

# A landscape-scale test of the predictive ability of a spatially explicit model for population viability analysis

D.B. LINDENMAYER\*†, I. BALL‡, H.P. POSSINGHAM‡,  
M.A. MCCARTHY\*‡ and M.L. POPE\*

\*Centre for Resource and Environmental Studies and the †The Department of Geography, The Australian National University, Canberra, ACT 0200, Australia; and ‡Department of Applied and Molecular Ecology, The University of Adelaide, Private Bag 1, Glen Osmond, SA, Australia

## Summary

1. Although population viability analysis (PVA) is widely employed, forecasts from PVA models are rarely tested. This study in a fragmented forest in southern Australia contrasted field data on patch occupancy and abundance for the arboreal marsupial greater glider *Petauroides volans* with predictions from a generic spatially explicit PVA model. This work represents one of the first landscape-scale tests of its type.

2. Initially we contrasted field data from a set of eucalypt forest patches totalling 437 ha with a naive null model in which forecasts of patch occupancy were made, assuming no fragmentation effects and based simply on remnant area and measured densities derived from nearby unfragmented forest. The naive null model predicted an average total of approximately 170 greater gliders, considerably greater than the true count ( $n = 81$ ).

3. Congruence was examined between field data and predictions from PVA under several metapopulation modelling scenarios. The metapopulation models performed better than the naive null model. Logistic regression showed highly significant positive relationships between predicted and actual patch occupancy for the four scenarios ( $P = 0.001–0.006$ ). When the model-derived probability of patch occupancy was high (0.50–0.75, 0.75–1.00), there was greater congruence between actual patch occupancy and the predicted probability of occupancy.

4. For many patches, probability distribution functions indicated that model predictions for animal abundance in a given patch were not outside those expected by chance. However, for some patches the model either substantially over-predicted or under-predicted actual abundance. Some important processes, such as inter-patch dispersal, that influence the distribution and abundance of the greater glider may not have been adequately modelled.

5. Additional landscape-scale tests of PVA models, on a wider range of species, are required to assess further predictions made using these tools. This will help determine those taxa for which predictions are and are not accurate and give insights for improving models for applied conservation management.

*Key-words:* arboreal marsupials, habitat fragmentation, metapopulation dynamics, model testing, population modelling.

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## Introduction

Computer simulation models, such as those used for population viability analysis (PVA), are increasingly being used to predict the fates of populations of plants

and animals, particularly those that are rare and/or threatened with extinction (Haig, Belthoff & Allen 1993; Lacy 1993; Lindenmayer *et al.* 1995a; Brook *et al.* 1997a; Ratner, Lande & Roper 1997). PVA has been completed for hundreds of species world-wide (reviewed by Boyce 1992; Lindenmayer & Possingham 1994) and it has been particularly widely used by the International Union for the Conservation of Nature

captive breeding specialist groups (Seal & Foose 1989). PVA models are also increasingly being used to set priorities for conservation and to underpin the development of strategies for biodiversity management throughout the world (Mace & Lande 1991; Lindenmayer *et al.* 1993; Possingham, Lindenmayer & Norton 1993; Ruggerio, Hayward & Squires 1994; Lindenmayer & Lacy 1995; McCarthy & Lindenmayer 1999). Despite their widespread use, there have been few field-based tests of PVA models. This has been a major criticism of PVA (Boyce 1992; Caughley & Gunn 1995) and the need for such testing has been highlighted by a number of authors (Soulé 1987).

Testing predictions from PVA can be difficult because, except for captive populations under highly controlled experimental conditions, it is not acceptable to drive a species to extinction simply to examine the predictive ability of a model. However, there are a number of other ways to test PVA models. One is to examine the historical fate of a given population over a prolonged period and compare actual dynamics with that predicted from simulation models. Brook *et al.* (1997b) completed such a study for the Lord Howe Island woodhen *Tricholimnas sylvestris*. They compared the simulated dynamics of the woodhen population using several PVA models with the behaviour of the real population.

Another approach for testing PVA metapopulation models is to examine localized extinctions and patch occupancy rates in habitat patches located within a fragmented landscape (Hanski *et al.* 1996; Wahlberg, Moilanen & Hanski 1996). Here, we report the results of a study in which predictions derived from the spatially explicit generic metapopulation model for PVA, ALEX (Possingham & Davies 1995), were tested in a

fragmented forest landscape. Our investigation involved modelling populations of the arboreal marsupial greater glider *Petauroides volans* Kerr in a set of 39 remnant patches of eucalypt forest in south-eastern Australia. Predicted values for animal abundance and patch occupancy were compared with the results of extensive field surveys in the same set of remnant patches. We conducted the study by parameterizing and running the model using the kind of data available to a land manager. This was achieved by a controlled flow of information between modellers and those who collected the data with which the model was tested.

## Methods

### STUDY AREA

The study area was the Buccleuch State Forest near Tumut in south-eastern Australia (148°40'E, 35°10'S), an extensive plantation of exotic softwood radiata pine *Pinus radiata* D. Don trees. The plantation has been developed over the past 65 years. Most of the *P. radiata* forest has been established on areas that formerly supported native *Eucalyptus* forest. A total of 39 patches of native *Eucalyptus* forest was left uncleared during the establishment of the plantation and these are now surrounded by extensive areas of radiata pine (Fig. 1). These patches vary in size, shape, forest type and a wide range of other attributes (Table 1). The dominant tree species are narrow-leaved peppermint *Eucalyptus radiata* Sieber, mountain swamp gum *Eucalyptus camphora* Baker, red stringybark *Eucalyptus macrorhynca* F. Muell and ribbon gum *Eucalyptus viminalis* Labill.

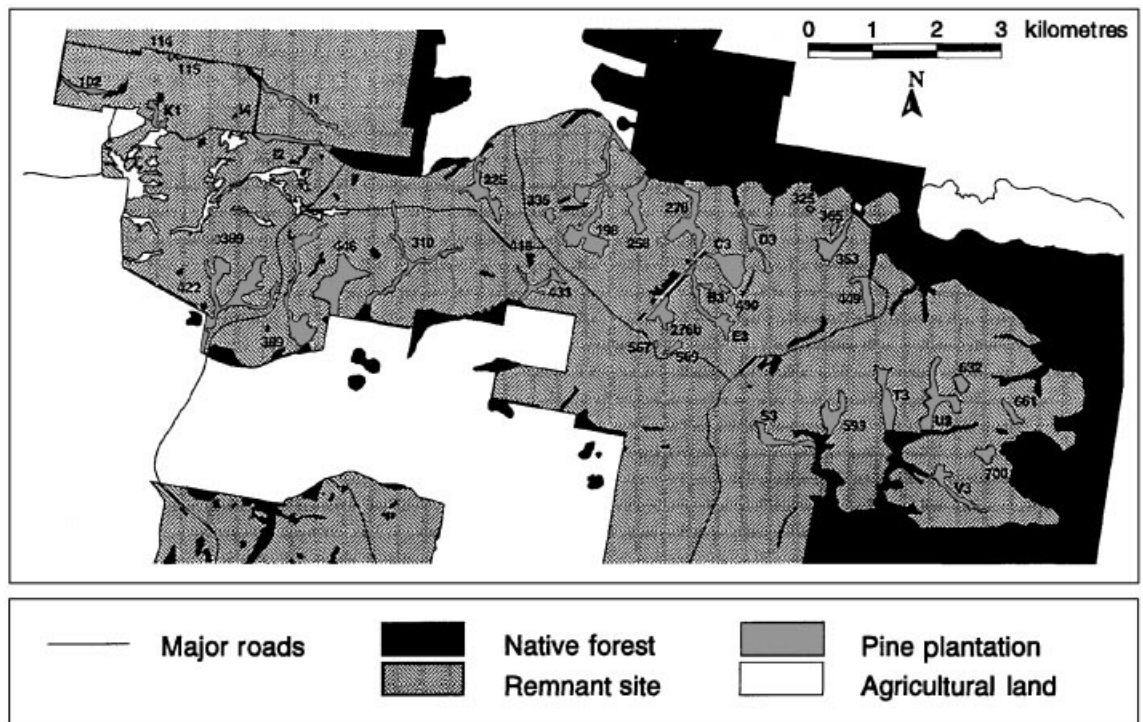


Fig. 1. The patch system modelled at Tumut.

**Table 1.** Information on the size and dominant tree species among patches of native *Eucalyptus* forest targeted for study in the Tumut region of south-eastern Australia. The single letter codes in the column for the dominant tree species in each patch are: r (*E. radiata*), v (*E. viminalis*), c (*E. camphora*), and m (*E. macrorhynca*). Two or more species are listed where they are codominant in a given patch. Columns S1–S4 show the predicted mean abundance for the greater glider in each patch derived from each of the four scenarios using ALEX. The actual number of animals detected by spotlighting is shown in the column denoted 'actual'. The predicted probability of patch occupancy for scenario 4 in the model is presented in the last column ( $P(\text{occ})$ )

Patch	Size (ha)	Species	S1	S2	S3	S4	Actual	$P(\text{occ})$
102	6.6	r	0.96	0.96	0.90	0.82	0	0.34
114	0.6	m, r	0	0	0	0	0	0.00
115	0.7	m, r	0	0	0	0	0	0.00
198	40.4	c, v, r	9.72	11.02	7.46	7.52	1	0.95
235	15.1	c, r, v	1.90	3.04	1.68	1.96	0	0.42
258	15.1	c, r	2.18	2.78	1.38	2.24	0	0.58
276a	20.7	v, r	4.04	5.46	2.14	3.48	2	0.64
310	18.8	v, r	5.24	5.24	6.66	6.44	1	0.93
325	1.0	r	0.02	0.24	0	0.36	0	0.17
335	2.4	r	0	0.08	0	0.06	0	0.03
353	12.7	v	2.58	3.14	2.96	3.4	5	0.70
365	1.7	r	0.02	0.28	0.08	0.30	1	0.15
369	18.9	r	5.04	5.62	4.20	4.74	0	0.83
389	0.4	r	0	0	0	0	0	0.00
418	1.6	c, r	0	0	0.04	0.02	0	0.01
422	38.0	c, v, r	10.64	9.80	12.02	12.38	0	0.97
433	22.1	c, v, r	4.16	4.68	2.78	2.92	0	0.63
446	30.1	r	8.16	8.14	6.92	6.66	6	0.91
449	9.0	v, r	1.26	1.58	1.84	2.30	1	0.61
490	1.6	r	0	0.14	0	0.16	1	0.08
567	0.7	r	0	0.02	0	0	0	0.00
569	2.3	r	0.02	0.12	0.04	0.1	0	0.05
599	16.2	v, r	4.04	3.90	4.30	4.96	10	0.83
632	4.9	r, v	0.16	0.48	0.12	0.40	1	0.17
661	4.4	r	0.72	1.12	1	0.94	1	0.40
700	5.6	r	0.1	0.52	0.18	0.42	0	0.19
276b	20.5	v, r	4.46	4.80	3.38	3.48	5	0.71
B3	0.8	r	0	0	0	0.02	0	0.01
C3	20.1	r	4.40	4.94	3.16	4.14	15	0.76
D3	8.7	v	0.90	1.92	1.32	1.68	2	0.47
E3	13.5	v	3.48	3.00	3.58	3.72	9	0.71
I1	9.1	c, v, r	1.38	1.82	1.24	1.46	0	0.46
I2	5.0	v, r	0.66	0.70	0.72	0.92	0	0.27
I4	2.0	r	0.06	0.06	0.06	0.08	1	0.03
K1	4.1	r	0.90	0.78	0.90	0.50	0	0.22
S3	10.5	c	2.08	2.20	1.12	1.46	1	0.38
T3	18.7	v	4.18	4.68	6.00	6.06	10	0.85
U3	20.5	r	4.72	5.84	3.84	4.20	7	0.82
V3	9.0	v	1.54	2.26	2.32	2.48	1	0.70

The total area of the 39 patches of *Eucalyptus* forest was approximately 437 ha, with the largest single patch exceeding 40 ha and the smallest being < 0.2 ha (Table 1). This information was derived from calculations based on aerial photography of the plantation coupled with extensive field reconnaissance in which all of the patches were walked and mapped (Lindenmayer *et al.* 1999a). The area to the east and south-east of the plantation supports a continuous cover of *Eucalyptus* forest. The southern and western parts of the study area are bounded by land that has been cleared for grazing or to establish extensive tracts of radiata pine plantation. Further details of the features of the study area are presented in Lindenmayer *et al.* (1999a).

The Tumut area was chosen for study because: (i) the isolation time of the patch system was well documented

as records of the establishment dates for compartments of radiata pine; (ii) the spatial definition of patches was clear (native forest can be readily differentiated from the surrounding plantation radiata pine trees); (iii) a range of patch sizes and shapes were available for study; and (iv) public ownership of both the native forest and the plantation meant that it was easy to access areas for field sampling.

#### THE ECOLOGY OF THE GREATER GLIDER

The greater glider was targeted for study because several investigations of the species were completed in the Tumut region prior to, and immediately following, the establishment of the radiata pine plantation (Smith 1969; Tyndale-Biscoe & Smith 1969a, 1969b). Information

**Table 2.** Life-history attributes for the greater glider used in simulation modelling. See text and Possingham *et al.* (1994) for further details on the values used for these parameters

Parameter	Value
Annual probability of death	
Newborn (0–1 years)	0.5
Juvenile (1–2 years)	0.15
Adult (2 years)	0.1
Annual probability a female glider has a female young*	0.35
Minimum area required for breeding	3 ha
Dispersal probability	0.5
Minimum proportion for migration†	0.3
Mean migration distance	2 km

\*ALEX models the fate of only one sex, typically females.

†Population density in a patch before young animals disperse.

from other field investigations on the biology and ecology of the greater glider has been used to parameterize ALEX (Table 2; Henry 1984; Kavanagh 1987; Norton 1988; Lindenmayer *et al.* 1990, 1995b; Comport, Ward & Foley 1996; M.L. Pope & D.B. Lindenmayer, unpublished data).

The greater glider weighs up to 1300 g and is entirely folivorous, feeding almost exclusively on the leaves of *Eucalyptus* spp. trees (Kavanagh & Lambert 1990). Its home range is 1–2 ha (Henry 1984; Comport, Ward & Foley 1996) and the species is usually solitary except during the breeding season, when pairs of animals are often recorded (Henry 1984). One offspring is produced annually, although up to half the females in a population may not breed in any given year. Rates of mortality among juvenile animals (those < 1 year old) may exceed 20% (Tyndale-Biscoe & Smith 1969a). Offspring disperse a year after birth and attain sexual maturity after a further 12 months. If dispersing animals are able to establish a suitable territory they may live up to 15 years. Many of the values for life-history parameters used in simulation modelling were similar to those used in a previous PVA of this species in a different forest region of south-eastern Australia (Possingham *et al.* 1994; Lindenmayer & Lacy 1995).

#### FIELD SAMPLING OF THE GREATER GLIDER IN THE PATCH SYSTEM

Night-time spotlighting surveys were used to count the greater glider in the 39 patches. Two survey methods were employed. First, a complete patch count was undertaken by spotlighting along a grid of flagged lines set 50 m apart and covering the entire patch. Secondly, spotlighting was undertaken along transects divided into 200-m lengths. The length of each transect was scaled according to the size of the patch: the total length of the transect was 600 m for patches > 3 ha; 400 m for sites 2–3 ha; and 200 m for patches measuring between 1 and 2 ha. For patches < 1 ha, a complete patch search was completed.

All spotlighting surveys in this study were restricted to clear still nights to minimize the effects of weather conditions on the detection of animals (Davey 1990). We terminated night-time surveys before 01:00 h each morning because arboreal marsupials typically become less active late into the evening (Thomson & Owen 1964) and, in turn, may be more difficult to detect. The same two observers were responsible for all field sampling completed in this study.

Four extensive field sampling surveys of each of the 39 patches were completed: one complete patch count and three transect surveys (see above). As expected, some differences occurred between the number of animals recorded from the complete patch search and the transects. The overall numbers of the greater glider detected were remarkably consistent across the three transect surveys, varying from 32 to 35 animals. Levels of patch occupancy showed consistent overall trends; we recorded only two instances where a patch occupied during a given survey was later found not to support an animal. The reverse occurred only once, where a patch previously thought to be empty was later found to support the greater glider. In addition, no statistical evidence was found for differences in the detection abilities of the two observers; the square root of the mean abundance of arboreal marsupials recorded by each observer was 0.639 vs. 0.655 (SE = 0.064).

We made formal statistical comparisons of the counts generated from the two types of spotlighting surveys using two approaches (i.e. the complete patch counts vs. the transect surveys). First, the square root of the mean abundance of animals per 3 ha detected in the complete patch searches (0.670) was not significantly different from that from the transect counts (0.632) (SE = 0.102). Secondly, two Poisson regression models were developed, one from the transect information and the other using the results of the complete patch search. The response variable in each case was a density estimate of the abundance of animals per 3 ha. These relationships were then compared with a straight line to test for bias in counts generated from the two survey methods. The results of these analyses are outlined in Lindenmayer *et al.* (1999a) and they showed that data derived from the 600-m transect were an unbiased estimate of the abundance of arboreal marsupials gathered using a complete search. These procedures meant that it was statistically valid to use the values from the complete patch search as an estimate of the number of greater gliders in each remnant.

Additional spotlighting surveys were completed to determine the presence and abundance of animals in the radiata pine plantation within which our remnant eucalypt patches were embedded. Forty transects, each measuring 600 m long and scattered widely throughout the plantation, were sampled. Transects in the radiata pine forest were surveyed once. Surveys were also conducted in large areas of continuous eucalypt forest adjacent to the plantation, and the forest types sampled were identical to those which characterized the 39

remnants in our study. A total of 40 sites, each comprising a flagged 600-m long transect, was spotlighted for greater gliders.

Data on all species of arboreal marsupials from the remnants, pine sites and sites in large continuous areas of eucalypt forest have been used in a statistically based analysis of habitat fragmentation and landscape context effects that has been reported elsewhere (Lindenmayer *et al.* 1999a).

#### OVERVIEW OF THE STRUCTURE OF ALEX

A number of earlier papers have outlined the general structure of ALEX (Possingham & Davies 1995). The key components of the model have been described as part of case studies where the package has been employed (Lindenmayer & Possingham 1994, 1995a, 1995b; Possingham *et al.* 1994; Goldingay & Possingham 1995). Consequently, the general structure and most important components of ALEX are only briefly outlined below. In addition, we describe features of the package that were modified specifically to address problems associated with modelling the patch system at Tumut.

ALEX is a spatially explicit population model that uses the Monte Carlo method to make probabilistic predictions of population dynamics. The key state variables in the model are the numbers, location and age class of animals (Possingham & Davies 1995). Each animal is assigned to one of three possible age classes: newborn (individuals born in that year), juveniles (animals > 1 year old but pre-reproductive) and adults. Animals remain in a given age class for a given number of years (specified by the user). There is a fixed probability distribution for the number of offspring produced by each adult female, which is calculated from information on sex ratio at birth and the number and the size of litters (Possingham & Davies 1995). There is an annual probability of mortality associated with each age class.

Each patch in the model has a number of key properties, including: (i) position, which is defined by a set of spatially referenced  $x, y$  coordinates; (ii) area (defined in hectares); and (iii) maximum habitat quality, defined as the suitability of the area for supporting the target taxon.

ALEX includes a 'migration' submodel that allows animals to move between patches. Each age class is assigned a probability of dispersal and individuals leave a given patch when the number of animals exceeds a user-defined threshold abundance. If the density of animals within a patch is low, then animals of dispersal age will become established in the natal patch. Animals move from their source patch in a straight line and a random direction. The chance a dispersing animal will reach another patch is a function of the distance to, and the size of, other habitat patches in the system of remnants (Possingham & Davies 1995). The nature of the migration function in ALEX is underpinned by

observations and theory that indicate that animals are more likely to contact large adjacent patches than smaller more remote ones (Fritz 1979; Smith 1980; Hanski 1994a, 1994b). A mean migration distance is the distance animals can move without contacting another patch before they die. For the greater glider, we set the mean migration distance to 2 km, a value based on observations made during extensive radio-tracking studies of the species in the patch system at Tumut (M.L. Pope & D.B. Lindenmayer, unpublished data).

#### SIMULATION OF THE DYNAMICS OF THE TUMUT LANDSCAPE

Our study area was formerly covered in *Eucalyptus* forest that had been largely converted to stands of exotic softwood radiata pine trees. Different areas of native forest had been cleared at different times in the past as the plantation expanded. To model the landscape dynamics, simulations began in the year 1800 and the population density was specified as the carrying capacity of the area. The model was run for 132 years until the first compartment of softwood trees was established. This enabled populations of the greater glider to reach a stochastic 'equilibrium' in the model. The model was then run from 1932 for a further 65 years until 1997 (the time when field surveys were completed), with new eucalypt remnants added sequentially as the surrounding forest was converted to stands of radiata pine. Each new compartment of radiata pine was treated as a new 'patch' in which the habitat quality value was reduced to zero when the original native forest was cleared and converted to softwoods. The timing of the introduction of new pine compartment 'patches' in the model corresponded to the known dates for these operations obtained from State Forests of NSW. Thus, for our simulations, the entire system started as an intact landscape supporting potentially suitable habitat for the greater glider. The area of suitable forest was reduced as the eucalypt forest was converted to compartments of radiata pine. Animals were then only able to persist within the 39 remnant eucalypt patches.

#### Scenarios completed

##### NAIVE NULL MODEL

Initially, a 'naive' null model (i.e. not a metapopulation model) was run in ALEX in which forecasts of animal abundance were made assuming there were no fragmentation effects and based simply on remnant patch area and observed densities from nearby extensive continuous eucalypt forest. We assumed that the average population density in patches was equal to the population density in continuous eucalypt forest. We also assumed that greater gliders were randomly distributed in space, such that the number of animals in a patch was distributed as a random variate. The mean of this distribution was obtained by assuming that the expected

**Table 3.** Density and habitat quality values for the greater glider in different forest types. The values have been derived from field surveys of the abundance of animals in large continuous areas of eucalyptus forest that are of identical forest type to those characterizing the remnant patches in the model system. Habitat quality values in ALEX determine the breeding area of animals and, in turn, the number of animals that may occur in a patch (Possingham & Davies 1995)

Tree species	Density (ha <sup>-1</sup> )	Habitat quality
<i>E. camphora</i>	0.109	0.21
<i>E. radiata</i>	0.133	0.23
<i>E. macrorhynca</i> / <i>E. dives</i>	0.231	0.44
<i>E. viminalis</i>	0.333	0.63

number of individuals was equal to the area of a given patch multiplied by the population density actually measured for the dominant forest type that characterized that patch (Table 3).

#### METAPOPULATION MODELLING SCENARIOS

Four scenarios were run to generate predictions of animal abundance and patch occupancy by the greater glider. In the first (baseline) scenario (see below), the 39 remnants were treated as a 'closed' system in which there was no immigration of animals from native forest outside the study area. In addition, habitat quality was assumed to be identical for all patches. Assumptions about the lack of immigration and uniformity of patch quality were relaxed in subsequent scenarios.

##### Scenario 1

The uniform habitat quality value used for all 39 patches was calculated from density estimates for the greater glider obtained from field surveys of 40 sites located in large areas of continuous eucalypt forest. The average density of animals observed in continuous eucalypt forest was 0.19 animals ha<sup>-1</sup>. A very large continuous patch of habitat was then simulated using different values for the habitat quality parameter until the appropriate density for the greater glider was obtained (i.e. 0.19 animals ha<sup>-1</sup>). The corresponding value for habitat quality in ALEX was 0.59. Thus, all 39 eucalypt remnants in the patch system were assigned a value of 0.59 in the model.

##### Scenario 2

Extensive continuous areas of native eucalypt forest occur to the north and east of the softwood plantation. These areas may be a source of colonists in our patch system. Given this, in scenario 2 we incorporated the effects of immigration of greater gliders from large continuous areas of eucalypt forest. To facilitate modelling this effect, five extra patches, each 500 ha in size and located at the margins of the radiata pine plantation,

were added to the simulations. The model allowed animals from populations in these large patches to move into the patch system. The additional blocks of forest had no other effect on the patch system. For scenario 2, the same value for habitat quality (0.59) was employed for all 39 patches in the study area (see scenario 1) and the five additional 500-ha patches.

##### Scenario 3

In scenario 3 we varied the quality of each patch depending on the dominant forest type it contained. Field surveys in large continuous areas of *Eucalyptus* forest indicated that the density of greater gliders varied between different forest types. Correspondingly, values for habitat quality were varied on the basis of these observed differences in density (Table 3). The habitat quality variable influenced the minimum breeding area required by the greater glider and thus, in turn, the number of animals that could reproduce in a patch. As in scenario 1, immigration into the system was ignored.

##### Scenario 4

The effects of both variable patch quality and immigration of animals from large blocks of forest adjacent to the study area were modelled in scenario 4. The values for the quality of each patch were identical to those employed in scenario 3. Immigration into the patch system was modelled as per scenario 2.

#### WHAT WAS NOT MODELLED

A myriad of interacting factors can be simulated using PVA models. However, we endeavoured to keep our study as simple as possible to examine the relationships between model predictions and actual field data. Therefore, we did not model temporal variation, catastrophes or variations in dispersal ability. The major catastrophic events in the Tumut region are wildfires. However, considerable effort is now expended to prevent and suppress wildfires both within the *P. radiata* plantation and in the surrounding *Eucalyptus* forests. The patch system has not experienced any major wildfires since fragmentation. We were unable to model other possible catastrophes because of lack of data. A second simplification is that the model makes no provision for the impact of losses of genetic variability that may occur in small and/or declining populations (Possingham & Davies 1995). Other models for PVA (e.g. VORTEX; Lacy 1993) are required to simulate these processes. Data are presently not available to parameterize this aspect of the ecology of populations of the greater glider at Tumut.

#### OUTPUT DERIVED FROM ALEX

A range of patch- and population-based estimates are generated from the application of ALEX (Possingham & Davies 1995). The ones of particular relevance to

this study were the mean abundance of animals per patch and the probability of occupancy of a given patch (Table 1). Predicted values for these measures were gathered from the model for the year 1997, the same time as field surveys for the greater glider were completed. The methods outlined below for model testing were used for predictions derived from all four scenarios.

Logistic regression analysis (Collett 1991) was employed to test whether there was a significant positive relationship between actual patch occupancy and model-predicted probability of patch occupancy. Here the response (dependent) variable was actual occupancy or non-occupancy. The explanatory (independent) variable was the predicted probability of occupancy generated by ALEX. To explore further patch occupancy data, values for the predicted probability of occupancy were divided into four classes: 0–0.25, 0.25–0.5, 0.5–0.75 and 0.75–1. We then compared the predicted number of patches in these probability classes with the actual number of patches where the greater glider was found to be present and where it was absent.

To compare abundance data, predicted mean values for each patch were plotted against actual values. For a subset of patches, we compared the actual number of animals with histograms generated for the probability distribution of the predicted number of animals.

## Results

### SPOTLIGHTING SURVEYS

A total of 81 greater gliders was detected in the 39 patches, and the number of animals per patch varied from zero to 15 (Table 1). Despite extensive surveys, the greater glider was not detected in the 40 sites dominated by stands of radiata pine trees. Surveys of 40 sites in large areas of continuous eucalypt forest showed that estimates of the density of greater gliders varied between forest types (Table 3), and these values were used to generate a habitat quality rating for the remnant patches based on dominant tree species.

### PVA MODELLING: CONTRASTS BETWEEN SCENARIOS

The primary aim of this study was to contrast the predictions from a PVA model with actual field results. Given this, we have limited the description of major results to a brief summary of key outcomes of the four scenarios.

Values for average patch occupancy and average total animal abundance (the summed number over all patches) were lower in scenarios in which a closed system was modelled (scenarios 1 and 3). Similarly, variations in habitat quality between the patches produced lower values for these measures than the uniform habitat quality value cases. Thus, the simulations that yielded the highest values for patch occupancy and overall animal abundance were those in scenario 2,

in which animals could immigrate to a patch system characterized by uniform habitat quality. However, the forecast average number of animals in the patch system did not vary greatly between scenarios, ranging from 84 [95% confidence interval (CI) = 2.9] and 89.5 (95% CI = 3.2) (scenarios 3 and 1, respectively) to 93 (95% CI = 2.7) and 101 (95% CI = 3.1) (scenarios 4 and 2, respectively).

### COMPARISONS BETWEEN FIELD DATA AND MODEL PREDICTIONS: NAIVE NULL MODEL

The naive null model, in which fragmentation effects were ignored and animal abundance was calculated simply using the summed area of all 39 remnants (437 ha), gave a predicted total of approximately 170 (95% CI = 3.7) animals. This was considerably higher than the actual number recorded ( $n = 81$ ). The predicted number of greater gliders in each patch was also, on average, higher than observed in field surveys.

### COMPARISONS BETWEEN FIELD DATA AND MODEL PREDICTIONS: PATCH OCCUPANCY DATA AND METAPOPULATION MODELS (SCENARIOS 1–4)

Values for the mean total number of greater gliders predicted by ALEX in scenarios 1–4 outlined above (84–101) were similar to the actual total numbers summed across all 39 patches. Thus, the metapopulation models in these scenarios provided better predictions of overall numbers of animals than a simple extrapolation from unfragmented eucalypt forest (i.e. the naive null model).

Logistic regression analysis showed highly significant positive relationships between predicted patch occupancy and actual patch occupancy; patches forecast by ALEX to be occupied by the greater glider were significantly more likely to be actually occupied. The corresponding probability values for the tests for each of the scenarios were: scenario 1 ( $P = 0.006$ ), scenario 2 ( $P = 0.003$ ), scenario 3 ( $P = 0.004$ ) and scenario 4 ( $P = 0.001$ ). The equations for the logistic regression relationships were:

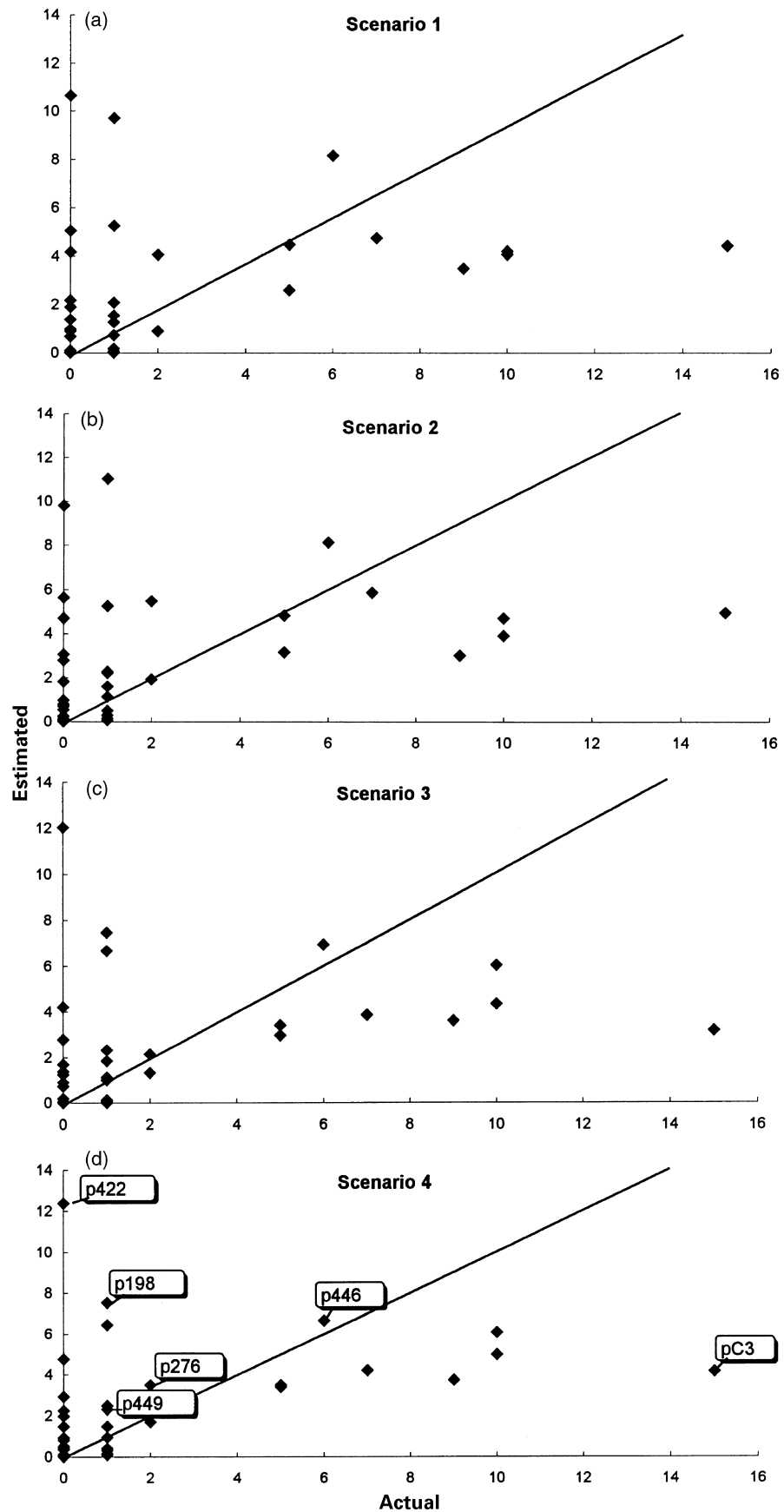
$$\text{Scenario 1: } \text{logit}(P) = -0.936 + 2.57 [1.10] \times (\text{predicted probability of patch occupancy})$$

$$\text{Scenario 2: } \text{logit}(P) = -1.24 + 2.90 [1.13] \times (\text{predicted probability of patch occupancy})$$

$$\text{Scenario 3: } \text{logit}(P) = -1.02 + 2.77 [1.14] \times (\text{predicted probability of patch occupancy})$$

$$\text{Scenario 4: } \text{logit}(P) = -1.38 + 3.33 [1.10] \times (\text{predicted probability of patch occupancy})$$

The response variable for these relationships was whether patches were or were not actually occupied. The number in square brackets in each equation is the standard error of the slope coefficient.



**Fig. 2.** Values for predicted and actual abundance of the greater glider for each patch from scenario 1 (a), scenario 2 (b), scenario 3 (c) and scenario 4 (d). For scenario 1, the patches have been assigned labels according to their size: small (< 3 ha), medium (3–10 ha), large (11–20 ha) and extra large (> 20 ha). The straight line in each diagram shows a hypothetical perfect fit between predicted and actual data. In (d), scenario 4, some key patches are highlighted by the associated identifying number.

COMPARISONS BETWEEN FIELD DATA AND  
MODEL PREDICTIONS: ABUNDANCE DATA AND  
METAPOPULATION MODELS (SCENARIOS 1–4)

Table 1 contains values for the mean predicted abundance and the actual abundance for each patch. Values for the predicted mean abundance of the greater glider in each scenario are plotted against actual counts for each patch in Fig. 2. The solid line in each figure is the 45° line, which would reflect perfect congruence between predicted and actual values for the abundance of the greater glider in all patches. Notably, we would not expect a perfect fit because the model predictions are averages (from 1000 runs for a given scenario) and the precise number of animals in a patch is influenced by demographic stochasticity (i.e. chance births, deaths and movements).

Inspection of Fig. 2 shows that, for several patches, either the model forecast many animals to occur and few were actually there or, conversely, few animals were predicted to occur but the patch was occupied by several greater gliders. These general themes were apparent from the comparisons of model output and actual abundance across all four scenarios, and thus irrespective of the level of model complexity invoked (i.e. the addition of habitat quality and immigration for external source areas) (Fig. 2). We tried to determine if there were particular patch sizes where there was major divergence between actual and predicted values, but no consistent trends were observed.

To determine if the actual number of animals was within the bounds of the predicted distribution, we compiled histograms of the variation in the predicted abundance of animals for a subset of sites from one set of simulations (scenario 4). The observed number of animals was overlaid on these histograms (Fig. 3). For some patches the observed occurrence was significantly higher (patch C3) or lower (patch 422) than predicted (Fig. 3).

Table 4 shows predicted and actual values for patch occupancy derived from scenarios 1–4, respectively, and the data they contain confirm the general findings illustrated in Fig. 3. For most scenarios, although the application of ALEX predicted low values (0–0.25) for the probability of patch occupancy, some animals were recorded in these patches. For example, in scenario 1, of 14 patches where the predicted probability of occupancy was 0–0.25, the greater glider was recorded in four (29%) patches (Table 4). Similar outcomes were recorded in scenarios 3 and 4 (Table 4). In general, congruence between actual patch occupancy and model forecasts improved for increased values for predicted probability of occupancy (e.g. 0.25–0.5 and 0.5–0.75; Table 4).

### Discussion

Our study represents one of the first landscape-scale tests of a spatially explicit population model. These types of tests are extremely important given the widespread

and increasing use of modelling tools for forecasting the fate of species in response to resource and conservation management. A key part of testing is to provide insights into how the structure and parameter settings could be changed to improve model predictions.

This investigation was a *post-hoc* exploration of the accuracy of predictions made by a widely available and relatively simple generic model for PVA. Except for data on the presence of animals in large continuous areas of native forest, the parameters input to the model were set without information from the field surveys. Hence, there was no *post-hoc* modification of the model in response to field results. This contrasts with other studies, such as the incidence model developed by Hanski (1994b), where tests involve using part of a data set to parameterize the model and then examining the predictive ability for the remaining patches in a system of fragmented remnants (Hanski *et al.* 1996; Wahlberg, Moilanen & Hanski 1996). Moreover, the study completed here examined a species with markedly different biological and ecological characteristics than the group (butterflies) targeted for testing of Hanski's (1994b) incidence model.

The naive null model, which assumed no fragmentation effects, substantially over-predicted the abundance of the greater glider. Despite the simplicity of the models in scenarios 1–4, there was considerable congruence between model forecasts and field data: the approximate total number of animals and patch occupancy patterns were well predicted. In these scenarios ALEX generated remarkably similar values to actual total numbers of greater gliders summed across all 39 patches (84–101, cf. 81). In addition, logistic regression analysis showed highly significant positive relationships between predicted patch occupancy and actual patch occupancy (values for *P* ranged from 0.001 to 0.006). Indeed, the likelihood of occupancy categories employed in our study provided a novel way for identifying patches where there was a high likelihood of successfully predicting actual patch occupancy. Our results demonstrated that when the model-derived values for the probability of patch occupancy were high (0.50–0.75, 0.75–1.00) there was greater congruence between actual patch occupancy and the predicted probability of occupancy.

### DISCREPANCIES BETWEEN FIELD DATA AND MODEL PREDICTIONS

We are acutely aware that even if model predictions accurately fit field data, it is possible that such congruence is fortuitous and the key factors and processes underpinning population dynamics have not been well captured within the model (Villard, Merriam & Maurer 1995). The model in this study substantially over-predicted the actual abundance for some patches, and in others it was considerably under-predicted (e.g. C3 and 422; Fig. 3).

Lack of congruence between field data and model predictions for some patches could have occurred because the remnant patches may vary in more ways than were

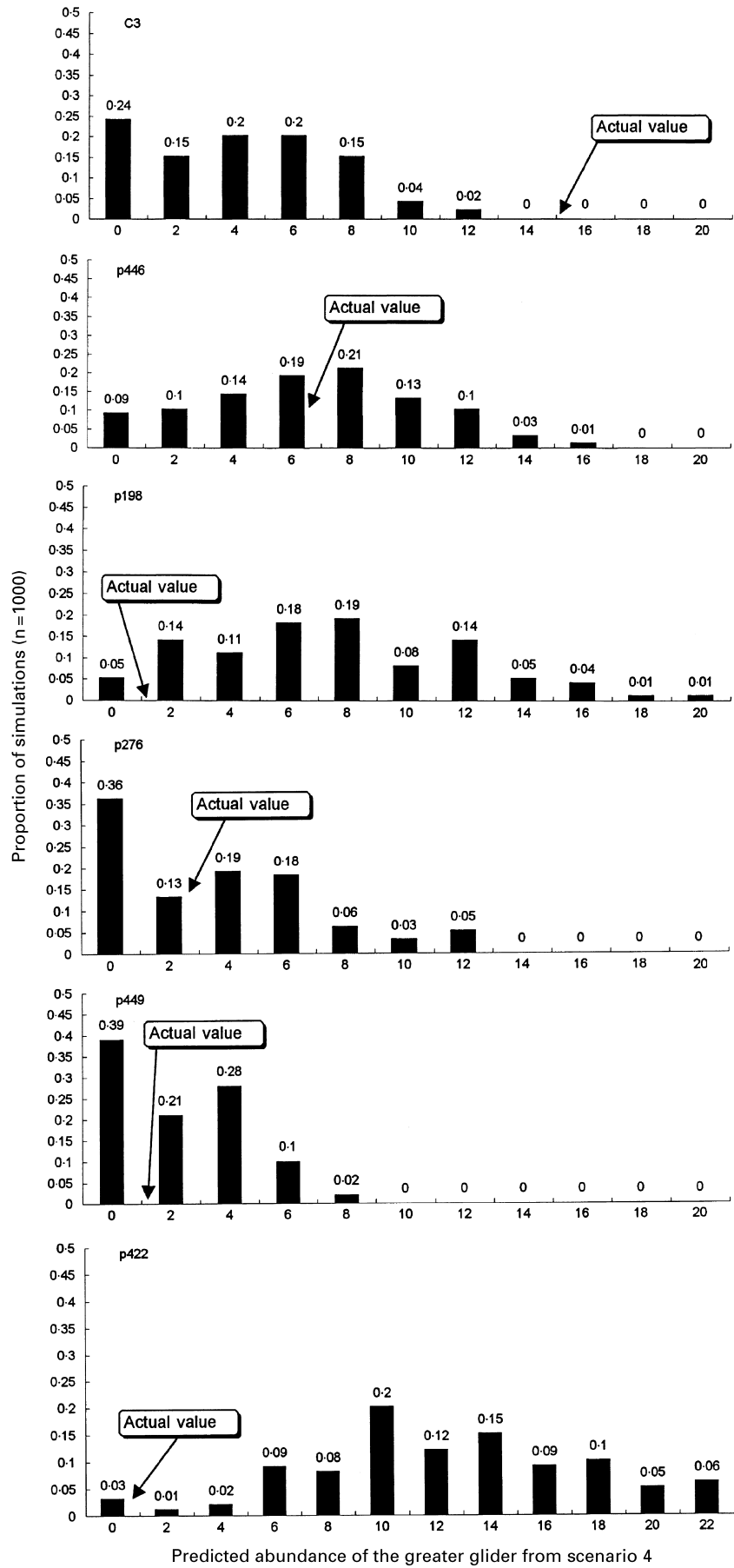


Fig. 3. Variations in the predicted values for the abundance of the greater glider in a subset of patches at Tumut. The patch identity is shown at the top of each diagram. The arrow denotes the actual value for observed abundance recorded from field surveys.

**Table 4.** Values for predicted probability of patch occupancy by the greater glider derived from the application of ALEX for four different scenarios (see text) compared with actual values for patch occupancy. The first row from each scenario shows the number of patches for a given predicted patch occupancy category that actually supported animals. The final row in each scenario gives values for the proportion of patches actually occupied for a given category for the forecast probability of occupancy

	Model derived value for predicted probability of patch occupancy			
	0–0.25	0.25–0.5	0.5–0.75	0.75–1
Scenario 1				
Predicted number of patches in class	14	11	8	6
Number of patches where animals actually present	4	5	7	4
Scenario 2				
Predicted number of patches in class	14	5	10	10
Number of patches where animals actually present	4	2	6	8
Scenario 3				
Predicted number of patches in class	14	11	7	7
Number of patches where animals actually present	4	5	6	5
Scenario 4				
Predicted number of patches in class	15	7	8	9
Number of patches where animals actually present	4	3	6	7

captured in the model. The mismatch is unlikely to be caused by errors in life-history information because an earlier series of detailed field studies focused on populations of the greater glider at Tumut (1969b; Tyndale-Biscoe & Smith 1969a). It is also unlikely to be due to errors in background information on landscape change because the history of fragmentation and patch creation has been well documented at Tumut. Some of the processes not included in the model and which might have caused the discrepancy are patterns of inter-patch dispersal and within-patch habitat suitability. Patterns of movement by the greater glider between habitat patches are poorly known but might substantially affect distribution patterns in a fragmented landscape. The ability of animals to move between patches may not be a simple function of inter-patch distance as modelled in this study, but rather it might be related to other factors such as the habitat suitability along water courses or other topographic features, as is believed to occur among populations of the bush rat *Rattus fuscipes* at Tumut (Hewittson 1997). Although we incorporated a habitat quality function based on differences in suitability between broad forest types for the greater glider (Table 3), we did not model within-forest type structural features of stands, such as the availability of hollow-bearing trees as nest sites. Inclusion of habitat quality associated with broad forest types did improve the model fit for some patches (e.g. for patch 198) but not for others. In the case of patch 422, a lack of trees with hollows (not included in ALEX) might explain the paucity of animals in this large patch and the low predictive ability of the model (Fig. 3). Unlike other parts of southern Australia where the abundance of trees with hollows is an important factor influencing the distribution of the greater glider (Lindenmayer *et al.* 1995b), extensive multivariate statistical analyses have indicated that this attribute of

stand structure is not a significantly explanatory variable in habitat models in the Tumut region (Lindenmayer *et al.* 1999a).

Factors such as demographic stochasticity can strongly influence the dynamics of very small populations of animals (McCarthy, Franklin & Burgman 1994). This could be important at Tumut, where many of the patches are relatively small (Table 1) and may support only a limited number of greater gliders. ALEX does incorporate the effects of demographic stochasticity, although the magnitude of its effects are unknown for the greater glider (like virtually all other species; McCarthy, Franklin & Burgman 1994) and it is possible we have under-estimated them.

#### FURTHER STUDIES

Our results indicate that an important future direction for our work at Tumut will be to test some of the assumptions employed in spatially explicit computer simulation models such as ALEX and, in turn, identify the various reasons why the model predictions were inaccurate for some patches. On this basis, we have instigated an intensive radio-tracking study of the greater glider in the patch system at Tumut. Blood samples have also been gathered from animals in an effort to use genetic techniques (Slatkin 1985) to track effective dispersal events between patches (Lindenmayer *et al.* 1999b). In addition, further tests are needed on a larger set of species with different life-history attributes from the greater glider. We plan to examine the level of congruence between model predictions and actual abundance for other arboreal marsupials as well as representatives of other groups for which extensive field data are being gathered at Tumut (birds and small mammals). These additional investigations will provide a detailed assessment of the

types of species for which model predictions are, and are not, accurate, and should give us insights for improving predictive models for conservation and management.

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