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The Predictive Accuracy of Population Viability Analysis: A Test Using Data From Two Small Mammal Species in a Fragmented Landscape

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Abstract

This study examines the predictive accuracy of the population viability analysis package, ALEX (Analysis of the Likelihood of EXtinction). ALEX was used to predict the probability of patch occupancy for two species of small native Australian mammals (*Antechinus agilis* and *Rattus fuscipes*) among 13 patches of suitable habitat in a matrix of plantation pines (*Pinus radiata*). The study was retrospective, running each simulation from 1900 until 1997, and the model parameterised without knowledge of the 1997 observed field data of patch occupancy. Predictions were made over eight scenarios for each species, allowing for variation in the amount of dispersal between patches, level of environmental stochasticity, and size of habitat patches. Predicted occupancies were compared to the 1997 field data of patch occupancy using logistic regression, testing H_{random} , that there was no relationship between observed and predicted occupancy, and H_{perfect} , that there was a perfect, 1:1 relationship between observed and predicted occupancies. Rejection of H_{random} and failure to reject H_{perfect} was taken as a good match between observed and predicted occupancies. Such a match was found for one scenario with *R. fuscipes*, and no scenarios with *A. agilis*. In general, patch occupancy was underestimated, with field surveys finding that 9 of the 13 patches were occupied by *R. fuscipes* and 10 by *A. agilis*. Nonetheless, PVA predictions were in the 'right direction', whereby patches predicted to have a high probability of occupancy were generally occupied, and *vice versa*. A *post hoc* search over additional scenarios found few scenarios with a better match than the original eight. The results of this study support the notion that PVA is best thought of as a relative, rather than absolute predictor of the consequences of management actions in threatened populations.

Keywords: ALEX; *Antechinus agilis*; habitat fragmentation; metapopulation, population viability analysis; *Rattus fuscipes*

Abbreviations: ALEX – analysis of the likelihood of extinction (PVA package); AUC – area under the curve; NSW – New South Wales; PVA – population viability analysis; ROC – receiver operating characteristic; SD – standard deviation.

Introduction

Population viability analysis (PVA) has become a popular tool in conservation biology and has been applied to the management of many threatened populations

(Brook et al. 1982; Boyce 1992; Lindenmayer et al. 1995; Beissinger and Westphal 1998). In most instances it is not possible to estimate population viability empirically since often we are trying to conserve only one or a handful of remaining populations. By using analytical or stochastic simulation methods (Beissinger and Westphal 1998), PVA provides a formal framework with which ecologists can explore the potential effects of different management strategies on population viability. While PVAs are popular, they are not necessarily reliable. Any model is a simplification of nature, and is therefore only a caricature of reality (McCarthy et al. 2001b). Important processes may be left out or modelled inappropriately, and it is often difficult to obtain reliable estimates for all the parameters in a model, even for the most extensively studied species.

A number of studies have assessed the predictive accuracy of PVA through retrospective comparisons between model predictions and field data. While the parameter of interest is usually extinction probability, this cannot be measured from single field studies. Therefore, ecologists have turned to other diagnostics with which to measure the fit between PVA predictions and data. For example, Brook et al. (1982) used trajectories of population size over time to assess the predictive accuracy of PVAs across a range of vertebrate taxa. With fragmented populations, patch occupancy can also be used to measure the fit between PVA predictions and data, and such an approach has been applied to several species of birds and arboreal marsupials in Australia (McCarthy et al. 2000, 2001a).

Because PVA models and the organisms they are applied to are so diverse, no single study can confirm nor discredit the general value of PVA (Beissinger and Westphal 1998). As such, it is important that ecologists test the predictive accuracy of different PVA models on a range of organisms, with the long-term goal of understanding some of the conditions that underlie PVA reliability. The aim of this study was to test the accuracy of the computer PVA package Analysis of the Likelihood of EXTinction (ALEX) (Possingham and Davies 1995) in predicting the patch occupancy of two species of small native Australian mammals in a fragmented landscape. The species studied were the agile antechinus (*Antechinus agilis*) and bush rat (*Rattus fuscipes*). While neither species is threatened with extinction, fragmentation of native forest can lead to their local decline (Barnett et al. 1977; Suckling and Heislars 1978; Bennett 1987; Dunstan and Fox 1996), and extensive habitat fragmentation has occurred in the chosen study region near Tumut, New South Wales, Australia. Although PVA is often applied to rare organisms for which few data are available, a wealth of published literature exists for *A. agilis* (or its closely related congener *Antechinus stuartii*), and *R. fuscipes* (Taylor 1961; Wood 1970; Warneke 1971; Wood 1971; Barnett et al. 1977; Cockburn et al. 1983, 1985; Wilson et al. 1986; Robinson 1987; Dickman 1989; Cockburn 1994; Sutherland and Predavec 1999).

PVA using the program VORTEX has previously been applied to *A. agilis* and *R. fuscipes* using the same data set as that used in the present study (Lindenmayer and Lacy 2002). Lindenmayer and Lacy (2002) found that, although some of their modelling scenarios gave reasonable predictions of the number of patches occupied by the two species, their models had moderate (*R. fuscipes*) to low (*A. agilis*) ability to

predict which patches were occupied. Important differences between VORTEX and ALEX (Lindenmayer et al. 1995) justify a comparison of model performance using the same data. In particular, ALEX is population-based, it models one sex only, has no genetic component and allows the user to model a wide variety of environmental processes; whereas VORTEX is individual-based, models both sexes, and allows for inbreeding depression.

The focus of this study was to measure how well an ecologist could predict the distribution of a species 97 years into the future when using (1) the PVA package ALEX, (2) knowledge of the intended fragmentation schedule of a region, and (3) all the available literature on the species in question. The approach taken was one of retrospective prediction, whereby the senior author made predictions for the 97 years following 1900. The year 1900 was chosen as a start point (with all patches occupied for both species) to allow for several decades of population dynamics before the first habitat fragmentation in 1932. Later start times were not used, as there were no data on patch occupancy for either species until 1997. Importantly, the model predictions were made without knowledge of the 1997 observed field distribution of *R. fuscipes* and *A. agilis*, with the senior author only given access to these data once the PVA was completed. Specifically, the aim was *not* to determine the best-fit parameter values for the observed data set. Instead, we were interested in a situation faced by conservation biologists in having to predict the likely consequences of habitat modification.

Methods

The study site

The distributions of *R. fuscipes* and *A. agilis* were studied in an extensive landscape matrix (approximately $15 \times 5 \text{ km}^2$) of exotic *Pinus radiata* plantation in the Buccleuch State Forest (148°40' E, 35°10' S) near Tumut, NSW, Australia. In what was originally continuous eucalypt forest, a patchwork of 32 plantation areas was created throughout the 1900s, with most plantations being established in the 1930s, 1970s and 1980s. Very little harvesting of these pine plantations had been conducted by the year 1997, although most had been subject to selective thinning operations. Within the pine matrix are 39 patches of remnant eucalypt forest, ranging in size from 0.6 to 40 ha, and the region is surrounded by open pasture with occasional scattered eucalypts. The eastern boundary of the plantation is bordered by a strip of eucalypt forest (approximately 2–3 km wide), and to the south are extensive areas of pine plantation and eucalypt forest (see Lindenmayer and Lacy 2002).

The species

R. fuscipes is a small (100–225 g) ground-dwelling native Australian rodent (Taylor 1961; Wood 1971; Strahan 1995). Individuals are sexually mature within their first year and generally produce several litters over the summer breeding season (Taylor

1961; Warneke 1971; Robinson 1987). The sex ratio at birth is close to parity, and there is an average of four newborns per litter, with a maximum of seven (Taylor 1961; Warneke 1971; Wood 1971). Individuals rarely live to breed beyond their first year (Wood 1971; Press 1987; Robinson 1987). Densities vary considerably among habitats and over time, with records of less than one individual per hectare in rainforest/wet open forest (Barnett et al. 1977), 6 ha⁻¹ in rainforest (Wood 1971), and 14 ha⁻¹ in heath (Wilson et al. 1986).

A. agilis is a small (15–40 g) carnivorous Australian marsupial (Dickman 1989; Strahan 1995; Sutherland and Predavec 1999). Originally not distinguished from the brown antechinus (*A. stuartii*), *A. agilis* was only recently recognised as a separate species (Dickman et al. 1988, 1998). As such, most insights into the biology of *A. agilis* must be drawn from literature under the name of its congener. Much of this literature, however, is based on studies conducted in southeastern Australia, where the species is likely to have been *A. agilis* (even though referred to as *A. stuartii* at the time). *A. stuartii* is scansorial, foraging on the sides of tree trunks, on the ground, and nesting in tree hollows (Warneke 1971; Cockburn 1994; Strahan 1995; Sutherland and Predavec 1999). Individuals become sexually mature within their first year, and females produce a single litter over the summer breeding season (Cockburn et al. 1985; Cockburn 1994). The sex ratio at birth is close to parity (Wood 1970; Cockburn 1994); however, sex ratio does vary among populations (Cockburn 1994). There are generally 7–10 newborns per litter (Wood 1970; Barnett et al. 1977; Cockburn et al. 1983; Wilson et al. 1986; Dickman 1989). All males die after their first year and very few females live to breed a second year (Wood 1970; Cockburn et al. 1985; Wilson et al. 1986). Densities of *A. stuartii* vary considerably among habitats and over time, with densities recorded at 1–2 ha⁻¹ in eucalypt forest (Dickman 1980), 1–3 ha⁻¹ in rainforest/wet open forest (Barnett et al. 1977), 7 ha⁻¹ in rainforest (Wood 1970), and 21 ha⁻¹ in heath (Wilson et al. 1986).

Field sampling

Surveys for both species were undertaken in 39 remnant eucalypt patches in 1997, as part of long-term study of a range of vertebrate taxa at the site (Lindenmayer et al. 2000, 2001). In each patch, a transect of aluminium box traps ('Elliott traps') was set, using a bait mixture of peanut butter, honey and rolled oats. Each transect was placed in a randomly chosen direction from the middle to the edge of the patch, and transect length was scaled to patch size: 200 m long for patches up to 2 ha in size; 400 m for patches of 2–3 ha, and 600 m for patches of 3 ha or larger. Traps were spaced at 50 m intervals along each transect, and set for five successive nights at each site.

The PVA model: ALEX

Predictions of patch occupancy were made using the PVA package ALEX (Possing-

ham and Davies 1995). ALEX is a computer simulation program that uses the Monte Carlo method, drawing pseudorandom numbers to simulate the stochastic processes that underlie population dynamics. This model has been used to study the population viability of a range of species, including marsupials (Possingham et al. 1994; Lindenmayer et al. 1995) and birds (McCarthy et al. 2000). Below is a summary of the main features of ALEX relevant to this study (for a detailed description see Possingham and Davies 1995).

- ALEX models one sex. This should be set as the limiting sex, and in the absence of specific information usually the female sex is chosen.
- There are three age classes: newborns (less than 1 year old), juveniles (greater than 1 year old but sexually immature), and adults (sexually mature).
- The species can occur in a number of patches, with each patch represented as a circle arranged on a two-dimensional landscape.
- There are two forms of dispersal between patches:
 - Migration*: this represents ‘unsafe’ dispersal through the matrix of non-breeding habitat that lies between patches. Each dispersing individual radiates in a straight line (of randomly allocated direction) from a patch. Individuals have a distance-specific probability of dying (user-specified), but immigrate into a patch that happens to intercept them before they die.
 - Diffusion*: this represents safe dispersal (zero mortality) along what are effectively habitat corridors between patches. The user specifies the arrangement and width of corridors, with corridor width determining the maximum number of diffusers between two patches in a given year.
- One or more catastrophes can be modelled, which occur randomly or can be triggered by a deterministic increase in patch biomass. Catastrophes decrease population size and/or biomass, and the occurrence of a catastrophe can be local (specific to a single patch) or global across all patches.
- Each patch has its own habitat quality, which represents the maximum number of individuals that can reproduce in a given year. Habitat quality varies stochastically between years, drawn from a normal distribution with a user-specified standard deviation. The degree of correlation between patches in this variation can be set. Furthermore, habitat quality may vary deterministically, as a function of habitat change.
- The user enters values for a range of demographic parameters including fecundity, age-specific death rates, migration rates and diffusion rates, minimum breeding area and living area per individual, and mean migration distance (Appendix 1).

Different PVA models have their own strengths and weaknesses (Lindenmayer and Possingham 1995). ALEX has the advantage of allowing for habitat quality to change over time, both stochastically and deterministically. This feature was particularly useful in this study, since patches in the Tumut region changed with time according to the establishment of pine plantations. Furthermore, because ALEX is not individual-based (i.e. it simply follows the *number* of individuals in each age class) it can simulate the dynamics of large populations relatively quickly using binomial distributions.

ALEX has some disadvantages. In particular, it has the potential to poorly represent the dynamics of very small populations. By following only the fate of females, ALEX ignores the possibility that males are limiting or absent. Furthermore, by not modelling genetic diversity, ALEX does not include the potential effects of inbreeding depression – a factor that may be important in small populations (Lacy 1993; Frankham 1998; Hedrick and Kalinowski 2000).

Habitat modelling

An initial step with many PVAs is the identification of suitable areas of breeding habitat. The chosen study site represents a challenge in this regard, with its complex mix of different habitat types, including eucalypt forest and pine plantations, streams and slopes. Suckling and Heislars (1978) studied the abundance of *R. fuscipes* and *A. stuartii* in a similar patchwork of eucalypt forest and pine plantations, and their work provides a valuable basis for modelling the habitat preferences of *R. fuscipes* and *A. agilis*. They found that:

- Of all habitat types studied, both *A. stuartii* and *R. fuscipes* were caught at the highest rate in eucalypt stream habitat.
- *R. fuscipes* did not occupy eucalypt slope habitat. The capture rate of *A. stuartii* on eucalypt slopes was approximately half that in eucalypt streams.
- The capture rate of *R. fuscipes* in pine plantation streams was very similar to that in eucalypt streams. The capture rate of *A. stuartii* in pine plantation streams was only half that in eucalypt streams.
- Neither species occupied mature pine slope habitat (20 years old).
- Both species occupied young pine slope habitat (8 years old), with capture rates similar to those in eucalypt stream habitat.

Using data from Barnett et al. (1977) and Dickman (1980) for *A. stuartii*, we set the density of *A. agilis* at 2 ha⁻¹. With evidence of *R. fuscipes* occurring at higher densities (or at least higher trap rates) than *A. stuartii* (Suckling and Heislars 1978; Stewart 1979), we set its density at 6 ha⁻¹. Given a sex ratio of 1:1 for both species (Taylor 1961; Wood 1970; Warneke 1971; Cockburn 1994), the density of female *A. agilis* was set at 1 ha⁻¹ and that of *R. fuscipes* at 3 ha⁻¹. These were assigned as the densities in optimal habitat (eucalypt stream habitat), with lower densities assigned to sub-optimal habitat types (Table 1). Furthermore, because of the association of both *R. fuscipes* and *A. stuartii* with dense understorey (Horner and Taylor 1965; Warneke 1971; Suckling and Heislars 1978; Dickman 1980; Sutherland and Predavec 1999), it was assumed that neither species occur in the open agricultural land surrounding the study site.

Based on the estimates of habitat suitability for these two species (Table 1), five types of habitat patches were identified: (a) eucalypt slope; (b) pine slope; (c) pine stream; (d) composites of eucalypt slope and eucalypt stream; and (e) composites of eucalypt slope, eucalypt stream and pine stream (see Appendix 2 for detailed descriptions). Using maps of the study region, 111 habitat patches were identified. Of the 39 eucalypt remnants sampled (see under 'Field sampling'), 16 were very small

Table 1. Values used to model the maximum densities of *Antechinus agilis* and *Rattus fuscipes* in different habitat types. Densities are given as the number of females per hectare.

Habitat type	<i>Antechinus agilis</i>	<i>Rattus fuscipes</i>
Eucalypt, stream	1.0	3.0
Young pine, stream	1.0	3.0
Mature pine, stream	0.5	3.0
Eucalypt, slope	0.5	0.0
Young pine, slope	1.0	3.0
Mature pine, slope	0.0	0.0

patches (less than 6 ha) of eucalypt slope habitat, expected to contain no *R. fuscipes*, and to support only small numbers of *A. agilis* (see Table 1). Because ALEX has difficulties modelling small populations (Possingham and Davies 1995), these patches were excluded from the analysis *a priori*. The remaining 26 sampled remnants were distributed among 13 of the composite patches of eucalypt slope, eucalypt stream and pine stream. The data were treated as presence/absence, and in composite patches containing more than one sampled remnant, the data from all samples were pooled to determine presence/absence. Despite data being available for only 13 of the 111 patches modelled, the additional 98 patches were an important part of the model for their potential influence (through dispersal) on the dynamics of the entire system. A total of 177 corridors were also included to allow individuals to diffuse between adjacent patches, with corridor width determined by measuring the length of shared boundary between patches.

Parameter settings and modelling scenarios

Where possible, parameter values for both species were estimated from the literature (Appendix 1), using data from *A. stuartii* to estimate parameter values for *A. agilis*. However, even for such extensively studied species as *R. fuscipes* and *A. stuartii*, some parameters in ALEX were poorly described in the literature. These included the amount of dispersal between patches, the level of environmental stochasticity, and the effective size of habitat patches. For these parameters, a number of scenarios were modelled based on disparate yet plausible parameter values.

We considered two levels of dispersal: none and 25%. For 25% dispersal, we allowed for both migration (radial dispersal with mortality) and diffusion (directed dispersal along corridors without mortality). Higher levels of dispersal were not studied because females of both species have high site fidelity, with males being the most active dispersers (Wood 1970, 1971; Warneke 1971; Greenwood 1980; Cockburn et al. 1985; Robinson 1987). We allowed for two levels of environmental variation, measured as the standard deviation in the normally distributed yearly habitat quality value. We used SD = 0.25 and SD = 0.50 (where the mean was always set at 0.75; see Appendix 1). Finally, we varied the amount of suitable habitat adjacent to streams. While the literature indicates that *R. fuscipes* uses eucalypt streams but not slopes, and that both species use mature pine streams but not mature pine slopes, it is not clear how far stream habitat extends into slopes. As such, we modelled two situat-

Table 2. List of scenarios, observed occupancy (1997 field data), patch area and predicted occupancy of the 13 patches modelled in ALEX for *Antechinus agilis* and *Rattus fuscipes*.

	Patch number													AUC ^a
	1	2	3	4	5	6	7	8	9	10	11	12	13	
<i>Antechinus agilis</i>														
OBSERVED OCCUPANCY														
PATCH AREA (ha)	0	1	1	1	1	1	0	0	1	1	1	1	1	
Stream width = 20 m	9.9	13.3	16.6	17.8	20.7	24.4	26.3	28.2	28.5	52.6	127.1	185.3	363.4	
Stream width = 40 m	16.4	18.9	23.7	20.6	32.0	37.0	32.3	37.4	35.7	98.2	149.8	225.6	464.3	
PVA OCCUPANCY PROBABILITIES														
SD = 0.25/dispersal = 25%/stream-20 m wide	0.268	0.170	0.456	0.492	0.372	0.324	0.650	0.514	0.774	0.266	0.924	0.946	0.988	
SD = 0.25/dispersal = 25%/stream-40 m wide	0.382	0.274	0.536	0.574	0.486	0.448	0.726	0.614	0.836	0.326	0.956	0.972	0.996	
SD = 0.25/dispersal = 0%/stream-20 m wide	0.002	0.056	0.082	0.110	0.144	0.174	0.224	0.256	0.262	0.006	0.834	0.934	0.964	
SD = 0.25/dispersal = 0%/stream-40 m wide	0.034	0.092	0.204	0.146	0.326	0.340	0.328	0.438	0.364	0.024	0.864	0.950	0.972	
SD = 0.50/dispersal = 25%/stream-20 m wide	0.004	0.008	0.018	0.024	0.016	0.026	0.070	0.042	0.094	0.016	0.204	0.222	0.322	
SD = 0.50/dispersal = 25%/stream-40 m wide	0.012	0.010	0.044	0.030	0.024	0.028	0.068	0.060	0.122	0.014	0.210	0.226	0.334	
SD = 0.50/dispersal = 0%/stream-20 m wide	0.000	0.000	0.000	0.000	0.000	0.002	0.002	0.004	0.004	0.000	0.070	0.102	0.174	
SD = 0.50/dispersal = 0%/stream-40 m wide	0.000	0.002	0.000	0.000	0.004	0.004	0.004	0.010	0.010	0.000	0.112	0.138	0.202	
<i>Rattus fuscipes</i>														
OBSERVED OCCUPANCY														
PATCH AREA (ha)	0	0	1	1	1	1	0	1	1	0	1	1	1	
Stream width = 20 m	7.4	7.4	8.8	4.4	14.5	13.7	10.0	12.5	9.2	47.2	30.7	54.0	119.0	
Stream width = 40 m	14.8	14.8	17.6	8.8	29.0	27.4	20.0	25.0	18.4	94.4	61.4	108.0	238.0	
PVA OCCUPANCY PROBABILITIES														
SD = 0.25/dispersal = 25%/stream-20 m wide	0.034	0.032	0.102	0.016	0.278	0.234	0.476	0.218	0.174	0.014	0.800	0.856	0.956	
SD = 0.25/dispersal = 25%/stream-40 m wide	0.242	0.346	0.464	0.180	0.626	0.604	0.738	0.582	0.520	0.194	0.940	0.966	0.984	
SD = 0.25/dispersal = 0%/stream-20 m wide	0.076	0.166	0.194	0.016	0.460	0.404	0.248	0.406	0.210	0.006	0.788	0.932	0.962	
SD = 0.25/dispersal = 0%/stream-40 m wide	0.340	0.522	0.614	0.188	0.760	0.722	0.628	0.756	0.596	0.178	0.918	0.978	0.994	
SD = 0.50/dispersal = 25%/stream-20 m wide	0.000	0.000	0.000	0.000	0.004	0.010	0.020	0.008	0.006	0.000	0.066	0.086	0.188	
SD = 0.50/dispersal = 25%/stream-40 m wide	0.002	0.012	0.014	0.006	0.034	0.046	0.064	0.028	0.028	0.002	0.168	0.198	0.296	
SD = 0.50/dispersal = 0%/stream-20 m wide	0.000	0.004	0.004	0.000	0.018	0.012	0.002	0.002	0.000	0.000	0.052	0.130	0.194	
SD = 0.50/dispersal = 0%/stream-40 m wide	0.000	0.000	0.016	0.002	0.044	0.028	0.014	0.030	0.016	0.004	0.116	0.194	0.300	

^aAUC refers to the area under the curve of ROC plots.

ions: one where stream habitat is effectively 20 m wide (10 m each side of the watercourse) and one where stream habitat is 40 m wide. Modelling all combinations of these variables ($2 \times 2 \times 2$) gave a total of eight scenarios for each species (Table 2).

Statistical analyses

ALEX was used to simulate population dynamics from the year 1900 until 1997, with 500 simulations per scenario. For each patch, the probability of occupancy was calculated as the proportion of simulations in which the patch was occupied in 1997. These probabilities were then compared to 1997 field data of patch occupancy using logistic regression analysis. Predicted probabilities of occupancy (P_{occ}) from the PVA were transformed into their logit, $\ln[P_{occ}/(1-P_{occ})]$, following McCarthy et al. (2001b). In the logistic regression model $p = e^{a+bX}/1+e^{a+bX}$, the independent variable X is replaced by these transformed data, $\ln[P_{occ}/(1-P_{occ})]$, while the response variable p is the probability of observed patch occupancy predicted from the logistic regression, and a and b are parameters to be estimated. We assumed that the chance of false negatives (species present in a patch but not detected) was negligible (see Discussion for implication).

Two null hypotheses were tested using these data. H_{random} was the hypothesis that there was no relationship between observed and predicted occupancy. In this case the intercept of the logistic regression model can take any value, but the slope is equal to 0. In contrast, $H_{perfect}$ was the hypothesis that there was a perfect, 1:1 relationship between observed and predicted occupancies, whereby the intercept equals 0 and the slope equals 1. Rejection of H_{random} and failure to reject $H_{perfect}$ was taken as a good match between observed and predicted occupancies. Hypotheses were rejected using $\alpha = 0.05$.

Results

The 1997 field survey found that 10 of the 13 patches were occupied by *A. agilis* (Table 2), and nine by *R. fuscipes* (Table 2). There was much overlap in the occupancy pattern of the two species, with *A. agilis* occupying eight of the nine patches occupied by *R. fuscipes*. Patch size varied by more than an order of magnitude within each scenario, and predicted patch occupancy probabilities varied considerably within and between modelling scenarios, ranging from 0.000 to 0.996 (Table 2). All scenarios with high environmental variation had very low occupancy probabilities (less than 0.34). For the purposes of logistic regression, occupancy probabilities of 0.000 (undefined when logit-transformed) were converted to 0.002, equivalent to only 1 of the 500 simulations having the chosen patch occupied in the year 1997.

Antechinus agilis

There was a poor match between observed and predicted patch occupancy for all eight

scenarios examined for this species (Figure 1, Table 3), with observed patch occupancy being consistently underestimated (indicated by the location of the fitted line above the 1:1 line). In no scenario was H_{random} , the hypothesis that the slope of the logistic regression equation equals 0, rejected. The closest fit between observed and predicted patch occupancy was for the scenario of low environmental variation/25% dispersal/stream width = 40 m; the scenario expected to have the highest patch occupancy. This was one of only two scenarios where H_{perfect} (the hypothesis of a 1:1 relationship between observed and predicted patch occupancy) was not rejected ($P > 0.05$). Not surprisingly, the worst fit was at the other extreme, of high environmental variation/0% dispersal/stream width = 20 m.

Rattus fuscipes

ALEX provided an accurate prediction of patch occupancy for one of the eight scenarios for *R. fuscipes* (low environmental variation/0% dispersal/stream width = 40 m), whereby H_{random} was rejected ($P = 0.037$), and H_{perfect} not rejected ($P \geq 0.85$). Although H_{random} was rejected for another four scenarios, H_{perfect} was also rejected in every case (Table 3). A close fit between observed and predicted occupancies was found for the scenario of low environmental variation/25% dispersal/stream width 5 40 m; however, H_{random} was not rejected in this instance ($P = 0.08$). For all eight scenarios, the observed patch occupancy was underestimated. The worst fit was for the scenario of high environmental variation/25% dispersal/stream width = 20 m.

Power analyses

Given that the analyses were based on data for only 13 habitat patches, we conducted power analyses to assess the probability of successfully identifying a good fit between model and data for each scenario. These probabilities were estimated through stochastic simulation by assuming for each scenario a perfect set of patch occupancy predictions. Thus, if ALEX predicted a patch occupancy probability of 0.90 for a particular patch under a certain scenario, then that patch was simulated as having a 0.90 probability of occupancy. A total of 200 simulations were run for each scenario, with statistical power recorded as the proportion of simulations resulting in simultaneous rejection of H_{random} (no relationship between observed and predicted occupancy) and non-rejection of H_{perfect} (1:1 relationship). Power estimates for the scenarios with low environmental variation ranged from 0.53 to 0.83 (Table 3). Power estimates were unavailable for those scenarios with high environmental variation, due to unstable logistic regression solutions (probably caused by the very low occupancy probabilities).

Alternative measure of predictive accuracy: receiver operating characteristic

As an alternative to hypothesis-testing of model performance, we also measured the area under the curve (AUC) of receiver operating characteristic (ROC) plots for

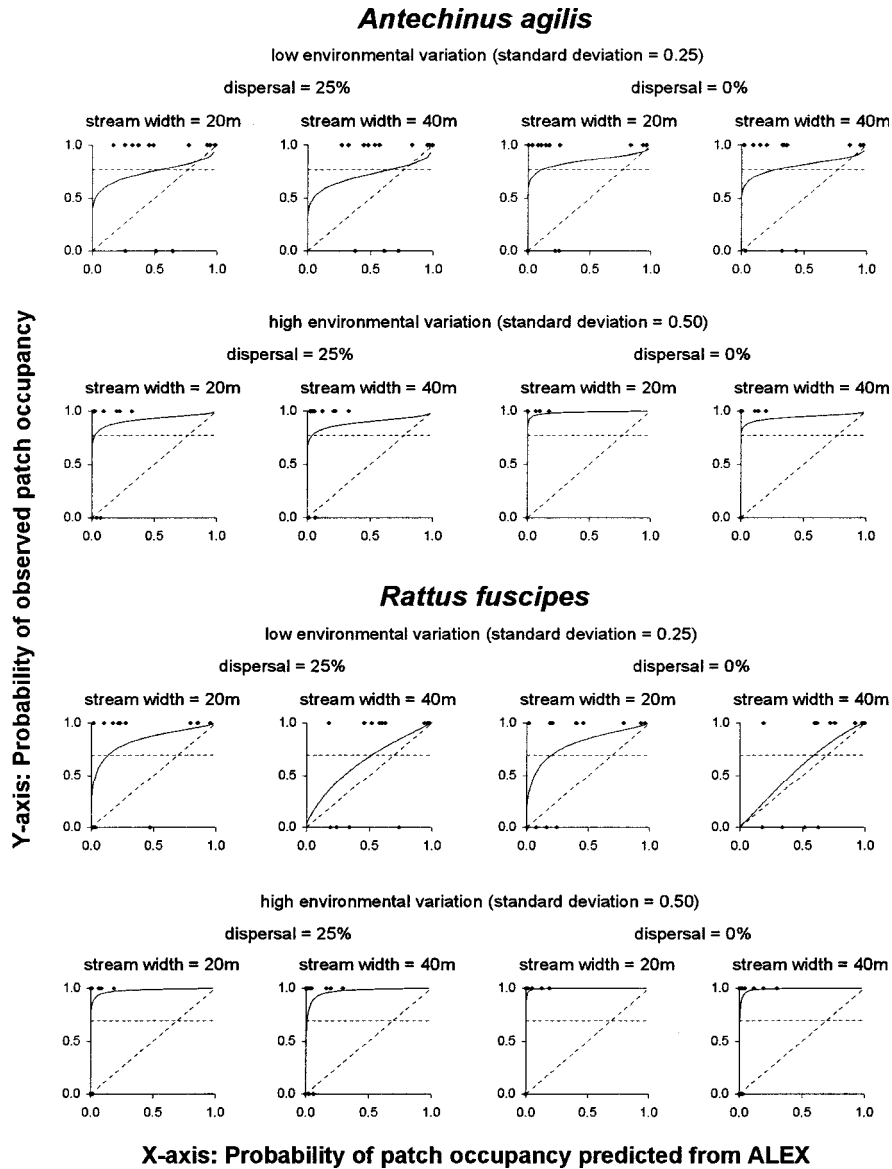


Figure 1. Results of logistic regression analyses for *Antechinus agilis* and *Rattus fuscipes*, describing the probability of observed patch occupancy (y-axis) as a function of predicted patch occupancies from ALEX simulations (x-axis), with both axes back-transformed from their logit. Shown are results of the eight original scenarios for each species. The diagonal broken line represents H_{perfect} , the hypothesis of a 1:1 relationship between observed and predicted occupancy, while the horizontal broken line represents H_{random} , the null hypothesis of no relationship between observed and predicted occupancy. The solid line is the line of best fit between observed and predicted occupancy, and the observed data for the 13 patches are represented as either a value of 1 for an occupied patch, or as 0 for an empty patch.

Table 3. Summary of logistic regression analyses for *Antechinus agilis* and *Rattus fuscipes*, describing the probability of observed patch occupancy as a function of patch occupancies predicted from ALEX simulations.

Scenario	<i>Antechinus agilis</i>						<i>Rattus fuscipes</i>																		
	Stream width = 20 m			Stream width = 40 m			Stream width = 20 m			Stream width = 40 m															
	B_{best}	A_{best}	L_{perfect}	POWER	B_{best}	A_{best}	L_{perfect}	POWER	B_{best}	A_{best}	L_{perfect}	POWER	B_{best}	A_{best}	L_{perfect}	POWER									
ORIGINAL SCENARIOS																									
Baseline (25% dispersal, environ. variation = 0.25)	0.34	1.12	9.19	0.090	0.450	0.55	0.34	0.96	8.10	0.250	0.450	0.53	0.64	1.96	13.57	0.001	0.070	0.79	0.90	0.71	7.02	0.550	0.080	0.60	
Dispersal = 0%	0.31	1.80	19.01	0.000	0.300	0.83	0.31	1.48	14.07	0.001	0.400	0.75	0.68	1.72	10.82	0.009	0.047	0.74	1.11	0.27	6.01	0.850	0.037	0.58	
Environmental variation = 0.50	0.42	2.63	31.21	0.000	0.450	-	0.34	2.22	29.20	0.000	0.600	-	0.73	4.54	39.37	0.000	0.150	-	0.96	4.61	27.70	0.000	0.038	-	
Dispersal = 0%, environmental variation = 0.50	0.66	4.89	49.51	0.000	0.300	-	0.34	2.92	46.29	0.000	0.450	-	1.33	8.12	39.25	0.000	0.039	-	1.32	6.79	29.71	0.000	0.011	-	
POST HOC SCENARIOS																									
Environmental variation = 0.10							0.30	0.85	7.64	0.450	0.500								0.94	0.47	6.74	0.800	0.090		
Drought effect: min. = 0.00, max. = 0.50							0.24	0.52	9.02	0.150	0.500								0.53	-0.69	9.79	0.060	0.150		
Drought probability = 0.10							0.38	0.63	7.17	0.600	0.400								0.67	-0.05	6.79	0.800	0.090		
Environmental correlation = 0.50							0.37	0.95	7.95	0.300	0.450								0.85	0.69	7.04	0.600	0.080		
Diffusion probability (newborns) = 0.50							0.40	1.04	8.42	0.200	0.400								0.79	0.86	7.46	0.400	0.080		
Migration probability (newborns) = 0.50							0.42	1.05	8.37	0.200	0.400								0.69	1.11	8.96	0.150	0.150		
Mean migration distance (10 km for $A. a.$, 5 km for $R. f.$)							0.74	0.65	6.68	0.700	0.250								1.39	0.41	5.88	0.750	0.027		
Minimum diffusion density = 0.25							0.47	0.81	7.26	0.500	0.350								0.76	0.57	7.06	0.650	0.100		
Minimum migration density = 0.50							0.45	1.07	8.39	0.200	0.400								0.71	1.23	9.33	0.080	0.150		
Living and breeding area (0.75 ha for $A. a.$, 0.25 ha for $R. f.$)							0.37	0.85	7.52	0.450	0.450								1.03	0.19	6.32	0.975	0.070		
Adult death rate = 0.85							0.33	0.53	7.50	0.450	0.400								0.80	-0.45	6.85	0.650	0.070		
Newborn death rate (0.450 for $A. a.$, 0.675 for $R. f.$)							0.58	0.09	6.68	0.700	0.250								0.72	-0.40	7.21	0.550	0.090		

Predicted patch occupancy, P_{occ} , was transformed to $\ln(P_{\text{occ}}/(1 - P_{\text{occ}}))$, before analysis. B_{best} and A_{best} are respectively the best-fit values for the slope and intercept. L_{perfect} is the negative log likelihood for the fit of observed occupancy data to H_{perfect} , the hypothesis of a 1:1 relationship between observed and predicted occupancy. Lower values of L_{perfect} indicate a closer fit to this hypothesis. P -values are given for both H_{perfect} and H_{random} , the null hypothesis of no relationship between observed and predicted occupancy probability. A good fit between observed and predicted patch occupancies was taken as rejection of H_{random} and failure to reject H_{perfect} at the 0.05 level. Such a fit was found for only two scenarios (underlined). Each scenario is described by stating how it differs from the baseline case of low environmental variation (SD = 0.25) and 25% dispersal. The first four rows of data represent the original scenarios examined, while the remaining rows represent *post hoc* scenarios explored in light of the results for the initial scenarios. The statistical power is given as the probability of successfully identifying a good model (i.e. when H_{perfect} is true). Power estimates were available only for scenarios with low environmental variation.

each scenario (plots not shown). ROC plots describe the proportion of true positives (patch correctly predicted to be occupied) as a function of the proportion of false positives (patch predicted to be empty, but is really occupied) (see Fielding and Bell 1997; Pearce and Ferrier 2000; Manel et al. 2001). A good model is one that can predict true positives without predicting false positives, and the area under a ROC plot provides an index of overall model predictive accuracy that is independent of the probability threshold chosen to predict occupancy. Thus, a model may be poor at making absolute predictions of patch occupancy, but still be identified as making good estimates of the relative probabilities of patch occupancy. Pearce and Ferrier (2000) defined a poor model as one having an AUC value of 0.5–0.7 (with 0.5 indicating a completely random predictor of occupancy); a reasonable model having an AUC between 0.7 and 0.9; and a very good model as having an AUC greater than 0.9. The AUC for the eight scenarios modelled for *A. agilis* varied from 0.52 to 0.60 (Table 2), indicating poor model performance for this species. In contrast, the AUC values for *R. fuscipes* ranged from 0.75 to 0.94, suggesting moderate to high model performance (Table 2). Interestingly, the best scenario as assessed by the ROC method (high environmental variation/0% dispersal/stream width = 40 m), had one of the worst fits as identified through logistic regression (Tables 2 and 3). This scenario predicted extremely low patch occupancy probabilities (10 values below 0.05 and none greater than 0.30 – see Table 2), and strongly underestimated observed patch occupancy (Figure 1). However, this was the best model (highest AUC) in terms of relative predictions of patch occupancy, with the four unoccupied patches having predicted occupancy probabilities less than 0.015 (Table 2). This highlights the potential discrepancy in goodness of fit between relative and absolute predictions of patch occupancy.

Additional scenarios

Following the consistent underestimation of patch occupancy for both species (Figure 1), a set of 12 additional scenarios were examined for each species to assess whether ALEX could achieve closer fits to the observed data. Since the scenario of low environmental variation/25% dispersal/stream width = 40 m represented the best fit for *A. agilis*, and a close second-best fit for *R. fuscipes* (Figure 1, Table 3), this was used as the baseline case from which parameter settings in ALEX were varied. With every additional scenario examined, a single parameter was varied in such a way as to increase patch occupancy. For example, environmental variation was decreased from 0.25 to 0.10.

For *A. agilis*, 8 of the 12 additional scenarios gave a better fit to the observed data than the original baseline scenario (i.e. the negative log likelihood, L_{perfect} , was lower). However, both H_{perfect} and H_{random} were accepted for each scenario. For *R. fuscipes*, 5 of the additional 12 scenarios gave a better fit to the data than the baseline scenario, and H_{perfect} was accepted for every additional scenario. However, H_{random} was only rejected for the scenario of increased mean migration distance. That scenario gave a closer fit to the observed data than the original best fit scenario for *R. fuscipes*

of low environmental variation/0% dispersal/stream width = 40 m ($L_{\text{perfect}} = 5.88$ compared with $L_{\text{perfect}} = 6.01$).

Discussion

This study found that among the eight scenarios initially modelled using the PVA ALEX, only one scenario accurately predicted the pattern of patch occupancy of *R. fuscipes* after 97 years of dynamics in a fragmented landscape. That scenario was one of low environmental variation, zero dispersal and large habitat patches (i.e. stream habitat was modelled as being 40 m wide). In contrast, none of the eight scenarios modelled for *A. agilis* provided such a match. What do these results mean in terms of the utility of PVA, and of ALEX in particular? Should we have expected more than one scenario to match the data for *R. fuscipes*, and should we be concerned that no scenarios matched the data for *A. agilis*?

Ideally we would be so well informed of a species' biology that we could expect to reliably represent its dynamics with a single PVA modelling scenario. The reality, however, is that information is limiting, and PVA studies must therefore consider a range of modelling scenarios (Goldingay and Possingham 1995; Hamilton and Moller 1995; Marmontel et al. 1997; Gaona et al. 1998), essentially casting a broad PVA 'net' within which we hopefully capture reality. Accordingly, we would hope to find an accurate match between observed and predicted patterns for one or several scenarios, rather than for every scenario. The fact that we did obtain such a match for a scenario with *R. fuscipes* is reassuring. At the same time it is important to acknowledge the possibility that this match arose by chance alone, given that we examined a total of eight scenarios for each species (excluding the 12 *post hoc* scenarios). Even if the null hypothesis were true for all eight scenarios, the overall probability of finding one or more good matches for each species (i.e. rejection of H_{random} , and non-rejection of H_{perfect}) may be higher than 0.05. The theoretical maximum of this combined probability for eight tests (each with two hypotheses) is 0.32, but probably much lower (depending on the probability of accepting the 1:1 hypothesis given that the null hypothesis is true, a value which cannot exceed 0.95). Thus, the pessimistic view is that there was up to a 32% probability of finding at least one good fit between model and data for *R. fuscipes* through chance alone. The fact that we found a scenario with a good fit to data should therefore not be seen as unqualified confirmation of ALEX as a good model for this species, but as a failure to reject it as a bad model.

In contrast, the lack of any good matches between the model and data for *A. agilis* suggests that the eight scenarios modelled in ALEX did not capture the real dynamics of this species. This lack of fit could be due to a number of reasons. First, it is important to acknowledge the potential inaccuracy of the parameter values and habitat modelling used for *A. agilis*, especially since we relied on the assumption that the literature for *A. stuartii* provides reliable insights into the biology of *A. agilis*.

The poor fit between model and data for *A. agilis* may also be associated with

having not considered (1) a wide enough range of scenarios, or (2) a fine enough gradation of scenarios. While the additional scenarios explored for *A. agilis* did produce better fits between predicted and observed occupancies (Table 3), none of these resulted in rejection of H_{random} , the hypothesis of no relationship between observed and predicted occupancy. This suggests that the lack of fit between the model and data for *A. agilis* is attributable to either inappropriate modelling of its biology or the failure to examine a fine enough gradation of scenarios. Interestingly, the search across additional scenarios for *R. fuscipes* found only a marginally better fit between observed and predicted occupancies, suggesting that the original eight scenarios included a reasonably close estimate of the true dynamics of the system.

There may be inherent deficiencies in ALEX which limit its predictive capabilities for particular species. It is important to note that ALEX models each patch as a circle, thereby removing the influence of patch shape on population dynamics and dispersal. Given that many patches in the Tumut study site contained long, thin strips of habitat along streams, patch shape may have been important. Furthermore, ALEX is a single-species approach to population modelling, and does not explicitly model the effects of predation, competition and disease on population dynamics. This may represent an oversimplification of the dynamics of some species.

Alternatively, it is possible that the scenarios modelled here in ALEX for *A. agilis* did in fact capture the real dynamics of the system, but that the 1997 field data represented a particularly unlikely data set of patch occupancies. The stochastic nature of metapopulation dynamics means that patches that had a high probability of being occupied in 1997 may by chance be unoccupied due to extinction, and that patches with a low probability of occupancy may be occupied due to recent colonisation. This is essentially an issue of statistical power, which was estimated as being relatively low (between 0.53 and 0.83) in this study. For tests with more statistical power, it would be useful to collect patch occupancy data over many years.

While several factors could be responsible for the low predictive accuracy of patch occupancy for *A. agilis*, we were unable to determine their relative importance here. As more data become available on the biology of this species in fragmented landscapes, and as data on the patch occupancy dynamics of *A. agilis* in the study site become available over time, it will be possible to gain greater insights into the reasons behind this initial lack of success in fitting the model to data.

The consistent underestimation of patch occupancy was a striking feature of our results for both species. Furthermore, this pattern would have been even stronger if we had assumed false negatives in the sampling process (i.e. the species being present but not detected during a survey). This underestimation across all scenarios for both species suggests that the Tumut landscape is in some way more conducive to population persistence and/or recolonisation than our modelling predicted. Indeed, both species had relatively high levels of patch occupancy: 9/13 patches occupied for *R. fuscipes* and 10/13 for *A. agilis*. In trying to understand the basis of this underestimation, it is important to question the validity of using parameter estimates from other studies to model these species at Tumut. Although both species have been extensively studied, there is large variation in the estimates of key demographic param-

eters among previous studies. For example, the density of *R. fuscipes* has been reported at 6 ha⁻¹ (Wood 1971), and 14 ha⁻¹ heath (Wilson et al. 1986), while that of *A. stuartii* (congener of *A. agilis*) has been reported at 1–2 ha⁻¹ (Dickman 1980), 7 ha⁻¹ (Wood 1970), and 21 ha⁻¹ (Wilson et al. 1986). While this variation is likely to be due to local population dynamics and the effects of habitat, it is impossible to resolve these factors from the available studies to make confident predictions of carrying capacity density at Tumut. This highlights the importance of site-specific empirical data in parameterising population models, and may represent a major challenge to the predictive ability of PVAs.

What does this study say about ALEX *per se*? A useful insight in this regard can be gained by comparison with a study by Lindenmayer and Lacy (2002), who used the PVA package VORTEX to study the same system (i.e. they assessed the viability of both *A. agilis* and *R. fuscipes* in the same study region, making retrospective predictions). Although VORTEX is quite different to ALEX (it is individual-based and incorporates genetic effects), and although Lindenmayer and Lacy (2002) modelled the system in a very different way to this study, they did find similar patterns for the predictive accuracy of the model, in terms of obtaining a moderately good fit between observed and predicted patch occupancy for *R. fuscipes*, but a poor fit for *A. agilis*. This suggests that the inaccuracy of patch occupancy predictions for *A. agilis* in this system is not attributable to model-specific deficiencies.

One encouraging pattern to emerge from this study is that for both species, the slope of the best-fit logistic regression line was positive for all eight scenarios (Table 3, Figure 1). The same was true of all 12 additional scenarios examined (Table 3). While the slope was significantly greater than 0 for only five of the original eight scenarios for *R. fuscipes*, and none for *A. agilis*, the consistent pattern of a positive slope suggests that ALEX was able to predict the *relative* occupancy probability of the different patches. This pattern was further qualified by the high AUC values of ROC plots, of between 0.75 and 0.94 for *R. fuscipes*, and low AUC values between 0.52 and 0.60 for *A. agilis*. As such, the results of these analyses support the notion that for at least some species, PVAs such as ALEX should be best thought of as relative, rather than absolute predictors of metapopulation dynamics. Day and Possingham (1995) were able to demonstrate that the relative value of habitat patches to metapopulation persistence is positively correlated to the probability of patch occupancy, where they defined the most valuable patch as the one whose removal causes the greatest increase in metapopulation extinction probability. Inasmuch as ALEX provides the basis for relative predictions of patch occupancy, this suggests that ALEX may provide the basis for useful insights into the management of fragmented populations.

This study adds another element to our understanding of the predictive capabilities of PVA modelling. In summary, we found a close fit between model predictions and data for only one of eight scenarios examined for *R. fuscipes*, and none of eight scenarios for *A. agilis*. This modelling process highlighted several key issues in relation to the testing of PVAs in general, and of the utility of ALEX in particular:

- Although these two small mammals, *R. fuscipes* and *A. agilis*, have been

extensively studied, a number of PVA parameters (e.g. density at carrying capacity) varied markedly between studies, while other parameters (e.g. the effects of environmental variation) were not measured at all and required estimates based purely on intuition.

- Some tests of PVA predictions can be inherently problematic. By trying to mimic a real PVA ecologist, we felt it was appropriate to model a number of scenarios to account for uncertainty in key parameters. This had the side effect of increasing the overall probability of finding at least one good fit between the model and data that had arisen purely by chance. In this context, the close fit between model and data for a single scenario for *R. fuscipes* may in fact be the outcome of multiple testing rather than a truly good prediction. An ideal test of a PVA would have parameter estimates good enough to justify modelling one or a few scenarios for each species.
- The two PVA models (ALEX and VORTEX) now tested against this data set both made considerably better predictions of patch occupancy for *R. fuscipes* than for *A. agilis*. This suggests that the problems encountered in modelling the dynamics of particular species may be common even across structurally different PVAs. At the same time, this pattern also suggests that the quality of PVA predictions is not common to the similar life history of these species as small mammals, but may vary at finer, perhaps species-specific levels.
- The consistent pattern of a positive relationship between predicted and observed patch occupancy, although not always statistically significant, suggests that ALEX was able to at least predict a relative trend of occupancy probability.

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Appendix 1

List of parameter values used to model *Antechinus agilis* and *Rattus fuscipes* in the population viability model, ALEX. Parameter values that differ between the two species are in bold. Refer to Possingham and Davies (1995) for a detailed description of the parameters.

Parameter	<i>Antechinus agilis</i>	<i>Rattus fuscipes</i>
Adult death rate	0.95	0.95
Newborn death rate	0.50	0.70
Number of juvenile age classes	0	0
Birth probabilities		
0 female offspring	0.0520	0.1661
1 female offspring	0.1459	0.0492
2 female offspring	0.3516	0.0799
3 female offspring	0.2895	0.1040
4 female offspring	0.1306	0.1258
5 female offspring	0.0271	0.1366
6 female offspring	0.0032	0.1259
7 female offspring	0.0001	0.0964
8 female offspring	0.0000	0.0614
9 female offspring	0.0000	0.0326
10 female offspring	0.0000	0.0145
11 female offspring	0.0000	0.0054
12 female offspring	0.0000	0.0017
13 female offspring	0.0000	0.0004
14 female offspring	0.0000	0.0001
Living area (ha)	1.00	0.33
Breeding area (ha)	1.00	0.33
Best quality	0.75	0.75
Worst quality	0.00	0.00
Minimum diffusion density	0.50	0.50
Quality effect on diffusion	0.50	0.50
Mean migration distance (km)	5.00	2.50
Minimum migration density	0.75	0.75
Probability of catastrophe ('drought')	0.143	0.143
Min. % population reduction from drought	25%	25%
Max. % population reduction from drought	75%	75%
Initial population size (N/K)	1.00	1.00
Environmental mean	0.75	0.75
Environmental standard deviation	0.25 (or 0.50)	0.25 (or 0.50)
Environmental correlation	0.75	0.75
Maximum quality	1.00	1.00
Deterministic growth rate (R)	1.24	1.30

The following sources were used as the basis for parameter estimation (superscript ^A denotes a source used for *A. agilis*, and ^R denotes one used for *R. fuscipes*). Adult death rate: Wood (1970)^A; Wood (1971)^R; Cockburn et al. (1985)^A; Press (1987)^R; Robinson (1987)^R. Newborn death rate: these were set at 0.5 for *A. agilis* and 0.7 for *R. fuscipes* so that growth rate, R, would be greater than 1 in optimal years. Number of juvenile age classes (a reflection of age at sexual maturity): Taylor (1961)^R; Wood (1970)^A. Birth probabilities: Taylor (1961)^R; Warneke (1971)^R; Wood (1971)^R; Robinson (1987)^R; Cockburn (1994)^A. Living and breeding areas: Barnett et al. (1977)^A; Suckling and Heislars (1978)^R; Stewart (1979)^R; Dickman (1980)^A (see Methods section for further explanation). Mean migration distance: *A. agilis* was modelled as having a greater migration tendency than *R. fuscipes* based on evidence (Suckling and Heislars 1978) that *A. agilis* was found at higher relative frequencies in mature *Pinus* forest (i.e. non-breeding habitat). Probability of catastrophe: following Lindenmayer and Lacy (2002) we modelled a 1/7 chance of 1-year drought.

Appendix 2

Description of the five types of habitat patches modelled in ALEX for *R. fuscipes* and *A. agilis* in the Tumut landscape. See Table 1 for a summary of the density estimates for the different habitat components. The 111 patches modelled in ALEX comprised:

(a) **16 eucalypt slope patches:** these remained as eucalypt slope habitat from 1900 to 1997. These areas did not contain streams, and therefore only represented breeding habitat for *A. agilis* (not for *R. fuscipes*).

(b) **32 pine slope patches:** each of these was converted from eucalypt slope to pine slope habitat. These were modelled as starting as eucalypt forest in 1900, supporting no *R. fuscipes* but 0.5 female *A. agilis* per hectare. Each patch had its own conversion history, representing the year in which it was converted to pine forest. For the 10 years following conversion, each patch had high quality – potentially supporting three *R. fuscipes* females and one *A. agilis* female per hectare. This represented a window of opportunity wherein young pine forest supports the high density of ground cover beneficial to both species (Suckling and Heislars 1978). The conversion of patches from eucalypt to pine was modelled in ALEX using the program's annual biomass increment as a proxy for time. Thus, at a critical time (specific to each patch), patch value was increased. Furthermore, the planting of pines would have caused local mortality. This was modelled as a patch-specific catastrophe of 100% mortality in the year of conversion, using the biomass increment as a trigger. In the 10 year following conversion to pine forest, the quality of each patch was reduced permanently to zero to represent the unsuitability of mature pine forest as breeding habitat for both species.

(c) **29 pine stream patches:** these all started as eucalypt stream habitat in 1900, and were converted to pine stream habitat, each patch with its own conversion history. Pine stream patches were demarcated as separate catchments, truncated upstream in their headwaters and downstream where they entered agricultural land. While many of these patches were highly branched, they were modelled in ALEX as circles (as were all patches). For *R. fuscipes*, patch quality remained high after this conversion, while for *A. agilis*, patch quality was modelled as decreasing by 50% once the pines mature (modelled as 10 years after conversion). Some pine stream patches were converted completely from eucalypt to pine stream habitat in a single year. In those cases, the conversion event was modelled as a patch-specific catastrophe of 100% mortality. In those stream patches converted to pine habitat over a number of years, a catastrophe of only 50% mortality was applied.

(d) **15 eucalypt slope/eucalypt stream composite patches:** these remained in this condition from 1900 to 1997.

(e) **19 eucalypt slope/eucalypt stream/pine stream composite patches:** a patch-specific catastrophe of 50% mortality was applied in the year when the stream component (or part of it) was converted to pine forest. Patch quality for *A. agilis* was reduced 10 years after conversion, with the final quality depending on the proportion of the patch converted (patch quality did not change for *R. fuscipes*).

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