A simple landscape-scale test of a spatially explicit population model: patch occupancy in fragmented south-eastern Australian forests

David B. Lindenmayer, Michael A. McCarthy, Hugh P. Possingham and Sarah Legge

The results of a landscape-scale test of ALEX, a widely used metapopulation model for Population Viability Analysis (PVA), are described. ALEX was used to predict patch occupancy by the laughing kookkaburra and the sacred kingfisher in patches of eucalypt forest in south-eastern Australia. These predictions were compared to field surveys to determine the accuracy of the model. Predictions also were compared to a "naïve" null model assuming no fragmentation effects.

The naïve null model significantly over-predicted the number of eucalypt patches occupied by the sacred kingfisher, but the observed patch occupancy was not significantly different from that predicted using ALEX. ALEX produced a better fit to the field data than the naïve null model for the number of patches occupied by the laughing kookaburra. Nevertheless, ALEX still significantly over-predicted the number of occupied patches, particularly remnants dominated by certain forest types – ribbon gum and narrow-leaved peppermint. The predictions remained significantly different from observations, even when the habitat quality of these patches was reduced to zero. Changing the rate of dispersal improved overall predicted patch occupancy, but occupancy rates for the different forest types remained significantly different from the field observations. The lack of congruence between field data and model predictions could have arisen because the laughing kookaburra may move between an array of patches to access spatially separated food and nesting resources in response to fragmentation. Alternatively, inter-specific competition may be heightened in a fragmented habitat. These types of responses to fragmentation are not incorporated as part of traditionally applied metapopulation models. Assessments of predictions from PVA models are rare but important because they can reveal the types of species for which forecasts are accurate and those for which they are not. This can assist the collection of additional empirical data to identify important factors affecting population dynamics.

D. B. Lindenmayer and M. A. McCarthy, Centre for Resource and Environmental Studies and Dept of Geography, The Australian National Univ., Canberra, ACT 0200, Australia (davidl@cres.anu.edu.au). – H. P. Possingham, Dept of Applied and Molecular Ecology, Univ. of Adelaide, Adelaide, SA 5064, Australia. – S. Legge, Div. of Botany and Zoology, Australian National Univ., Canberra, ACT 0200, Australia.

Predictions of the response of species to fragmentation are important because they may help identify those taxa at risk and, in turn, allow land and wildlife managers to adopt proactive conservation approaches before expensive, high risk management strategies such as reintroduction and translocation are required (Burgman and Lindenmayer 1998). However, predicting the effects of landscape change on biota can be difficult because taxa respond very differently to the same perturbations (Robinson et al. 1992). Even species that are closely related, share life history, dietary and other characteristics, may respond differently (e.g. Simberloff and

Dayan 1991, Thiollay 1992, Lindenmayer et al. 1999a). In addition, the influence of multiple factors operating at different scales (Laurance 1991), together with the potential for cumulative impacts (sensu McComb et al. 1991, Cocklin et al. 1992) can thwart attempts to accurately forecast the long-term response of any given species to landscape change (Burris and Canter 1997). Carefully designed field experiments can help better inform the understanding of landscape change (e.g. Margules et al. 1994), but these too can have limitations (Huston 1997). The complementary use of models (e.g. those for Population Viability Analysis) can also help forecast population dynamics in fragmented systems (McCarthy 1995, Possingham and Davies 1995, Hanski et al. 1996, Wahlberg et al. 1996). They also can be used to predict the effects of landscape change on species decline (Lamberson et al. 1994, Possingham et al. 1994, Akçakaya et al. 1995, McCarthy and Lindenmayer 1999). However, the accuracy of forecasts made using these tools have only rarely been tested (Hanski et al. 1995, Hanski and Simberloff 1997, Lindenmayer et al. 1999a). Indeed, predictions from these modelling tools may not be particularly robust or ecologically meaningful unless they are compared with field data (McCarthy et al. 1997). Given this, we completed a simple test of congruence between patch occupancy predicted by a metapopulation model and actual data on patch occupancy gathered from extensive field surveys. The aim of our study was to determine if the metapopulation model could make reasonable predictions of patch occupancy. We used ALEX (Analysis of the Likelihood of Extinction; Possingham and Davies 1995), a generic, widely used, and spatially explicit PVA package, to model the dynamics of populations of two distinctive species of kingfishers in a fragmented forest landscape in south-eastern Australia. These were the laughing kookaburra (*Dacelo novaeguineae*) and sacred kingfisher (*Todiramphus sanctus*). We examine the accuracy of forecasts of patch occupancy made by ALEX and discuss these comparisons in terms of how spatially explicit models might be improved.

Study area

The region targeted for study was the Buccleuch State Forest (148°40′ E, 35°10′ S) near Tumut in southern New South Wales (NSW), south-eastern Australia (Fig. 1). The region is characterised by 60000 ha of exotic conifers (almost all of which is radiata pine [*Pinus radiata*] forest).

We focussed on a 5050-ha sub-section within the Buccleuch State Forest that surrounds approximately 450 ha of remnant *Eucalyptus* forest distributed as 39 small to medium-sized patches (0.4 ha to 40.5 ha; Appendix 1, Fig. 2). The radiata pine forest within the

study area was established over a period exceeding 50 yr between 1930 and the mid-1980s (Lindenmayer et al. 1999b). The area directly north of the study area supports 20000 ha of radiata pine plantation. A similar expanse of exotic softwood forest occurs to the south of the radiata pine plantation. The eastern edge of the study area is fringed by large, continuous areas of native *Eucalyptus* forest exceeding 100000 ha. The length of the boundary between the eastern edge of the study area and the adjacent native forest is approximately 18 km. The continuous native forest supports a range of types of mixed-species eucalypt stands similar to those which characterise the remnant eucalypt patches located within the softwood plantation.

Data on vegetation cover within the boundaries of our study area were collected by State Forests of NSW using aerial photography and ground-truthing. Remnant patches were mapped, digitised, assigned unique polygon numbers, and the associated data entered into a Geographic Information System (GIS). For our study, information on the size and location of each remnant was extracted from the GIS database and its accuracy subsequently confirmed by on-ground surveys.
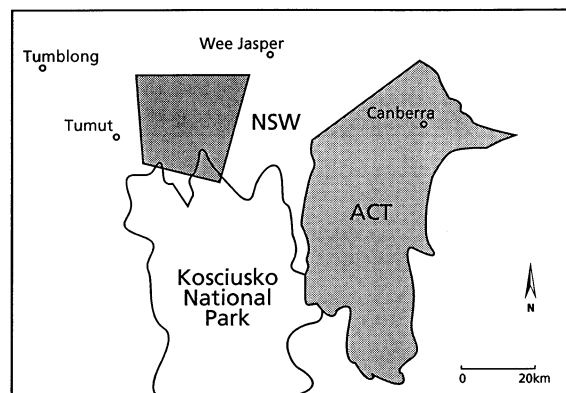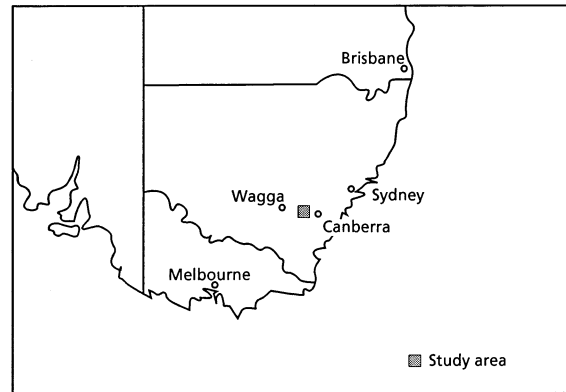

Fig. 1. The general location of the study area at Tumut, south-eastern Australia.
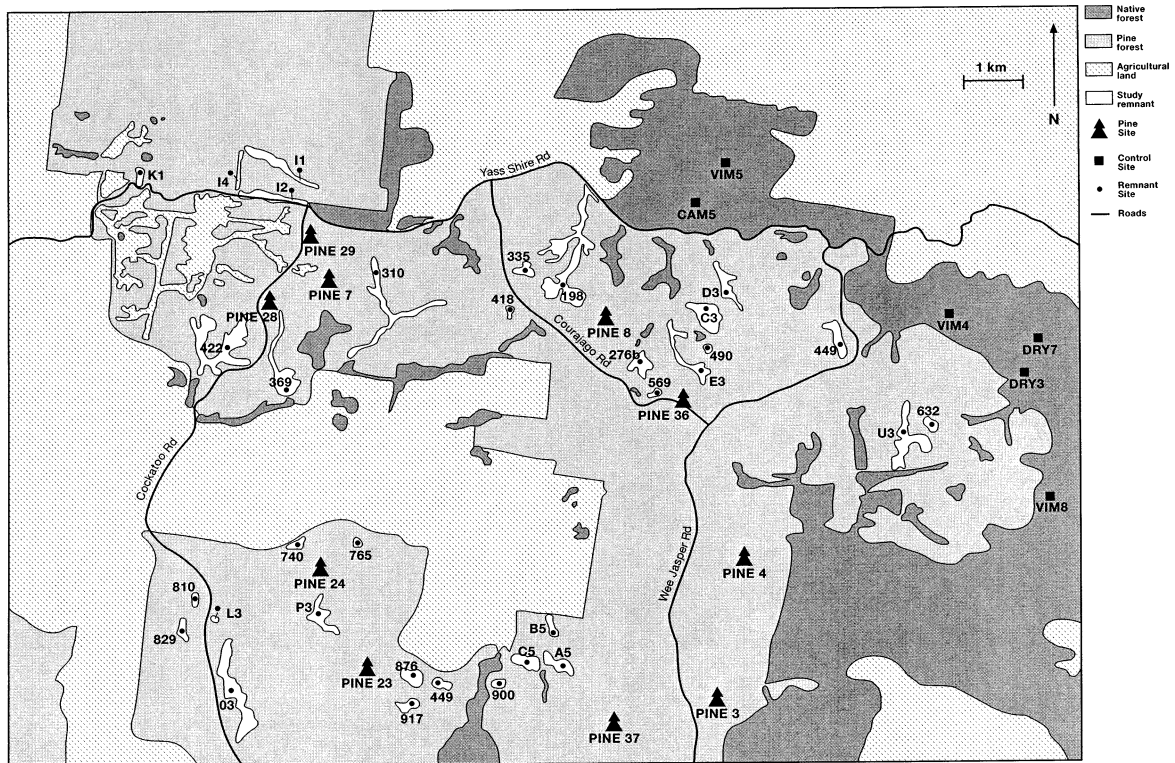
Fig. 2. The patch system modelled at Tumut.

Extensive field reconnaissance indicated that the 39 remnant patches were dominated by four different species of eucalypt – ribbon gum (*Eucalyptus viminalis*), narrow-leaved peppermint (*Eucalyptus radiata*), red stringybark (*Eucalyptus macrorhynca*), and swamp gum (*Eucalyptus camphora*) (Appendix 1).

Target species

We selected two species of birds for detailed investigation – the laughing kookaburra and the sacred kingfisher. They were chosen because:

1) Both species are relatively large and have distinctive calls (Readers Digest 1990, Pizzey and Knight 1997) making them more likely to be detected than some other more cryptic bird taxa present at Tumut (Lindenmayer et al. 1997, Cunningham et al. 1999). In addition, earlier field trials (Cunningham et al. 1999) indicated that standard bird census methods like point interval counts (see Ralph et al. 1997) readily record the presence of the laughing kookaburra and the sacred kingfisher (Cunningham et al. 1999). This provided considerable confidence in the accuracy of surveys to detect birds in the habitat fragments. This is important because it limited the potential that sampling error would contribute sub-

stantially to differences between field data and model predictions.

2) The biology and ecology of the two species is comparatively well known (reviewed by Higgins 1999) – a factor assisting with model parameterisation. Good data were available on population density across different habitat types in eastern Australia (Ford and Bell 1981, Legge 2000), social systems (Parry 1973, Legge and Cockburn 2000), and fecundity (Readers Digest 1990, Legge 2000). One species is a seasonal latitudinal migrant (sacred kingfisher) and the other is a year-round resident (laughing kookaburra), making an interesting contrast in model predictive ability between species which exhibit large differences in movement patterns. Differences in life history attributes and movement patterns can facilitate interesting comparisons in predicted population trajectories (Burgman et al. 1993).

3) Previous extensive field surveys of 40 sites dominated by stands of radiata pine (Lindenmayer et al. 2001) indicated the sacred kingfisher and laughing kookaburra were absent or rare in the pine matrix surrounding the eucalypt patches at Tumut. This suggested that both species were behaving as metapopulations, making them good candidates for modelling as metapopulations and for completing tests of predicted patch occupancy.

Field sampling protocols

Two types of surveys were employed to sample bird populations on our study sites – point-interval counts (sensu Pyke and Recher 1983) and automatic bird call recording devices (Lindenmayer et al. 1997). These are outlined below.

Point interval counts

Many field techniques are available for bird census (Recher 1988, Ralph et al. 1997). Various bird counting protocols were subject to detailed assessment in the Tumut region (Lindenmayer et al. 1997). The point interval count method (sensu Pyke and Recher 1983) was shown to be a robust technique for the detection of relatively large birds with distinctive calls such as the laughing kookaburra and sacred kingfisher (Cunningham et al. 1999).

To facilitate point interval count sampling, a 600-m transect divided into 100-m units was used to census birds. The 0-m, 100-m, 200-m, 300-m, 400-m, 500-m, and 600-m points along each transect were marked with distinctively coloured flagging tape and metal disks. A 5-min point interval count was employed to count birds at the each of the seven marked locations along the transect.

The same experienced field observer (DBL) was responsible for undertaking all counts. This avoided the problems of observer bias and observer heterogeneity which are typically associated with multiple observer surveys (Kavanagh and Recher 1983, Link and Saur 1997, Cunningham et al. 1999). In addition, field sampling was confined to clear, still mornings to limit the effects of variable weather conditions on our data (Slater 1994). Finally, field surveys were completed during late October and early November 1996 when all seasonal migrants (e.g. sacred kingfisher) had arrived in the Tumut region (Lindenmayer et al. 1997). The sacred kingfisher and laughing kookaburra are calling frequently at this time as part of territory establishment and breeding behaviour (Parry 1973).

Point interval counts in remnants

All 39 patches of remnant eucalypt forest in the study area were surveyed repeatedly using point interval counts for the presence of the sacred kingfisher and laughing kookaburra. A 600-m transect (see above) was established at all eucalypt remnants 3 ha or larger. For remnants smaller than this, we scaled the transect length according to the remnant size; 200 m for 1–2-ha patches; and 400 m for 2–3-ha patches. Transects commenced at a randomly selected edge of a patch. Surveys were repeated 14 times for each

remnant in the study. Thus, considerable effort was employed to establish the presence or absence of the sacred kingfisher and the laughing kookaburra in each remnant eucalypt patch.

Point interval counts in continuous (unfragmented) eucalypt forest

A number of authors have shown that the densities of Australian forest birds may vary between different forest types (Ford and Bell 1981, Mac Nally 1997). Given this, we completed counts of the sacred kingfisher and laughing kookaburra at 40 sites located within large continuous areas of native forest that occurred at the boundaries of the radiata pine plantation in the Buccleuch State Forest. The same forest types which characterised the remnants (see above and Appendix 1) were targeted for survey in continuous areas of native eucalypt forest. At least eight replicates of each of the four forest types were surveyed. To reduce the potential for spatial dependence, sites in continuous forest were more than 1 km apart and located within extensive stands of a given forest type. The field protocols for sampling bird populations were identical for the 39 eucalypt remnants and the 40 sites in large continuous areas of native forest (i.e. point interval counts along a 600-m marked transect).

We derived habitat quality values for the different remnant habitat patches in the fragmented forest at Tumut (see section below on modelling scenarios). The different habitat quality values were based on numbers of point count observations made during field surveys in continuous eucalypt forest dominated by the different forest types. Data from continuous forest enabled us to scale the frequency of detection within a given eucalypt forest type relative to corresponding values for the other forest types. We then scaled these relative values against estimates of actual densities for the laughing kookaburra and sacred kingfisher gathered in similar vegetation communities to those at Tumut (e.g. Mac Nally 1997, Higgins 1999). This approach allowed us to generate density estimates for use in modelling the four different forest types in our study (see Table 1). Notably, we did not use density estimates directly obtained from our field surveys of continuous eucalypt forest. This was because of the risk of double-counting the same individuals at successive census stations located 100 m apart (see above). Hence, unlike presence/absence data for patch occupancy, there may have been large errors in density estimates for the sacred kingfisher and the laughing kookaburra derived using repeated point interval counts.

Automatic bird call recording devices

Automatic bird call recording was the second method employed to detect forest birds. Automatic bird call recorders were set at the 0-m and 400-m points along the marked transect established in 20 of the 39 remnant eucalypt patches. These devices also were deployed at the 0-m and 400-m points along the transects established at each of the 40 sites located within large continuous areas of native forest. The automatic bird call recording devices provided continuous recording of bird calls for a specified interval (Lindenmayer et al. 1997, unpubl.). For this study, call boxes were synchronized so that a 30-min period was recorded at dawn, and a further three 10-min segments were completed during each of the following three hours (i.e. 08.00–08.10, 09.00–09.10 and 10.00 to 10.10). Thus, a profile of bird calling was obtained across the morning and the chances of detecting the target taxa if they occurred within a given area was maximised. Audio tapes made of calls were removed from each bird call recorder at the completion of a taping session and then analysed to determine the number of calls made by the sacred kingfisher and the laughing kookaburra.

The frequency of calling by large kingfishers such as the sacred kingfisher and the laughing kookaburra (Parry 1973, Reyer and Schmidl 1988) means there is a very high probability of detection of bird call recording devices. Although automatic bird call recording devices may not yield 100% detection rates of the target species, the same extensive sampling regime was employed both in continuous eucalypt forests and in the remnant eucalypt patches. Hence, it was the relative outcome of the comparison of methods across the array of sites in this study that was important.

Estimating the probability of detection

All sites in the study were surveyed using point interval counts. The automatic call box recording devices were deployed at all 40 sites in large continuous areas of native eucalypt forest and 20 of the 39 eucalypt remnants. Although extensive surveys were completed using repeated point interval counts, the use of call box recorders gave detections of the laughing kookaburra and sacred kingfisher that were overlooked using human census methods. This enabled us to make corrections for observer error resulting from the point interval count, which were accounted for when comparing the field data and model predictions. Results from the automatic bird call recorders were used to estimate the probability of detecting the sacred kingfisher and the laughing kookaburra with the point interval count method.

The laughing kookaburra was detected at 18 sites using the automatic bird call recorders and at 15 of these 18 sites by point interval count method, giving an estimated detection probability of 0.833. For the sacred kingfisher, the equivalent results were detection at 16 sites by call box recording devices and 10 of these 16 sites by point interval counts. Thus, the detection probability for the sacred kingfisher was 0.625. These detection probabilities were used to correct for observer error by multiplying them by the predicted patch occupancy values obtained from simulation modelling.

The ALEX simulation model

Earlier papers have outlined the general structure of ALEX (Possingham et al. 1992, Possingham and Davies 1995), and its key components have been described as part of various case studies (e.g. Possingham et al. 1994, Lindenmayer and Possingham 1996). Consequently, the general structure and most important components of ALEX are only briefly outlined below. We describe features of the package 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. Each eucalypt patch embedded within the radiata pine matrix has a number of properties: (1) position, which is defined by a set of spatially referenced x,y co-ordinates, (2) area defined in hectares, and (3) habitat quality, defined as the suitability of the area for supporting the target taxon. Habitat quality for each patch was parameterised using density estimates for the sacred kingfisher

Table 1. Life history attributes for the sacred kingfisher and laughing kookaburra used in simulation modelling. The values used for these parameters are based on information in the literature, data summarised in a major review by Higgins (1999) and field data gathered by Legge and Cockburn (2000) and Legge (2000) (see text).

Parameter	Values for laughing kookaburra	Values for sacred kingfisher
Annual probability of death		
New born	0.6	0.85
Adult	0.1	0.3
Mean no. female young per pair per year[a]	0.35	3.94
Density (females per ha)[b]		
E. camphora forest	0.14	0.14
E. macrorhyncha forest	0.17	0.20
E. viminalis forest	0.20	0.20
E. radiata forest	0.11	0.20
Dispersal mortality (km^{-1})	0.05	0.05

[a] ALEX models the fate of only one sex – typically females.
[b] Population density values are based on extensive field surveys in continuous (unfragmented forest in the four forest types – see text). 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 and Davies 1995; see text).

and the laughing kookaburra in large continuous areas of native forest (see above and Table 1).

Model initialisation

Our study area was formerly covered in *Eucalyptus* forest that has been largely converted to stands of exotic softwood radiata pine trees. Areas of native forest have been cleared at different times in the past as the plantation expanded and the model initialisation process took this sequential landscape change into account. The first compartments of radiata pine were established in 1932 and further ones were added until 1985 (see Appendix 1). To model the landscape dynamics, simulations were commenced in the year 1800 and the model was run for 132 yr until the first compartment of softwood trees was established. This enabled populations of the sacred kingfisher and the laughing kookaburra to reach a stochastic "equilibrium" in the model. 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 sacred kingfisher and the laughing kookaburra. 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.

Life history attributes and dispersal

The key state variables in ALEX are the number, location and age class of animals (Possingham and Davies 1995). Each animal was assigned to one of two possible age classes; newborn (individuals born in that year) and adults. 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 clutches. There is an annual probability of mortality associated with each age class.

ALEX includes a "dispersal" submodel that allows animals to disperse between patches. Each age class was assigned a probability of dispersal and individuals moved from a given patch when the number of animals exceeded a user-defined threshold abundance. If the density of animals within a patch was low then animals of dispersal age will become established in the natal patch. 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 and Davies 1995). The nature of the dispersal function in ALEX is underpinned by observations and theory which indicates that animals are more likely to contact large, adjacent patches than smaller more remote ones (Fritz 1979, Smith 1980, Hanski 1994a, b). To reflect the increased probability of death during dispersal, a mortality rate was specified for the movement of individuals, with the actual dispersal mortality dependent on the straight-line distance between patches.

Parameter estimation for ALEX

Table 1 summarises the parameter values used in simulation modelling. These were based on information in the literature including a major review by Higgins (1999) as well as field data gathered by one of us (Legge 2000, Legge and Cockburn 2000). Notably, these values were determined *without* information on actual patch occupancy in the Buccleuch State Forest. We outline below a few key features of the laughing kookaburra and the sacred kingfisher that relate to our comparative modelling study.

The laughing kookaburra is endemic to mainland eastern Australia. Its diet includes a wide array of invertebrate and vertebrate prey. The majority of nests are in cavities in trees. The species lives in family groups comprised of an adult pair in a long-term monogamous relationship, 0–6 auxiliaries or helpers, and 0–3 juvenile birds. The adult breeding pair typically produces one clutch per year with a mode of three eggs. A second clutch is occasionally produced, particularly if the first one is lost. Brood reduction, facilitated by siblicide, limits fledging success. Little is known about dispersal in the laughing kookaburra, although banding records show that animals may move > 50 km from the natal territory. However, most marked birds are recovered < 10 km from the initial banding site. Mature birds can be long lived and records of birds exceeding 15 years old are known.

The sacred kingfisher occurs throughout large parts of coastal and inland Australia as well as New Guinea, south-east Asia, New Zealand and the Pacific Islands. The diet of the sacred kingfisher includes a diverse range of prey items including invertebrates and small vertebrates. Nesting usually occurs in tree hollows or termite mounds. The species lives in pairs and may produce at least two broods annually. Clutch size is typically four and fledging success is about 70%. Populations of the sacred kingfisher in southern Australia are migratory and depart in late summer or autumn and move to northern Queensland, New Guinea and Indonesia. Banding records suggest that adult sacred kingfishers may return to the same breeding sites in

successive years. We assumed in the model that after fledging, young adult birds migrated north and in the following (spring) season returned to the study area in an attempt to breed. The dispersal model in ALEX entailed the assumption that these new breeders were more likely to attempt to breed close to their natal site rather than in patches that were far away. In contrast, it was assumed that previous breeders always returned to the same patch. These assumptions are broadly consistent with patterns of natal dispersal, including those documented for migratory birds, where the modal dispersal distance is often short and the distribution of dispersal distances is highly skewed (Wolfenbarger 1949, Waser 1985, McCarthy et al. 1997).

Large continuous areas of native eucalypt forest occur at the north and east of the radiata pine plantation. Immigration from these areas into the patch system was included in the model in the following way. Five eucalypt patches, each measuring 500 ha in size were added to the patch system in the model. These additional patches were located to the north and east of the system of eucalypt remnants – locations consistent with the actual location of the extensive areas of continuous eucalypt forest at Tumut. Birds could disperse from these five large patches into the array of 39 eucalypt remnants targeted for modelling. The dispersal parameters used were the same as those described above for the laughing kookaburra and sacred kingfisher.

Scenarios used for model testing

Spatially explicit population models have a large number of input parameters and they can be modified to fit almost any data. Consequently, we employed a simple modelling protocol that involved comparing actual field data on patch occupancy with predictions of patch occupancy forecast from (1) a "naïve null" model, and (2) the ALEX metapopulation model. One thousand runs were completed for each scenario. Notably, there was limited variability in the predicted probability of patch occupancy across runs (typically 2%–3%) indicating that such variation was insignificant relative to other forms of variation (e.g. changes in habitat quality; see below).

"Naïve null" model

In the naïve null model it was assumed there were no fragmentation effects and that animals were distributed randomly. Thus, the probability of patch occupancy was derived from a Poisson distribution assuming that the expected density in each patch was the same as in nearby continuous (unfragmented) areas characterised by the same forest type. The population densities used were obtained from the surveys of the 40 sites in large

continuous areas of native forest (Table 1). As one of the main foci of our work was to model the impacts of habitat fragmentation, the naïve null model was an attempt to ignore fragmentation effects on the dynamics of sacred kingfisher and laughing kookaburra populations.

The ALEX metapopulation model

For the ALEX model, we incorporated the key life history parameters outlined in Table 1 and assumed there was a fragmentation effect. An important component of the application of the ALEX model was variation in habitat quality values between the eucalypt remnants. These were varied as a function of the dominant forest type within a patch (see Table 1). Four eucalypt forest types were recognised: those dominated by *E. viminalis*, *E. radiata*, *E. macrorhyncha* and *E. camphora*. Habitat quality estimates were included in simulations using the ALEX model to determine if it could help explain differences between field data and model predictions for patch occupancy. This helped to ascertain, for example, if predictions by ALEX were equally (in)accurate in patches dominated by different forest types.

Statistical comparisons between predictions from metapopulation models and field surveys

Values for patch occupancy derived from computer simulation modelling were compared with field data in two ways-logistic regression and log-likelihood values. Logistic regression (Hosmer and Lemeshow 1989) was used to investigate the relationship between the observed occupancy and the predicted probability of occupancy (Cox 1958, Miller et al. 1991). The logistic regression approach does not provide information on the relative goodness-of-fit (e.g. the fit of the ALEX model compared with the naïve null model). Given this, log-likelihood values were calculated to quantify the goodness-of-fit for the predictions of the ALEX model compared with those of the naïve null models given the observed (field) data.

Testing using logistic regression used the equation

$$\mathrm{logit}(Y) = \ln[Y/(1-Y)] = A + B\,\mathrm{logit}(X)$$

where Y is the observed presence or absence (1 or 0), X is the predicted probability of occupancy, and A and B are the regression coefficients. The predictions were significantly different from the observations if A was significantly different from zero, or if B was significantly different from one (Cox 1958, Miller et al. 1991). The statistical significance of the difference between the

predictions and observations was determined from the change in the deviance (Hosmer and Lemeshow 1989). The resulting equation estimated the relationship between the predicted probability of occupancy and the actual probability of occupancy. The ability of the model to predict occupancy within the different forest types was assessed by including forest type as a categorical variable in the logistic regression and testing for significant effects.

Log-likelihood values were calculated using the equation

$$\ln L = \Sigma \, \text{obs} \ln(Y) + (1 + Y) \ln(1 - X)$$

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

Results

Observed versus predicted patch occupancy for the sacred kingfisher

Field surveys by point interval counts showed that of the 39 remnant eucalypt patches in the study, nine were occupied by the sacred kingfisher. In comparison, the naïve null model predicted an average of 16.3 occupied patches whereas the ALEX model predicted an average of 9.3 patches. The log-likelihood value for the naïve null model for the sacred kingfisher was 28.9 and 15.9 for the ALEX model. The logistic regression relationship between the observed patch occupancy (Y) and the model-predicted patch occupancy (X) for the simulations using ALEX was

$$\text{logit}(Y) = -0.745 + 0.841 \, \text{logit}(X)$$

The slope of this relationship was significantly greater than zero ($p = 0.025$) and the observed patch occupancy was not significantly different from predicted ($p = 0.485$). Hence, patches that the model predicted to

Table 2. Predicted and actual numbers of occupied patches for the sacred kingfisher in different forest types. Unmodified ALEX model

Forest type	Predicted no. of occupied patches	Actual no. of occupied patches
E. viminalis	3.0	4
E. radiata	2.9	1
E. macrorhyncha	0.3	0
E. camphora	3.0	4

have a high probability of occupancy were more likely to be found to be actually occupied during field surveys. We also compared the mean predicted number of occupied patches to the actual number for the different forest types (Table 2) and there was no significant effect of forest type ($p = 0.23$). Given the fit between the actual and predicted patch occupancy for the sacred kingfisher, we did not further modify ALEX.

Observed versus predicted patch occupancy for the laughing kookaburra

Field surveys by point interval counts showed that of the 39 remnant eucalypt patches, eight were occupied by the laughing kookaburra. In comparison, the naïve null model predicted an average of 25.8 occupied patches, whereas the ALEX model predicted an average of 21.6 patches. The log-likelihood value for the naïve null model for the laughing kookaburra was 53.3, and was 29.9 for the ALEX model. The logistic regression relationship between the observed patch occupancy (Y) and the model-predicted patch occupancy (X) for the simulations using the ALEX model was

$$\text{logit}(Y) = -2.15 + 1.14 \, \text{logit}(X)$$

The slope of this relationship was significantly greater than zero ($P = 0.005$) and the observed patch occupancy was significantly different from predicted ($P = 0.000$).

The ALEX model produced a better fit to the field data than the naïve null model, but nevertheless it still significantly over-predicted the number of patches occupied by the laughing kookaburra. The discrepancy between model predictions and the observations was examined by comparing occupancy rates in the four different eucalypt forest types which characterised the patches. Comparing the mean predicted number of occupied patches to the actual number for the different forest types indicated that the occupancy rates in *E. viminalis* and *E. radiata* forest were too high (Table 3a). Including forest type as a categorical variable in the logistic regression revealed a significant effect of forest type on occupancy rates ($p = 0.012$). This indicated that differences between the predictions of the model and the observations varied with forest type. Given this, we modified the ALEX model by reducing the habitat quality of *E. radiata* and *E. viminalis*-dominated patches. However, the predictions still remained significantly different from observations, even when habitat quality was reduced to zero (Table 3b). This occurred because even if habitat quality in some of the eucalypt remnants was low, animals did not avoid them and the model still allowed individuals to disperse into these patches (although successful breeding did not occur).

Hence, occupancy predicted by the model remained higher than the actual patch occupancy.

A second modification was then made to model to decrease the number of animals dispersing into the patch system from large neighbouring areas of continuous eucalypt forest. This was done by reducing the size of these neighbouring areas from 500 ha to 100 ha. This improved the fit, with the predictions not significantly different from observations ($p = 0.464$). The logistic regression equation for the relationship between the revised predictions of patch occupancy and actual occupancy was

$$\mathrm{logit}(Y) = -0.526 + 0.994\,\mathrm{logit}(X)$$

However, the occupancy rates for the patches characterised by different forest types still remained significantly different from the observations (Table 3c, $p = 0.011$). The forecast occupancy was still over-predicted for E. viminalis and E. radiata but under-predicted for E. camphora (Table 3c).

Table 3. Predicted and actual numbers of occupied patches for the laughing kookaburra in different forest types. (a) shows values for the unmodified ALEX model where both reasonably high levels of dispersal from neighbouring continuous forest and high habitat quality values for E. viminalis and E. radiata-dominated patches were included in the simulations. The patch occupancy predictions from simulations where the habitat quality values were zero in E. viminalis and E. radiata-dominated patches are shown in (b). (c) shows values where immigration from neighbouring continuous forest was reduced.

a) Unmodified ALEX model

Forest type	Predicted no. of occupied patches	Actual no. of occupied patches
E. viminalis	6.6	1
E. radiata	7.9	1
E. macrorhyncha	0.8	0
E. camphora	6.2	6

b) Zero habitat quality for E. viminalis and E. radiata patches

Forest type	Predicted no. of occupied patches	Actual no. of occupied patches
E. viminalis	6.4	1
E. radiata	7.7	1
E. macrorhyncha	0.9	0
E. camphora	6.2	6

c) Reduced immigration into the patch system

Forest type	Predicted no. of occupied patches	Actual no. of occupied patches
E. viminalis	3.7	1
E. radiata	3.7	1
E. macrorhyncha	0.4	0
E. camphora	3.4	6

Finally, we completed further extensive sensitivity analysis of the ALEX model for the laughing kookaburra by varying parameters such as survival rates, fecundity rates, and dispersal distance. However, we were unable to identify a combination of parameter values that provided a good fit between predicted and observed data for occupancy of patches dominated by different forest types (results not shown).

Discussion

Spatially-explicit simulation models such as those used for PVA have been widely employed in conservation biology and, in turn, used to guide options for resource and conservation management. Indeed, there have been many hundreds of applications of the approach in the past decade (Boyce 1992, Lindenmayer and Possingham 1996). However, the accuracy of predictions from PVA have only rarely been tested (Brook et al. 1997a, b, Lindenmayer et al. 1999a). This is a problem that has been the basis for criticism of PVA modelling by some authors (e.g. Caughley 1994).

Outcomes for the sacred kingfisher

The results of our investigation showed a reasonable fit between field data on patch occupancy and model predictions from ALEX for the sacred kingfisher, but not for the laughing kookaburra. Before the start of the work, the reverse outcome was expected for the two species. We anticipated that the long-distance movements made by the sacred kingfisher, due to it being a seasonal latitudinal migrant, would make patch occupancy in the remnant system at Tumut much harder to accurately forecast than the resident (i.e. non-migratory) laughing kookaburra. Indeed, most spatially explicit models (including ALEX) do not take long distance migration behaviour into account.

We are aware that congruence between observed patch occupancy and model predictions does not necessarily mean that the model is correctly simulating the dynamics of populations of the sacred kingfisher at Tumut. Rather, it is possible the model construction (and the assumptions underlying the model) may be incorrect and any consistency between actual and forecast values is purely fortuitous. Indeed, by definition, no model can be a totally accurate description of reality (Starfield and Bleloch 1992, Burgman et al. 1993). Thus, as noted by Rykiel (1996), the purpose of testing models is not to "prove" they are true or false, but rather to determine how they need to be improved. However, empirical tests by experiments and observational studies of the assumptions that underpin PVA programs like ALEX, such as the movement sub-model, provide a strong additional approach to testing

the validity of models and one that is complementary to the one applied in this paper. On this basis, it will be important to couple tests of the accuracy of forecasts from ALEX with field-based empirical studies of, for example, patterns of inter-patch movement exhibited by the sacred kingfisher. One approach to empirical model testing will be to instigate a colour banding study of sacred kingfishers mist-netted in the patches at Tumut. Repeated field observations in successive years and completed across the network of patches, could provide data on whether marked adult birds return to the same patches each breeding season and how far banded juveniles move from the natal patch to neighbouring patches (if at all).

Outcomes for the laughing kookaburra

ALEX considerably over-predicted patch occupancy for the laughing kookaburra. The reasons for this are not clear, but there are several possible explanations. These include (among others)

1) ALEX is a single-species PVA model and it does not include interactions between species such as competition, predation and parasitism that can influence distribution patterns (and thus patch occupancy) (Possingham and Davies 1995). For example, the laughing kookaburra depends on cavities in trees for breeding and it is possible there is competition for hollows with other species at Tumut. Cavities used by the laughing kookaburra may be usurped by other animals such as feral bees (*Apis mellifera*) and arboreal marsupials (Parry 1973, Ashton 1985, 1987). Notably, patches dominated by *E. viminalis* and *E. radiata* at Tumut supported the highest densities of arboreal marsupials such as the greater glider (*Petauroides volans*) (Lindenmayer et al. 1999b). In addition, large flocks of sulphur-crested cockatoos (*Cacatua galerita*) nest in these types of remnant patches (Lindenmayer et al. 1996). Pairs of sulphur-crested cockatoos have been observed to behave aggressively toward other species of large birds that approach roosting and nesting sites (D. Lindenmayer pers. obs.). The sacred kingfisher is also a hollow-dependent species (Higgins 1999) but model forecasts of patch occupancy were not significantly different from field values. The sacred kingfisher is smaller than the laughing kookaburra and would be expected to use smaller cavities (Gibbons and Lindenmayer 1996). This may mean it is less likely than the laughing kookaburra to compete with the sulphur-crested cockatoo and the greater glider for nesting hollows. Multi-species PVA models would be needed to capture aspects of population dynamics created by processes like inter-specific competition.

2) ALEX may have problems simulating the dynamics of species with reasonable dispersal capability and that display some form of habitat selection during dispersal (e.g. selection for structural or floristic attributes within different types of forest). This may explain why changes in habitat quality values did not produce a substantially better fit of the model for the laughing kookaburra within particular forest types (those dominated by *E. viminalis* and *E. radiata*) (Table 3b). While changes in immigration rates did improve congruence between actual and predicted patch occupancy, there was still discrepancy between values not only for *E. viminalis* and *E. radiata*-dominated patches, but subsequently also for patches of *E. camphora* forest when such changes were implemented (Table 3c). More sophisticated movement and habitat quality sub-models than are currently available in ALEX (and indeed other PVA models-see Lindenmayer et al. 1995) may be needed to predict the dynamics of patchy populations such as the laughing kookaburra in complex landscapes like the one at Tumut.

3) There may be important Allee effects (sensu Allee 1931) occurring, but which are not incorporated as part of model specifications in ALEX. However, since the laughing kookaburra can breed successfully without living in a group (Legge 2000), these problems probably do not go beyond finding a mate. In addition, it is hard to determine why Allee effects would occur in only some patch types.

In summary, a range of possible factors may explain why ALEX poorly modelled the dynamics of the laughing kookaburra. However, it is presently not possible to conclusively identify the key reasons for the lack of congruence. Nevertheless, the results of our study have highlighted a number of important new areas of field research that will explore population processes that have contributed to the discrepancy between observed and predicted patch occupancy.

Patchy populations as metapopulations

As the laughing kookaburra and the sacred kingfisher were virtually absent from the radiata pine matrix surrounding the eucalypt patches, we assumed before the start of this study that both species could be distributed as classic metapopulations. That is, discrete (patch) sub-populations linked by occasional inter-patch dispersal. However, our results indicate that the laughing kookaburra may perceive the landscape somewhat differently. For example, the species may fly across the radiata pine matrix and use several different patches, including very small ones. Territory size may increase if "patchiness" reduces territory quality, or if frequent "commuting" necessitates a larger resource

base. This would result in generally lower population densities and lower rates of overall patch occupancy; outcomes that would typically not be predicted by traditional metapopulation models. Field data from a set of more extensive field surveys of bird populations over a larger part of the Tumut region (Lindenmayer et al. 2001) provided tentative evidence for this effect. Over a set of 86 eucalypt patches that was surveyed, the occurrence rate of the laughing kookaburra was consistently about 18%, irrespective of patch size (1 ha to > 120 ha) (Lindenmayer et al. 2001). In this investigation, the simulation model predicted the classic metapopulation outcome that larger patches were more likely to be occupied. An entirely different type of population model than the one tested here would be required to simulate the dynamics of the type of population structure hypothesised to occur in the laughing kookaburra (e.g. frequent inter-patch movements and changed territory use resulting from fragmentation). Notably, metapopulation models generally do not accommodate changes in home range sizes that may occur with habitat fragmentation (e.g. Barbour and Litvaitis 1993) and frequent movements between an array of patches to gather spatially separated food resources (e.g. Boone and Hunter 1996, Arnold and Weeldenburg 1998).

Deficiencies in modelling capability are an important source of differences between model predictions and actual observation. Thus, one of the key outcomes of our analysis is the need to be careful in the application of models such as those generic and widely applied packages that are frequently used in PVA. The limited predictive ability of the model for the laughing kookaburra indicates there may be species for which models are simply unsuited and new ones need to be developed. It also highlights the need to have a good understanding of how particular models are constructed and the assumptions underpinning the estimation of parameters (Wiens 1994, Lindenmayer et al. 1995). Indeed, our study has clearly shown that it is important to not assume automatically that all patchily distributed species necessarily behave as metapopulations (Doak and Mills 1994, Hanski and Simberloff 1997).

Data quality

An important problem in tests of the accuracy of predictions from PVA is the quality of the field data used in the comparisons. Poor quality field data (for example, recorded cases of absences of a target species from patches when it is in fact present) can thwart attempts to test PVA models. Sampling errors will occur in any field study and the extent of such errors needs to be quantified where possible. In this investigation, we used two different field methods (automatic call box recorders and extensive numbers of point-inter-

val counts) to estimate observer error associated with field sampling. In addition, we worked hard to maximise the quality of field data. This was done by (1) timing our field surveys when the seasonal migrant in our study (the sacred kingfisher) had arrived in the patch system, (2) targeting our work during the onset of the breeding season when birds are calling often (Parry 1973) and are most likely to be detected, (3) focussing on two large and highly visible species with distinctive calls, making them relatively easy to detect when present (Lindenmayer et al. 1997), (4) using data gathered by one experienced field observer (DBL) to limit potential problems created by observer heterogeneity in detection ability (Cunningham et al. 1999), (5) maximising the opportunities to detect a bird in a patch by undertaking multiple counts on the same site, (6) including a large number of patches in the study (39) to limit the overall extent of any field sampling errors on the outcomes of model testing, (7) conducting extensive surveys of 40 sites in large continuous areas of native eucalypt forest to generate values for bird density (and thus habitat quality) in an unfragmented spatial setting, (8) choosing a field counting protocol (point interval counts and bird call recordings) most likely to detect large birds with distinctive calls such as the sacred kingfisher and the laughing kookaburra (Cunningham et al. 1999), and, (9) undertaking extensive surveys in the radiata pine matrix ($N = 40$ sites) surrounding the eucalypt patches to determine the presence or absence of the species occurring there.

An important component of our work was to report not only where the model produced outcomes broadly consistent with actual field data (the sacred kingfisher), but also where it did not (the laughing kookaburra). Differences between the sacred kingfisher and the laughing kookaburra in their responses to fragmentation and related factors such as movement patterns in modified landscapes may explain the marked inter-specific differences in the level of congruence between model predictions and field data. We also plan to test ALEX on other species of birds as well as small mammals and arboreal marsupials to give a greater insight into those taxa for which population dynamics are predicted well and those for which they are poor. This is important because a lack of congruence highlights where models like ALEX need to be modified or where new models are required. It also indicates where greater ecological understanding of particular phenomena (e.g. dispersal and other forms of inter-patch movement) is needed to improve model predictions.

There is a tendency in many aspects of conservation science to report only successful outcomes of studies. For example, this characterises much of the literature on re-introduction and translocation biology (Reading et al. 1997). Yet, much can be learnt from failures or negative results in ecology as it can stimulate further and deeper thinking and subsequent empirical testing

about the basis for observed patterns in nature (such as animal distribution in patchy landscapes). The results of this study have stimulated a number of new field-based projects to better inform patterns of inter-patch movement by a range of vertebrate taxa.

References

Akçakaya, H. R., McCarthy, M. A. and Pearce, J. L. 1995. Linking landscape data with Population Viability Analysis: management options for the Helmeted Honeyeater. – Biol. Conserv. 73: 169–176.

Allee, W. C. 1931. Animal aggregations. A study in general sociology. – Univ. of Chicago Press.

Arnold, G. W. and Weeldenburg, J. R. 1998. The effects of isolation, habitat fragmentation and degradation by livestock grazing on the use by birds of patches of Gimlet *Eucalyptus salubris* woodland in the wheatbelt of Western Australia. – Pac. Conserv. Biol. 4: 155–163.

Ashton, C. B. 1985. The birds of the Aldinga-Sellicks Beach Scrub. – South Austr. Ornithologist 29: 169–179.

Ashton, C. B. 1987. The breeding of birds in the Aldinga Scrub Conservation park, South Australia. – Austr. Bird Watcher 12: 73–82.

Barbour, M. S. and Litvaitis, J. A. 1993. Niche dimensions of New England cottontails in relation to habitat patch size. – Oecologia 95: 321–327.

Boone, R. B. and Hunter, M. L. 1996. Using diffusion models to simulate the effects of land use on Grizzly Bear dispersal in the Rocky Mountains. – Landscape Ecol. 11: 51–64.

Boyce, M. S. 1992. Population viability analysis. – Annu. Rev. Ecol. Syst. 23: 481–506.

Brook, B. W., Lim, L., Harden, R. and Frankham, R. 1997a. How secure is the Lord Howe Island Woodhen? A population viability analysis using VORTEX. – Pac. Conserv. Biol. 3: 125–133.

Brook, B. W., Lim, L., Harden, R and Frankham, R. 1997b. Does population viability software predict the behaviour of real populations? A retrospective analysis of the Lord Howe Island Woodhen *Tricholimnas sylvestris* (Sclater). – Biol. Conserv. 82: 119–128.

Burgman, M., Ferson, S. and Akçakaya, H. R. 1993. Risk assessment in conservation biology. – Chapman and Hall.

Burgman, M. A. and Lindenmayer, D. B. 1998. Conservation biology for the Australian environment. – Surrey Beatty and Sons.

Burris, R. K. and Canter, L. W. 1997. Cumulative impacts are not properly addressed in environmental assessments. – Environ. Impact Assessment Rev. 67: 5–18.

Caughley, G. C. 1994. Directions in conservation biology. – J. Anim. Ecol. 63: 215–244.

Cocklin, C., Parker, S. and Hay, J 1992. Notes on cumulative environmental change I: concepts and issues. – J. Environ. Manage. 35: 31–49.

Cox, D. R. 1958. Two further applications of a model for binary regression. – Biometrika 45: 562–565.

Cunningham, R. B., Lindenmayer, D. B., Nix, H. A. and Lindenmayer, B. D. 1999. Quantifying observer heterogeneity in bird counts. – Aust. J. Ecol. 24: 270–277.

Doak, D. and Mills, L. S. 1994. A useful role for theory in conservation. – Ecology 75: 615–626.

Ford, H. and Bell, H. 1981. Density of birds in eucalypt woodland affected to varying degrees by dieback. – Emu 81: 202–208.

Fritz, R. 1979. Consequences of insular population structure: distribution and extinction of spruce grouse populations. – Oecologia 42: 57–65.

Gibbons, P. and Lindenmayer, D. B. 1996. A review of issues associated with the retention of trees with hollows in wood production forests. – For. Ecol. Manage. 83: 245–279.

Hanski, I. 1994a. Patch occupancy dynamics in fragmented landscapes. – Trends Ecol. Evol. 9: 131–134.

Hanski, I. 1994b. A practical model of metapopulation dynamics. – J. Anim. Ecol. 63: 151–162.

Hanski, I. and Simberloff, D. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. – In: Hanski, I. and Gilpin, M. E. (eds), Metapopulation biology, ecology, genetics and evolution. Academic Press, pp. 5–26.

Hanski, I., Pakkala, T., Kuussaari, M. and Lei, G. 1995. Metapopulation structure of an endangered butterfly in a fragmented landscape. – Oikos 72: 21–28.

Hanski, I., Moilanen, A., Pakkala, T. and Kuussaari, M. 1996. The quantitative incidence function model and persistence of an endangered butterfly metapopulation. – Conserv. Biol. 10: 578–590.

Higgins, P. (ed.) 1999. Handbook of Australian New Zealand and Antarctic Birds. Vol. 4. Parrots to Dollarbird. – Oxford Univ. Press.

Hosmer, D. W. and Lemeshow, S. 1989. Applied logistic regression. – John Wiley.

Huston, M. A. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. – Oecologia 110: 449–460.

Kavanagh, R. and Recher, H. F. 1983. Effects of observer variability on the census of birds. – Corella 7: 93–100.

Lamberson, R. H., Noon, B. R., Voss, C. and McKelvey, R. 1994. Reserve design for territorial species: the effects of patch size and spacing on the viability of the Northern Spotted Owl. – Conserv. Biol. 8: 185–195.

Laurance, W. F. 1991. Ecological correlates of extinction proneness in Australian tropical rain forest mammals. – Conserv. Biol. 5: 79–89.

Legge, S. 2000. The effects of group size on reproductive success in the Laughing Kookaburra. – J. Anim. Ecol. (in press).

Legge, S. and Cockburn, A. 2000. Social and mating systems of co-operatively breeding Laughing Kookaburras. – Behav. Ecol. Sociobiol. 47: 220–229.

Lindenmayer, D. B. and Possingham, H. P. 1996. Modelling the relationships between habitat connectivity, corridor design and wildlife conservation within intensively logged wood production forests of south-eastern Australia. – Landscape Ecol. 11: 79–105.

Lindenmayer, D. B., Burgman, M. A., Akçakaya, H. R. et al. 1995. A review of three models for metapopulation viability analysis – ALEX, RAMAS/Space and VORTEX. – Ecol. Model. 82: 161–174.

Lindenmayer, D. B., Pope, M., Cunningham, R. B. et al. 1996. Roosting in the Sulphur-Crested Cockatoo (*Cacatua galerita*). – Emu 96: 209–212.

Lindenmayer, D. B., Cunningham, R. B., Nix, H. A. et al. 1997. Counting birds in forests: a comparison of observers and observation methods. – CRES Working Paper. 1997/6. 25 pp.

Lindenmayer, D. B., McCarthy, M. A. and Pope, M. L. 1999a. A test of Hanski's simple model for metapopulation model. – Oikos 84: 99–109.

Lindenmayer, D. B., Cunningham, R. B., Pope, M. and Donnelly, C. F. 1999b. The Tumut fragmentation experiment in south-eastern Australia: the effects of landscape context and fragmentation of arboreal marsupials. – Ecol. Appl. 9: 594–611.

Lindenmayer, D. B., Cunningham, R. B., Donnelly, C. F. and Nix, H. A. 2001. Novel effects of fragmentation: birds in a eucalypt and exotic pine mosaic in south-eastern Australia. – Ecology (in press).

Link, W. A. and Saur, J. R. 1997. New approaches to the analysis of population trends in land birds: comment. – Ecology 78: 2632–2634.

McCarthy, M. A. 1995. Extinction dynamics of the helmeted honeyeater: effects of demography, stochasticity, inbreeding and social structure. – Ecol. Model. 85: 151–163.

McCarthy, M. A. and Lindenmayer, D. B. 1999. Incorporating metapopulation dynamics of Greater Gliders into reserve design in disturbed landscapes. – Ecology 80: 651–667.

McCarthy, M. A., Lindenmayer, D. B. and Dreschler, M. 1997. Extinction debts and the risks faced by abundant species. – Conserv. Biol. 11: 221–226.

Mac Nally, R. 1997. Population densities in a bird community of a wet sclerophyllous Victorian forest. – Emu 97: 145–156.

Margules, C. R., Milkovits, G. A. and Smith, G. T. 1994. Contrasting effects of habitat fragmentation on the scorpion *Cercophonius squama* and an amphipod. – Ecology 75: 2033–2042.

McComb, W. C., McGarigal, K., Fraser, J. D. and Davis, W. H. 1991. Planning for basin-level cumulative effects in the Applachian coal fields. – In: Rodiek, J. E. and Bolen, E. C. (eds), Wildlife habitats in managed landscapes. Island Press, pp. 138–151.

Miller, M. E., Hui, S. L. and Tierney, W. M. 1991. Validation techniques for logistic regression models. – Statist. Med. 10: 1213–1226.

Parry, V. 1973. The auxilliary social system and its effect on territory and breeding in Kookaburras. – Emu 73: 81–100.

Pizzey, G. and Knight, F. 1997. Field guide to the birds of Australia. – Angus and Robertson.

Possingham, H. P. and Davies, I. 1995. ALEX: a model for the viability analysis of spatially structured populations. – Biol. Conserv. 73: 143–150.

Possingham, H. P., Davies, I., Noble, I. R. and Norton, T. W. 1992. A metapopulation simulation model for assessing the likelihood of plant and animal extinctions. – Math. Comput. Simulation 33: 367–372.

Possingham, H. P., Lindenmayer, D. B., Norton, T. W. and Davies, I. 1994. Metapopulation viability of the Greater Glider in a wood production forest in a wood production area. – Biol. Conserv. 70: 265–276.

Pyke, G. H. and Recher, H. F. 1983. Censusing Australian birds: a summary of procedures and a scheme for the standardisation of data presentation and storage. – In: Davies, S. J. (ed.), Methods of censusing birds in Australia. Proceedings of a symposium organised by the Zoology section of the ANZAAS and the Western Australian Group of the Royal Australasian Ornithologists Union. Dept of Conservation and Environment, Perth, pp. 55–63.

Ralph, C. J., Sauer, J. R. and Droege, S. 1997. Monitoring bird populations by point counts. – U.S.D.A. Forest Service. General Technical Report PSW-GTR-149. Pacific Southwest Research Station, Albany CA.

Recher, H. F. 1988. Counting terrestrial birds: use and application of census procedures in Australia. – Aust. Zool. Rev. 1: 25–45.

Readers Digest 1990. Readers Digest complete book of Australian birds. – Readers Digest.

Reading, R. P., Clark, T. W. and Griffith, B. 1997. The influence of valuational and organisational considerations on the success of rare species translocations. – Biol. Conserv. 79: 217–225.

Reyer, H. U. and Schmidl, D. 1988. Helpers have little to laugh about: group structure and vocalisation in the Laughing Kookaburra *Dacelo novaeguineae*. – Emu 88: 150–160.

Robinson, G. R., Holt, R. D., Gaines, M. S. et al. 1992. Diverse and contrasting effects of habitat fragmentation. – Science 257: 524–526.

Rykiel, E. J. 1996. Testing ecological models: the meaning of validation. – Ecol. Model. 90: 229–244.

Simberloff, D. and Dayan, T. 1991. The guild concept and the structure of ecological communities. – Annu. Rev. Ecol. Syst. 22: 115–143.

Slater, P. J. 1994. Factors affecting the efficiency of the area search method for censusing birds in open forests and woodlands. – Emu 94: 9–16.

Smith, A. T. 1980. Temporal changes in insular populations of the Pika (*Ochotona principes*). – Ecology 61: 8–13.

Starfield, A. M. and Bleloch, A. L. 1992. Building models for conservation and wildlife management. – Burgess International Group, Edina.

Thiollay, J. 1992. The influence of selective logging on bird species diversity in a Guianian rain forest. – Conserv. Biol. 6: 47–63.

Wahlberg, N., Moilanen, A. and Hanski, I. 1996. Predicting the occurrence of endangered species in fragmented landscapes. – Science 273: 1536–1538.

Waser, P. M. 1985. Does competition drive dispersal? – Ecology 66: 1170–1175.

Wiens, J. 1994. Habitat fragmentation: island vs landscape perspectives on bird conservation. – Ibis 137: S97–S104.

Wolfenbarger, D. O. 1949. Dispersion of small organisms. – Am. Midl. Nat. 35: 1–152.

Appendix 1

The size and dominant forest type of remnant patches of eucalypt forest in the study region at Tumut. Extensive field reconnaissance was used to identify the dominant tree species in each remnant.

Patch number	Dominant tree species	Patch size (ha)	Year of isolation
102	*E. radiata*	6.6	1985
114	*E. macrorhynca*	0.6	1985
115	*E. macrorhynca*	0.7	1985
198	*E. camphora*	40.5	1978
235	*E. camphora*	15.2	1977
258	*E. camphora*	15.1	1978
272	*E. radiata*	1.0	1979
276a	*E. camphora*	20.7	1979
276b	*E. camphora*	20.5	1982
310	*E. viminalis*	18.8	1977
335	*E. radiata*	2.4	1978
353	*E. viminalis*	12.7	1980
365	*E. radiata*	1.7	1980
369	*E. radiata*	18.9	1982
389	*E. radiata*	0.4	1983
418	*E. camphora*	1.6	1976
422	*E. macrorhynca*	38.0	1983
433	*E. camphora*	22.1	1976
446	*E. radiata*	30.1	1977
449	*E. viminalis*	9.0	1980
490	*E. radiata*	1.6	1982
567	*E. radiata*	0.7	1982
569	*E. radiata*	2.3	1982
599	*E. viminalis*	16.2	1983
632	*E. radiata*	4.9	1984
661	*E. radiata*	4.4	1985
700	*E. radiata*	5.6	1985
B3	*E. radiata*	0.8	1979
C3	*E. radiata*	20.1	1979
D3	*E. viminalis*	8.7	1979
E3	*E. viminalis*	13.5	1982
I1	*E. camphora*	9.1	1986
I2	*E. viminalis*	5.0	1983
I4	*E. radiata*	2.0	1985
K1	*E. radiata*	4.1	1985
S3	*E. camphora*	10.6	1973
T3	*E. viminalis*	18.7	1983
U3	*E. radiata*	20.5	1984
V3	*E. viminalis*	9.0	1985