypt trees. At night, they travel distances of up to 2 km and have large home ranges on the order of 35 ha or more (Goldingay and Kavanagh, 1993). Yellow-bellied gliders have a distinctive call that can be heard at distances of up to 400 m (Russell, 1995).

2.3. Models

The models for the four species were developed using ALEX, a stochastic model of metapopulation dynamics (Possingham et al., 1992; Possingham and Davies, 1995). ALEX models stochastic population dynamics within patches and movement of individuals between patches. Patches vary in size, location and quality. Details of ALEX are provided elsewhere (Possingham et al., 1992; Lindenmayer and Possingham, 1994; Possingham and Davies, 1995), and the description here is limited to features that are unique to this study. The model of greater gliders was the same as that used in the study of Lindenmayer et al. (2000), while the models of the other three species were developed specifically for this study by drawing on data gathered from previous investigations (Possingham et al., 1994; Goldingay and Possingham, 1995). Parameter estimates were derived from a range of sources, and the values used are shown in Table 1. The habitat quality of each patch depended on the forest type, with the habitat quality chosen such that the simulated density in large (1000 ha) patches matched that observed in adjacent areas of continuous forest (Table 1; see also next section Field data). Effects of animals dispersing into the patch network from adjacent areas of continuous native eucalypt forest were simulated by modelling five large (500 ha) patches to the north and east of the patch system. Probabilities of occupancy of each patch were predicted from 1000 iterations of each model.

For each species, the model was initiated in the year 1800, and run until 1995, the year that the patches were surveyed for arboreal marsupials. The year 1800 was chosen because it was a sufficient length of time to allow the populations to reach a stochastic equilibrium prior to the onset of fragmentation. Areas of native forest that were converted to pine plantation were modeled in ALEX by reducing the habitat quality of those patches at the time they were cleared. With the exception of the ringtail possum, the arboreal marsupials require hollows to breed and these will not develop in the pine plantation because of the short rotation time (30 years). Thus, the habitat quality of a patch for greater gliders, yellow-bellied gliders and mountain brushtail possums was set to zero when it was converted to pine plantation. In contrast, ringtail possums are able to construct nests made of vegetation in pine plantations, and surveys revealed that they persist at low densities in these areas (Lindenmayer et al. 1999b). Therefore, we assumed that when an area of eucalypt forest was converted to pine plantation, the habitat quality for ringtail possums allowed them to persist at a low density (Table 1; see also Section 2.4. Field data).

To compare the predictions of the ALEX models, two simplified models were also developed. These can be considered null models that ignore aspects of landscape structure that we believe are important to population dynamics in fragmented landscapes. In the first, it was assumed that fragmentation had no effect on population density in the patches, and population densities were estimated from observed densities in the surrounding continuous forest (Table 1). The probability of occupancy of each patch was predicted using the Poisson probability distribution by assuming that animals were distributed randomly across the landscape. Thus, the probability of occupancy was equal to $[1-\exp(-N)]$, where N is the expected number of animals in the patch.

In the second "null" model, it was assumed that population dynamics occurred within patches, but that there was no dispersal between patches. This allowed the local extinction of populations in patches due to stochasticity, but did not allow recolonization of empty patches following extinction. These two different models were chosen because they represented extremes of the basic ALEX model. In the first case, it was assumed that fragmentation had no effect on the average population density in patches. In the second case, only local population dynamics were modeled, ignoring metapopulation effects. It was expected that the first model would tend to produce higher probabilities of patch occupancy than the basic ALEX model, and that the second model would produce lower probabilities of patch occupancy.

2.4. Field data

Repeated nocturnal spotlight surveys were conducted in the remnant eucalypt patches of the study area, with animals detected by their eye-shine, vocalizations and

Table 1
Parameter estimates used in the ALEX simulations of the four species of arboreal marsupial, derived from Possingham et al. (1994), Goldingay and Possingham (1995), and Lindenmayer (1997)

	Greater glider	Mountain brushtail possum	Ringtail possum	Yellow-bellied glider
Annual adult survival	0.9	0.95	0.64	0.8
Age of first breeding	2 years	3 years	1 year	2 years
Mean newborn females/breeder	0.35	0.38	1.23	0.5
Survival of newborns	0.5	0.3	0.33	0.7
Survival of juveniles	0.85	0.87	–	0.6
Mean dispersal distance (km)	2	10	5	10
Densities in forest types (ha^{-1})				
Eucalyptus camphora	0.11	0.06	0.1	0.01
Eucalypytus macrohyncha	0.23	0.005	0.04	0.01
Eucalypytus radiata	0.13	0.01	0.02	0.01
Eucalyptus viminalis	0.33	0.02	0.02	0.01
Pinus radiata	0	0	0.005	0

movements. Between September and October 1995, all 39 patches were surveyed twice for arboreal marsupials to reduce the chance of obtaining false absences (Lindenmayer et al., 1999b). The first survey involved a complete search of the entire area of the patch, while the second survey was conducted along a 600-m transect marked with flagging tape and randomly located within each patch. All spotlight surveys were confined to still clear nights to minimize effects of weather conditions on our results. Surveys were terminated within 4 h of dusk as arboreal marsupials tend to be most active at this time and are most likely to be seen (Thomson and Owen, 1964; Goldingay, 1984).

To determine the presence and density of animals in the absence of fragmentation, 40 sites (600 m transects) located in continuous eucalypt forest adjacent to the BSF were surveyed. These sites were selected by stratified random sampling to match the forest types, climate and geology of the eucalypt patches in the study area. Surveys were also undertaken at 40 sites (600 m transects) in the pine plantation to determine the rate of occurrence of the arboreal marsupials in the matrix. These sites were also selected from a stratified random sample to match the geology and climate of the eucalypt patches.

2.5. Statistical comparisons

Directly comparing the predicted probabilities of occupancy with field data requires the assumption that false absences are never recorded. This is an unlikely assumption even in the most intensive field program, so the predicted occupancy rates were modified to account for the possibility of observation error. The predicted probability of observing a patch as being occupied was calculated by multiplying the predicted probabilities of occupancy by the estimated conditional probability of observing the presence of the species given that a patch was in fact occupied. These conditional probabilities of observing a patch as being occupied were estimated using data on the frequency with which the species were seen in each patch on one night of survey but not on the other. The estimates obtained were 0.9 for greater gliders, 0.8 for ringtail possums, and 0.5 for common brushtail possums (see also Lindenmayer et al., 1999a). Due to their absence from the patches, it was not possible to obtain an estimate for the probability of detecting yellow-bellied gliders. Because of its distinctive and far-reaching call, it is unlikely that this species would remain undetected in the patches if present, so we used a value of 0.9, and checked the sensitivity of the results to variation in this parameter.

The models were compared qualitatively to field data using the mean predicted number of occupied patches and the actual observed number. Quantitative comparisons were made using logistic regression (Hosmer and Lemeshow, 1989) to investigate the relationship between the observed occupancy and the predicted probability of occupancy (Cox, 1958; Miller et al., 1991). This was achieved with a logistic regression equation of the form:

$$\text{logit}(o) = \ln[o/(1-o)] = A + B \times \text{logit}(\rho),$$

where o is the observed presence or absence, p is the predicted probability of occupancy, and A and B are the regression coefficients. The predictions are significantly different from the observations if A is significantly different from 0, or if B is significantly different from 1 (Cox, 1958; Miller et al., 1991). The statistical significance of the difference between the predictions and observations was determined from the change in the deviance (Hosmer and Lemeshow, 1989). The resulting equation estimated the relationship between the predicted probability of occupancy and the actual probability of occupancy.

The predictions of the different models were compared by calculating the log-likelihood values for each model given the observed data:

$$\ln(L) = \Sigma o \times \ln(\rho) + (1 - o) \times \ln(1\text{-}\rho),$$

where the summation was over all the patches. Values of $\ln(L)$ will always be less than or equal to zero, because p is always a fraction between 0 and 1, so $\ln(p)$ and $\ln(1-p)$ are never greater than 0. Models with higher $\ln(L)$ values (closer to zero) produced predictions that more closely matched the observed data.

Comparisons of the models were formalized using Bayesian statistics (Hilborn and Mangel, 1997). It was assumed that prior to the simulations, the three different models were equally likely for each of the four species, so the prior probabilities were 1/3 for each of the three models. Our confidence in the different models given the data was calculated for each species using Bayes' theorem. Thus, the posterior probabilities of the models (M_i) for each species, assuming that the prior probabilities were equal, was calculated as (Hilborn and Mangel, 1997):

$$\text{Prob}(M_\text{i}) = L_i / \Sigma L_i,$$

where the sum of the likelihoods (L_i) is over the three competing models. These posterior probabilities were used to compare the relative performance of the three competing models, although the best model is not necessarily a good model.

After comparing the predictions and observations, the ALEX models that performed poorly were subjected to a sensitivity analysis in which the mortality rates were varied in an effort to identify parameter combinations such that the predicted occupancy rate matched the observed rate. This was done to determine whether biologically plausible changes in life history rates in fragments could explain the discrepancy.

3. Results

Twenty of the surveyed patches were observed to be occupied by greater gliders, 11 by mountain brushtail possums, 23 by ringtail possums, and zero by yellow-bellied gliders (Table 2). The mean number of patches predicted to be occupied by ALEX was close to the observed number for greater gliders and yellow-bellied gliders, but less than the observed number for ringtail possums and mountain brushtail possums (Table 2). For the latter two species, the model assuming no effect of fragmentation provided better predictions, but this model also underestimated the observed occupancy. The observed density of mountain brushtail possums and ringtail possums was greater in patches than in the continuous forests, which was different from the predictions of all three models.

The probabilities of occupancy predicted by ALEX were not significantly different from the occupancy observed in the patches for the greater glider and yellow-bellied glider, but were significantly different for the ringtail possum and the mountain brushtail possum (Fig. 1). The predicted occupancy by ringtail possums in patches matched that observed in the field when mortality rates were reduced by approximately 40%. Similarly, the predicted occupancy by mountain brushtail possums matched the observations when mortality rates were reduced by 10%. However, the sensitivity analyses were unable to generate parameter combinations such that the density predicted in patches was greater than that in contiguous forest.

Table 2
The observed number of occupied patches in 1995 in the Buccleuch state forest and the mean predicted number for the three different models (the basic ALEX model, the model without fragmentation effects and the model without dispersal) for each of the four species of arboreal marsupial

	Greater glider	Mountain brushtail possum	Ringtail possum	Yellow-bellied glider
Observed	20	11	23	0
ALEX	21.8	2.85	0.778	0
No fragmenation	23.1	5.96	8.05	3.59
No dispersal	7.9	2.64	0.441	0

Log-likelihood values indicated that ALEX provided the best fit to the observed data in 1995 for the greater gliders. The model assuming no effect of fragmentation provided the best fit for mountain brushtail possums and ringtail possums, and ALEX and the model without dispersal provided equally good fits for the yellow-bellied glider (Table 3). The posterior probabilities indicated that, given the survey data, the ALEX models should be rejected in favor of the model with no fragmentation effects for the mountain brushtail possums and ringtail possums (Table 4). ALEX is much more likely than the other models for greater gliders, and the model without fragmentation effects was unlikely to be the best model for yellow-bellied gliders (Table 4). The results did not change qualitatively when using different estimates of the predicted probability of detecting yellow-bellied gliders. Surveys of the patches in more recent years have also failed to detect yellow-bellied gliders (Lindenmayer, unpublished), so we are confident that this species is absent from the patches.

In summary, ALEX appeared to make reasonable predictions of patch occupancy for the greater glider and yellow-bellied glider, but made poor predictions for the mountain brushtail possum and the ringtail possum. For these latter two species, the model assuming no effect of fragmentation made better predictions, but even in this case, the actual occupancy of patches was underestimated. None of the models predicted that densities of animals in patches would be greater than in

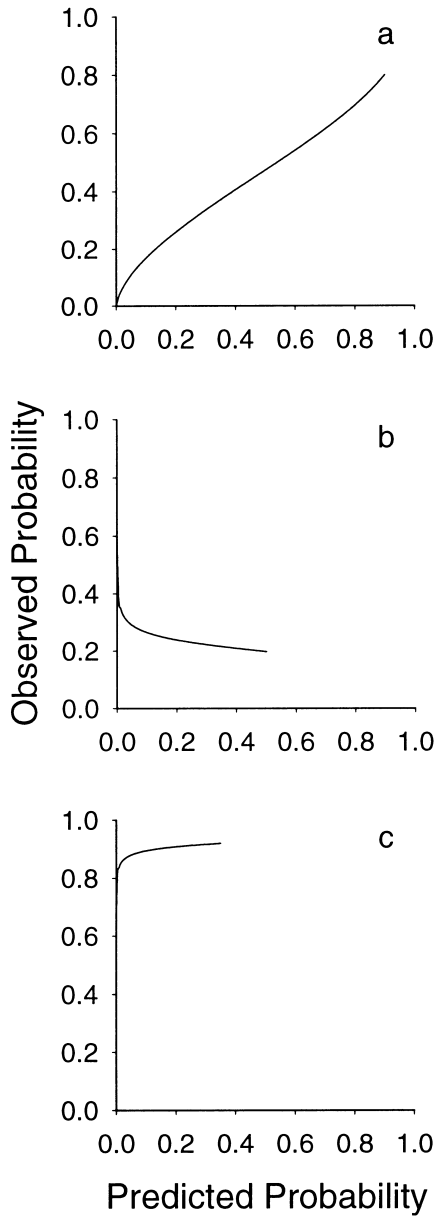

Fig. 1. Relationships between the probability of occupancy of patches predicted by ALEX for arboreal marsupials and the actual occupancy observed in the field. The comparisons are based on logistic regression (Hosmer and Lemeshow, 1989), and test for significant differences between the predicted probability of occupancy and observations (Cox, 1958; Miller et al., 1991). Results are shown for the greater glider (a; logit[o] = −0.101 + 0.678 × logit[p]; predictions and observations were not significantly different, $P = 0.399$), the mountain brushtail possum (b; logit[o] = −1.40 − 0.173 × logit[p]; predictions and observations were significantly different, $P = 0.000$), and the ringtail possum (c; logit[o] = 2.56 + 0.190 × logit[p]; predictions and observations were significantly different, $P = 0.000$). Results are shown across the range of predicted values. Results are not shown for the yellow-bellied glider, because predicted probabilities of occupancy were 0.000 for all patches and no animals were observed, making the predictions not significantly different from observations ($P = 1.000$).

Table 3
Log-likelihood values for the three different models (the basic ALEX model, the model without fragmentation effects and the model without dispersal) for each of the four species of arboreal marsupial based on the survey data in 1995 in the Buccleuch state forest[a]

	Greater glider	Mountain brushtail possum	Ringtail possum	Yellow-bellied glider
ALEX	−20.9	−55.5	−∞	0
No fragmenation	−23.7	−29.2	−39.6	−3.90
No dispersal	−∞	−∞	−∞	0

[a] Values closer to 0 indicate better a fit to a given set of data. Log-likelihood values of negative infinity indicate cases in which occupied patches were predicted to be empty (predicted occupancy equal to 0.0), and values of zero indicate cases in which all predicted probabilities were zero and no individuals were observed.

Table 4
Posterior probabilities for the three different models (the basic ALEX model, the model without fragmentation effects and the model without dispersal) for each of the four species of arboreal marsupial based on the survey data in 1995 in the Buccleuch state forest[a]

	Greater glider	Mountain brushtail possum	Ringtail possum	Yellow-bellied glider
ALEX	0.943	0.000	0.000	0.495
No fragmenation	0.057	1.000	1.000	0.010
No dispersal	0.000	0.000	0.000	0.495

[a] Higher probabilities indicate greater confidence in a model relative to the others being examined, given the survey data

continuous forest, as was observed for the mountain brushtail possum and the ringtail possum.

4. Discussion

Attempts to prove that a model is true or false are futile and misguided. By definition, any model can only be a good approximation in certain circumstances. Model testing is simply a process by which the predictions of a model are compared to data. In a traditional hypothesis-testing framework based on significance tests, a significant result leads to the rejection of the null hypothesis. However, the literal extension of this framework to model testing is illogical. When a significant result is obtained, the aim should be to modify the model where appropriate, not to reject it entirely. When the sources of error are not obvious, sensible modifications will rely on perceptive ecological intuition. The tests may sometimes indicate that the model will be unable to make realistic predictions regardless of modifications, and new modelling approaches (e.g. multi-species models) would be required.

Bayesian statistics provide a natural approach to model assessment, because it is possible to quantitatively

express the relative confidence in different models or different parameterizations of a model (Hilborn and Mangel, 1997; Wade, 2000). Bayesian methods allow refinement of parameter estimates as additional data become available. In theory, it would be possible to conduct a thorough Bayesian analysis using, for example, the MCMC algorithm (Wade, 2000), but the computational burden may be prohibitive. In the current study, simulations for each set of parameters took several hours on a 233 MHz Pentium computer. Given that more than 10,000 simulations are typically required for such an analysis, the computer time required would be more than 3 years. Nevertheless, Bayesian approaches remain useful for comparing different models with particular parameterizations. A more complete Bayesian approach of the type envisioned by Wade (2000) would be preferable to the one conducted in this study if the population model was simpler such that predictions could be obtained more efficiently.

In the current study, both Bayesian statistics and tests of significance provided similar insights on the models. They both indicated that the ALEX model was reasonable for predicting patch occupancy by greater gliders and yellow-bellied gliders, but much less suitable for ringtail possums and mountain brushtail possums. Both approaches can usefully contribute to assessing PVA models. Bayesian methods are useful for comparing different models, while significance tests are useful for assessing their accuracy.

The ALEX models for the four species of arboreal marsupial predicted that the population densities in the patches would be lower than in continuous forest, and hence, patch occupancy rates would also be lower. This qualitative prediction only received conclusive support from the field data for greater gliders. In the case of yellow-bellied gliders, there was some evidence for reduced density in the patches but this was not conclusive because of the overall low density of this species. It is not surprising that the yellow-bellied glider was absent from the patch network, given its large home range (30–60 ha) relative to the size of the eucalypt patches ($\leqslant$40 ha). For the other two species (mountain brushtail possums and ringtail possums), densities observed in the patches were higher than those in continuous forest, indicating that metapopulation models of the type developed here are incapable of describing the response of these species to fragmentation. The discrepancy cannot be eliminated by modifying the model parameters within reasonable bounds, because even when it was assumed that there was no effect of fragmentation (effectively perfect movement between patches and no stochastic effects due to small population size), the occupancy of patches was still underestimated (Table 2).

The discrepancy between the observed data and the predictions of the models for mountain brushtail possums and ringtail possums was not due to the particular model structure that we used. Any basic metapopulation model would predict lower abundance in patches compared to continuous habitat. Incidence function metapopulation models developed for mountain brushtail possums and ringtail possums in the BSF also made predictions that were not supported by field surveys (Lindenmayer et al., 1999a). There are factors affecting the population dynamics of these species that are difficult to explain with these models. Extra complexity would need to be added to the metapopulation models to improve their predictions for these species.

Ringtail possums and mountain brushtail possums occur infrequently in the pine matrix, which may help to explain the discrepancy between the model predictions and the observations. Ringtail possums eat pine needles, construct nests in pine trees and use pine needles as a nest-building material (Friend, 1980). The ability to use resources from both pine forest and native eucalypt forest may increase the habitat quality of patch edges, and consequently favor patches embedded in pines over continuous areas of eucalypt forest. During the spotlight surveys, ringtail possums were often observed near the edge of the eucalypt patches (Lindenmayer, unpublished), and occurred more frequently in narrow patches with large edge to area ratios than in more rounded patches (Lindenmayer et al., 1999b). In contrast, the field surveys did not indicate an effect of patch edges on mountain brushtail possums.

A second explanation for higher than expected occupancy of patches by ringtail possums and mountain brushtail possums is the influence of inter-specific interactions. Predators of arboreal marsupials (such as the powerful owl *Ninox strenua*, Tilley, 1982; Kavanagh, 1988; Cooke et al., 1998) may be rare or absent in pine forests (Lindenmayer, unpublished), preferring continuous areas of open eucalypt forest. The absence of such predators from remnant eucalypt patches may allow some species to increase in abundance. A similar effect may occur if fragmentation limits transmission of parasites. Competition may be another inter-specific effect contributing to the higher than expected occupancy rate of patches by ringtail possums and mountain brushtail possums. If the population dynamics of these two species were influenced by competition with other arboreal marsupials, such as common brushtail possums (*Trichosurus vulpecula*), release from such competition may allow population sizes to increase in patches. The sensitivity analyses of the ALEX models for ringtail possums and mountain brushtail possums demonstrated that mortality rates would need to be reduced by approximately 40 and 10%, respectively for the mean predicted occupancy rate of patches to match that observed. Changes in mortality of this magnitude might be expected due to release from predators and competitors, making this a realistic explanation for the discrepancy.

An alternative explanation is that populations of animals are initially inflated following perturbation in the

environment surrounding a remnant area (e.g. Darveau et al., 1995), but there is then a decline as population sizes "relax" to the carrying capacity of patches. This is unlikely to be occurring in the patch system at Tumut because many of the remnants have been surrounded by a radiata pine matrix for more than 20 years and inflated abundances would be expected to have subsided before now.

Understanding the reason for the higher than expected occupancy rate of patches by mountain brushtail possums and ringtail possums is important for understanding the response of species to fragmentation. The generality of basic single-species metapopulation models has been questioned on the basis that many species are not confined to discrete habitat patches connected by infrequent dispersal (Harrison and Taylor, 1997). In such circumstances, qualitative predictions of the response of species to fragmentation may be invalid. Results for the mountain brushtail possum and ringtail possum suggest that even when habitat is discrete, these models may make unrealistic predictions of the effects of fragmentation. Increases in abundance of some species following fragmentation have also been observed in other studies (Gaines et al., 1992; McCarthy et al., 1997). Models may need to be more sophisticated than the ones commonly in use if they are to be sufficiently general to accommodate the response of all species to fragmentation. Incorporating edge effects and inter-specific interactions may be necessary to accurately model the diversity of responses. Estimating parameters for these more complex models and making meaningful predictions may be difficult for most real-world situations. If inter-specific interactions are the main cause of the discrepancy between the predictions and the observations, it has serious implications for using risk assessment to predict impacts of fragmentation. As far as we know, multi-species PVAs do not exist.

Despite being first used more than 20 years ago (Shaffer, 1981) PVA models have rarely been tested. This is partly because any available data are usually used for model development, and partly because of the difficulty of testing the predicted risk of extinction, which is the primary prediction of PVA models. However, secondary predictions of PVA models can be tested, and improving these predictions will inevitably improve predictions of the risk of extinction. An iterative process of model development, testing, refinement and re-testing is likely to be the best framework for improving models and making them a useful predictive tool for conservation management (Possingham et al., 1993).

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