

## TESTING SPATIAL PVA MODELS OF AUSTRALIAN TREECREEPERS (AVES: CLIMACTERIDAE) IN FRAGMENTED FOREST

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**Abstract.** Population viability analysis (PVA) and other stochastic population models are frequently built and often used, but rarely tested. Stochastic metapopulation models of the White-throated Treecreeper (*Cormobates leucophaea*) and the Red-browed Treecreeper (*Climacteris erythroptus*) were developed in a system of 39 remnant patches of eucalypt forest in southeastern New South Wales, Australia. Parameters of the model were estimated using data obtained outside the fragmented system. Field surveys of the patches were conducted to test the predicted probabilities of patch occupancy, which is one of few instances where stochastic population models have been tested with empirical data. The initial models underestimated the occupancy of the patches, and the models were modified using the results of the tests in conjunction with further information on the biology of the species. A number of different modifications were made to determine changes that produced results that matched the observations. The best of these modifications made reasonable predictions, although this is not equivalent to a test with independent data because the data were known prior to the modifications. The best-fitting modified models were tested by comparing the observed number of extinction and colonization events to the predicted number. The models underestimated the observed number of events, although imperfect survey methods may have contributed to these differences. The tests of the stochastic models contributed to their development by highlighting the nature of the predictive error. The modified models predicted that the White-throated Treecreeper would be likely to persist over the next 100 years in most of the 39 patches. In contrast, the Red-browed Treecreeper was predicted to become extinct in most patches within approximately 50 years of fragmentation. This study illustrates how spatial patterns can be used to test the

predictions of population dynamic models, although we note that the tests are limited by survey error and spatial correlation in occupancy data.

**Key words:** *Cormobates leucophaea*; *Climacteris erythroptus*; *extinction risk*; *fragmentation*; *metapopulation*; *model validation*; *Pinus radiata*; *population viability*; *Red-browed Treecreeper*; *southeastern Australia*; *spatial population dynamics*; *White-throated Treecreeper*.

### INTRODUCTION

Population viability analysis (PVA) is an established and increasingly used tool for conservation biology. It is used to assess threats faced by species and to determine effective management strategies to mitigate these threats (Shaffer 1981, Gilpin and Soulé 1986, Boyce 1992, Burgman et al. 1993, Possingham et al. 1993, Beissinger and Westphal 1998). PVA models were first developed approximately 20 years ago (Shaffer 1981) and it is recognized that their predictions may be subject to considerable error (Taylor 1995, McCarthy et al. 1996). Despite this, they have rarely been tested (Lacy 1993, Brook et al. 1997). The predictions of PVA models are often expressed in terms of the risk of extinction within a given time period. Such predictions are difficult to test because of problems of replication (Burgman et al. 1993, Lacy 1993). Nevertheless, some aspects of PVA models can be tested with data that are typically available, such as the mean and variance of the population growth rate (Lacy 1993), patterns of patch occupancy (Lindenmayer et al. 1999), and rates of local extinction and colonization (Hanski 1997). These tests can help identify the aspects of a PVA model that are most inaccurate and that need to be rectified to improve the model.

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Habitat destruction and fragmentation is the greatest threat faced by biodiversity throughout many parts of the world (Bennett 1998, Burgman and Lindenmayer 1998). Worldwide, the loss of native vegetation has contributed to the decline and extinction of numerous species, which continue to be lost from remnant fragments of native vegetation (Soulé 1988, Groombridge et al. 1992, McCarthy et al. 1997). In Australia, large areas of native vegetation have been cleared for agriculture, housing, and forestry (Resource Assessment Commission 1992). It is often difficult to predict the impacts of habitat loss and fragmentation, and PVA using metapopulation models is a potentially useful tool for this purpose (Burgman et al. 1993). Several PVA models have been developed to assess management strategies for mitigating the impacts of the loss and fragmentation of habitat (Lindenmayer and Possingham 1994, Noon and McKelvey 1996, McCarthy and Lindenmayer 1999, in press), and PVA has been proposed as a method for assisting the optimal design of nature reserves (Burgman et al. 1993, Lindenmayer and Possingham 1994). However, the paucity of model testing means that responses to habitat loss and fragmentation predicted by these models are subject to considerable uncertainty.

The aim of this study was to develop, test, and modify stochastic metapopulation models, and to use the models to predict the fate of species in a fragmented system. We developed PVA models of two Australian treecreepers (class Aves, family Climacteridae), White-throated Treecreepers (*Cormobates leucophaea*) and Red-browed Treecreepers (*Climacteris erythropis*), that inhabit a system of remnant patches of eucalypt forest in southeastern Australia. The models were parameterized using data available from other studies. The predictions were tested against field data on the occupancy of the eucalypt patches to identify model errors. We used the tests to indicate how to modify the models, thereby providing an improved understanding of how these species respond to fragmentation. For both species, different modifications were made to the model to determine which modifications resulted in the best fit between predictions and observations. The modified models that best fit the data were subsequently tested using data on local extinction and recolonization events, and were used to predict the fate of the species over the next 100 years. This paper is one of only a few attempts to test the predictions of spatially explicit population models that have been parameterized with data collected independently of the test data.

## METHODS

### *Study area*

In southeastern Australia, large areas of land have been converted to exotic radiata pine (*Pinus radiata*) plantations, with plans for further expansion (Dargavel 1995,

Department of Primary Industries and Energy 1997). A typical example is the Buccleuch State Forest (BSF) near Tumut, New South Wales, which constituted our study area. The original native eucalypt forest was converted to a plantation of radiata pine between the 1930's and the 1980's (Routley and Routley 1975). A total of 192 remnant patches of native eucalypt forest (<1 - >100 ha, total area of approximately 2,600 ha) still exist within the matrix of radiata pine of the BSF (total area of approximately 45,000 ha). Numerous plant and animal species persist in this system of remnant eucalypt patches of the BSF and in the adjoining areas of contiguous native forest (Lindenmayer et al. in press b). This study was confined to a relatively isolated network of 39 patches that ranged in area from 0.5 to 40 ha.

### *Study species*

PVA models were developed for the Red-browed Treecreeper (*Climacteris erythropis*) and the White-throated Treecreeper (*Cormobates leucophaea*). These species were chosen because they both require hollow-bearing trees for nesting and are largely restricted to eucalypt forest, making them potentially useful indicators of the effects of fragmentation for a range of hollow-dependent species. Additionally, there is concern about population declines of Red-browed Treecreepers and other Australian treecreepers (Stokes 1995, Garnett and Crowley 1995). Both species are similar in size (length: Red-browed 160 mm; White-throated 175 mm; Longmore and National Photographic Index 1991), and have a similar diet of arthropods (especially ants) obtained from the bark of trees, although there are subtle differences in foraging behavior. Both species nest in tree hollows, which are typically absent from pine plantations. Red-browed Treecreepers breed cooperatively, whereas White-throated Treecreepers breed as pairs. Both species are year-round residents and defend breeding territories. Dispersal by adults of both species is rare, although they will occasionally move to take advantage of nearby breeding opportunities. Juvenile White-throated Treecreepers appear to have good dispersal abilities, whereas juvenile Red-browed Treecreepers tend to remain close to their natal site (Noske 1982, 1991). Red-browed Treecreepers occur at lower densities than White-throated Treecreepers in most eucalypt forests (Disney and Stokes 1976, Driscoll 1977, Noske 1982, Baker et al. 1997). Red-browed Treecreepers appear to forage preferentially on eucalypts with smooth bark, whereas White-throated Treecreepers appear to favor rough-barked species (Noske 1985). Disney and Stokes (1976) did not record breeding by either species of treecreeper in radiata pine plantations. Similarly, Driscoll (1977) did not observe any Red-browed Treecreepers in pine plantations, and the number of White-throated Treecreepers in pines was approximately 1/20th of that observed in native eucalypt forest.

### The models

The metapopulation models of the treecreepers were developed in two stages. An initial model was developed for each species, based on the best available information obtained from studies outside the fragmented system. The models were then tested by comparing their predictions to field data on patch occupancy in 1996, and were subsequently modified in an effort to improve their fit. The predictions of these modified models were compared to occupancy data from 1996 and 1997, and by comparing the predicted and observed number of extinction and colonization events.

Models for the two treecreepers were developed using ALEX, a generic PVA package for stochastic simulation of metapopulation dynamics (Possingham and Davies 1995). ALEX models suitable habitat as patches that may vary in size, location, and quality. Stochastic population dynamics are simulated within patches, and dispersal is modelled by allowing individuals to move probabilistically between patches. A habitat-quality variable in ALEX controls the maximum number of females that can breed in each patch. General information about the model can be found elsewhere (Possingham et al. 1992, Lindenmayer and Possingham 1994, Possingham and Davies 1995). Our description is limited to those details that are specific to our case study on treecreepers. Data on survival and reproductive performance were obtained from studies by Noske (1982), Tidemann et al. (1988), and Baker et al. (1997). These studies provided consistent parameter estimates, with the exception of the value for annual adult survival of White-throated Treecreepers. Data in Noske (1982) and Tidemann et al. (1988) suggest a mean annual adult survival of approximately 0.7, while Baker et al. (1997) estimated this parameter to be 0.53. We used the value of 0.7 because the analyses of Baker et al. (1997) included first year birds and likely heterogeneity in recapture rates, which may produce biased estimates of adult survivorship. Additionally, an adult survival rate of 0.53 would not be sufficient to allow the species to persist given the birth rates estimated by Noske (1982).

There are limited quantitative data on dispersal by the two species of treecreepers. We used what is known (Noske 1982, 1991) to derive parameter estimates and used a range of mean dispersal distances in a sensitivity analysis. Dispersal distance had a relatively small influence on the predictions, so results are only shown for the estimated values (Table 1). The minimum home range size was 2.5 ha for White-throated Treecreepers and 10 ha for Red-browed Treecreepers, although these areas were larger in different forest types. The habitat quality of each patch was assumed to depend on forest type. The values of habitat quality were obtained by modifying them until the density of adult females in large (1,000 ha) simulated patches matched that observed in areas of contiguous forest (Lindenmayer et al. unpub.). The parameters used in the

model are summarized in Table 1.

**TABLE 1.** Original parameters used in ALEX (Possingham and Davies 1995) for simulating the population dynamics of White-throated Treecreepers and Red-browed Treecreepers, based on studies by Noske (1982), Tidemann et al. (1988), Baker et al. (1997), Lindenmayer et al. (unpub.).

Parameter	White-throated	Red-browed
annual adult survival	0.7	0.8
prob. of newborn females/breeder:		
0 newborns/year	0.194	0.472
1 newborn/year	0.444	0.430
2 newborns/year	0.306	0.098
3 newborns/year	0.056	0.0
survival of newborns to adulthood	0.4	0.4
standard deviation in environment	0.2	0.2
mean dispersal distance (km)	5.0	1.0
densities in contiguous forest (ha <sup>-1</sup> ):		
<i>E. camphora</i> forest	0.2	0.1
<i>E. macrohyncha</i> forest	0.4	0.025
<i>E. radiata</i> forest	0.4	0.05
<i>E. viminalis</i> forest	0.4	0.1

The population dynamics of the two treecreepers were simulated in a relatively isolated section of the BSF. This area contains 39 remnant eucalypt patches ranging in area from 0.5 ha to 40 ha. The effects of birds migrating from areas of contiguous native eucalypt forest that are adjacent to the BSF were simulated by modelling five large (500 ha) patches to the north and east of the patch system. Simulations were initiated in the year 1800 to allow the metapopulation to reach a stochastic equilibrium prior to fragmentation. This was done to ensure that the results were not dependent on initial conditions. Compartments that are now pine forest were modelled as patches. Conversion of these patches to pine forest was simulated by reducing their habitat quality to zero in the year that the pines were established. This was done because potential nest sites are rare or absent in pine plantations (Lindenmayer et al. 1999c), so hollow-nesting species such as the two treecreepers examined in this study would be unlikely to breed there. Simulations were conducted to the year 1997, with 1000 iterations of the model. The occupancy of each of the 39 remnant eucalypt patches in 1996 and 1997 was estimated as the proportion of iterations in which the patch was occupied.

### Field surveys of birds

We used a 600 m long transect divided into 100 m units to sample birds populations on all remnants 3 ha or larger. For smaller remnants, we scaled the transect length according to their size; 200 m for 1-2 ha patches and 400 m for 2-3 ha patches. Each transect commenced at a randomly selected

edge of a patch and tracked a path along a fixed compass bearing to the center of the remnant. The entire length of each transect was permanently marked with flagging tape and metal discs at all sites. The 0, 100, 200, 300, 400, 500, and 600 m points along each transect were uniquely marked with distinctively colored flagging tape. The point-interval count method (Pyke and Recher 1983) was employed to count birds at the each of the seven marked locations set 100 m apart. Each point interval count took five minutes during which time birds were identified visually and by their calls (see Lindenmayer et al. 1997, Cunningham et al. 1999). Each remnant was surveyed twice each year in 1996 and 1997. Thus, up to 14 five-minute point interval counts were completed for each remnant in the study. The same experienced field observer (DBL) conducted all the survey work. This avoided the problems of observer bias and observer heterogeneity that typically occur with multiple observer surveys (Kavanagh and Recher 1983, Link and Saur 1997, Cunningham et al. 1999).

Field sampling was confined to clear, still mornings to limit the effects of variable weather conditions on our data (Slater 1994), and were completed during late October and early November in 1996 and 1997. Earlier pilot studies (Lindenmayer et al. 1997) indicated that most species including the White-throated Treecreeper and Red-browed Treecreeper are calling frequently at this time of year as part of breeding behavior. This, together with the distinctive and far-carrying calls made by both species and the extent of field sampling (see above), substantially limited the likelihood of birds being overlooked if present in a remnant.

#### *Model testing and modification*

The models were tested by comparing the predicted probability of occupancy to the observed occupancy in 1996 using logistic regression (Hosmer and Lemeshow 1989). The predicted probability of occupancy was used as the explanatory variable and the observed presence or absence was used as the response variable. Such an analysis indicates whether there is a significant positive relationship between the predictions and observations (Lindenmayer et al. 1999). Logistic regression was also used to test whether the predicted probabilities of occupancy were significantly different from the observed rates of occupancy, and the nature of any differences (Cox 1958, Miller et al. 1991).

Differences between the predictions of the model and the observed occupancy in 1996 indicated that aspects of the initial models were particularly erroneous (see Results section below). The models were subsequently modified in an effort to improve the congruence between the predictions and observations. The subsequent comparisons to the occupancy data are not equivalent to tests of the models using independent data, because the modifications were made in light of the results from the original tests. These modifications should be regarded as a process of model calibration rather than validation.

In the case of the White-throated Treecreeper, predicted absences from numerous small eucalypt patches in which it was present suggested that persistence of the species was underestimated in these patches. Four possible reasons were identified: dispersal distances were too short; population densities were underestimated; population growth rates were too low; or the species was able to use the pine matrix. The population density estimates appeared reasonable, so the model was modified by doubling the mean dispersal distance, increasing the adult survival rate from 0.7 to 0.8, and allowing the White-throated Treecreepers to use the pine matrix. White-throated Treecreepers are known to forage in pine forest (Driscoll 1977, Friend 1980, Smith 1982, Lindenmayer et al. 1997), so the model was modified to allow individuals to forage up to 100 m into the matrix of pine forest. This distance was chosen because it reflects the approximate radius of home range movements by White-throated Treecreepers (3 ha). This modification effectively increased the size of each patch as a linear function of the perimeter, so there was a proportionally larger increase in small patches.

The original model of Red-browed Treecreepers consistently underestimated the occupancy of all patches, irrespective of their size. Three possible reasons for this were identified. Firstly, the density of the species in different forest types may have been underestimated, increasing the predicted probability of local extinction. However, we believed that the density estimates were reasonable, so this was not thought to contribute to the error. The second possible source of the underestimation of occupancy was that the population growth rate was too low. The simulated population growth rate of Red-browed Treecreepers in the absence of density limitation was only 1.05, which is low for most bird species. The survival rate of adults was increased from 0.8 to 0.85, increasing the maximum population growth rate to 1.1. The third possible source of error was that effective dispersal was too low, so the model was modified by doubling the mean dispersal distances.

Simulations were then conducted with the modified models of the two species of treecreepers, and the predicted probabilities of patch occupancy in 1996 were compared to the data obtained from the field surveys. The modified models that best fit the data were then chosen for subsequent analysis. Because presence/absence data were obtained for two consecutive years (1996 and 1997), it was possible to test the predicted number of local extinction and colonization events. The number of these events was recorded in each of the 1000 iterations of the model to determine the probability distribution of the number of extinction and colonization events. These distributions were then compared to the observed number of events predicted by the best-fitting modified models. Finally, the modified models that best fit the data were used to predict the fate of the two species of treecreepers in the BSF by

determining the probability of patch occupancy over the next 100 years.

## RESULTS

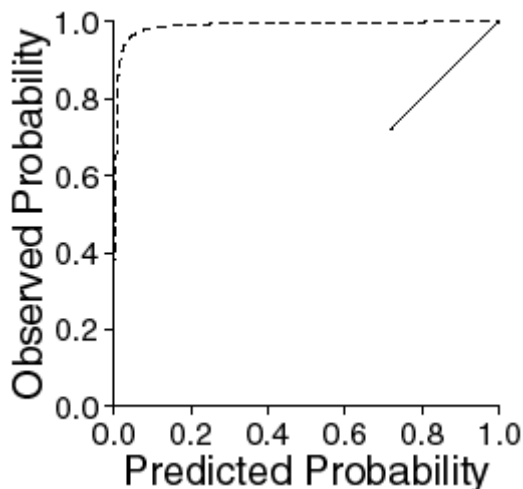
### *Initial models*

The initial models underestimated the occupancy of patches by both White-throated and Red-browed Treecreepers in 1996. In the case of White-throated Treecreepers, the average predicted probability of patch occupancy was 0.64, less than the observed rate of 0.9. Logistic regression demonstrated a significant ( $P < 0.05$ ) positive relationship between the predictions and observations, although the predicted probabilities of occupancy were significantly different from the observations (Fig. 1). The predictions for the smallest patches tended to be the most inaccurate. In the case of Red-browed Treecreepers, the average predicted probability of patch occupancy was 0.04, less than the observed rate of 0.28. Logistic regression demonstrated a significant ( $P < 0.05$ ) positive relationship between the predictions and observations, although there was imperfect correspondence between the two, with the model consistently underestimating occupancy (Fig. 2).

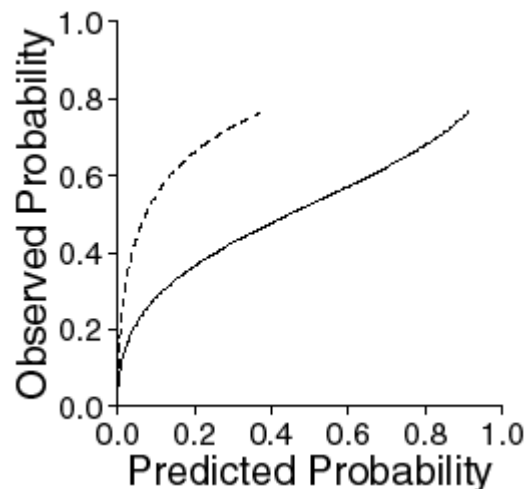
### *Modified models*

Doubling the mean dispersal distance and increasing the annual survival rate of adults to 0.8 failed to make the predictions match the observations for White-throated Treecreepers, with predicted probabilities of occupancy

being significantly different from the observations ( $P < 0.001$ , mean predicted occupancy rates 0.66 and 0.73 respectively). These modifications failed to increase the predicted occupancy rate of the smallest patches to that observed. In contrast, the modification to accommodate foraging in the pine matrix improved the predictions of the model of White-throated Treecreepers. For this latter model, the average predicted occupancy in 1996 was 0.96, close to the observed rate of 0.9. Logistic regression demonstrated that the predicted probabilities of patch occupancy were not significantly different from the observations in 1996 ( $P > 0.1$ ), and there was a significant positive relationship between the predicted occupancy and the observed occupancy ( $P < 0.01$ ) (Fig. 1). Thus, the model that allowed foraging outside the patches was chosen as the best-fitting model of White-throated Treecreepers. Similar results were obtained for this model using the 1997 data. The average predicted occupancy in 1997 was 0.96, close to the observed rate of 0.95. Logistic regression demonstrated that the predicted probabilities of patch occupancy were not significantly different from the observations in 1997 ( $P > 0.45$ ), but neither was there a significant positive relationship between the predicted occupancy and the observed occupancy ( $P > 0.4$ ). The predicted numbers of local extinction and colonization events were both between zero and three in the period from 1996 to 1997. One apparent extinction event was observed in the field, which is close to the middle of the distribution. Three apparent colonization events were observed in the field, a number that was predicted to be rare (Fig. 3).



**FIG. 1.** Fitted relationship between the predicted probability of patch occupancy by White-throated Treecreepers in 1996 and the observed probability, using logistic regression (Cox 1958, Miller et al. 1991). The broken line is the relationship obtained for the initial model, and the solid line is the relationship obtained for the best-fitting modified model. The relationships are truncated because results are only shown over the range of the predicted values.

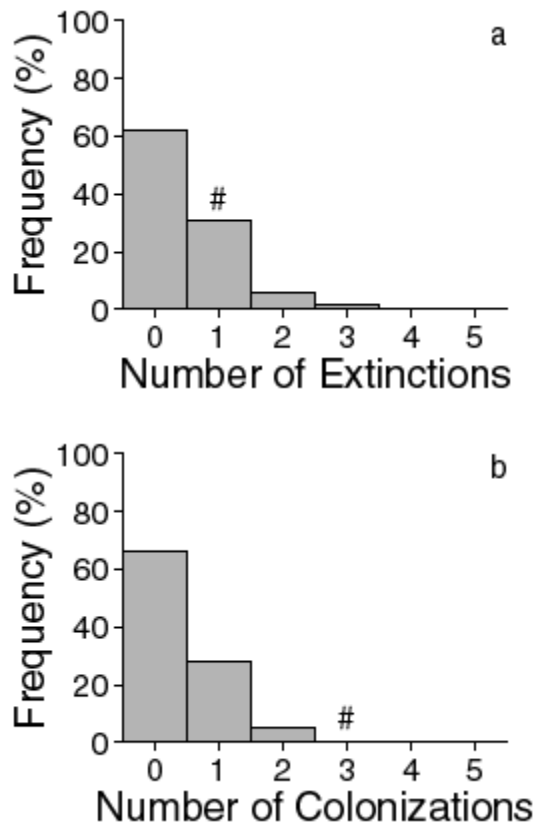


**FIG. 2.** Fitted relationship between the predicted probability of patch occupancy by Red-browed Treecreepers in 1996 and the observed probability, using logistic regression (Cox 1958, Miller et al. 1991). The broken line is the relationship obtained for the initial model, and the solid line is the relationship obtained for the best-fitting modified model. The relationships are truncated because results are only shown over the range of the predicted values.

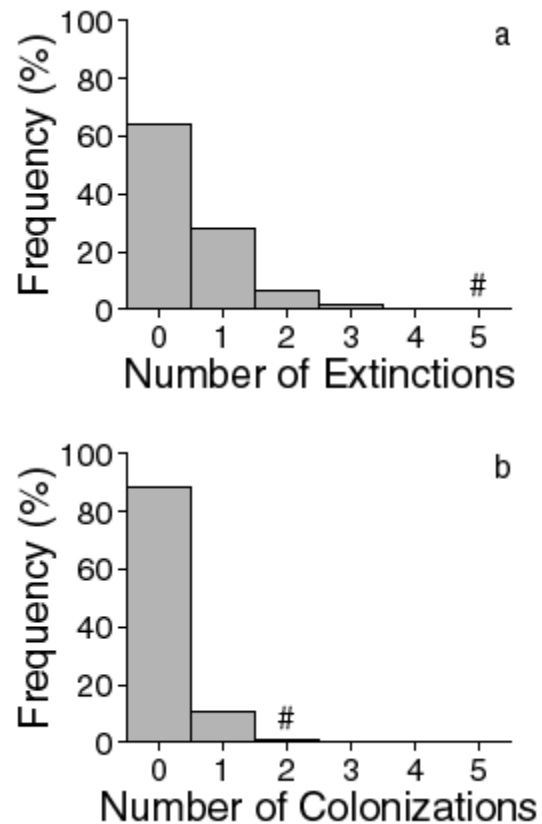
Doubling the mean dispersal distance only increased the mean occupancy rate of patches by Red-browed Treecreepers from 0.04 to 0.05, well below the observed occupancy rate of 0.28. In contrast, the model for Red-browed Treecreepers improved substantially when the adult survival rate was increased to 0.85. The average predicted occupancy in 1996 was 0.21, close to the observed rate of 0.28. Logistic regression demonstrated a significant positive relationship between the predicted occupancy and the observed occupancy in 1996 ( $P < 0.005$ ). However, the predicted probabilities of patch occupancy were significantly different from the observations in 1996 ( $P < 0.05$ ), with a Red-browed Treecreeper observed in one patch where the predicted probability of occupancy was close to zero (Fig. 2). Thus, the model with the increased survival rate of adults was chosen as the best-fitting model of Red-browed Treecreepers. The average predicted occupancy in 1997 using this model was 0.19, close to the observed rate of 0.18. Logistic regression demonstrated that the predicted probabilities of patch occupancy were not significantly

different from the observations in 1997 ( $P > 0.3$ ), and there was a significant positive relationship between the predicted occupancy and the observed occupancy ( $P < 0.02$ ). The predicted number of local extinctions was between zero and four in the period from 1996 to 1997, compared to the five that were observed. The predicted number of colonization events was between zero and two in the period from 1996 to 1997, compared to the two that were observed. Both these values are at, or beyond, the extremes of the predicted distributions (Fig. 4).

The best-fitting modified models predicted markedly different fates for the two bird species. The White-throated Treecreeper was predicted to persist throughout most of the network of 39 patches over the next 100 years, with the mean occupancy greater than 0.9 (Fig. 5). In contrast, the Red-browed Treecreeper was predicted to continue to decline, with the mean occupancy less than 0.03 after 100 years, although the full effect of fragmentation was not predicted to be apparent for several decades (Fig. 5).



**FIG. 3.** Frequency distribution of the predicted number of local extinction (a) and colonization (b) events from 1996 to 1997 for the best-fitting modified model of White-throated Treecreepers. The observed number based on field surveys is indicated by the asterisk.



**FIG. 4.** Frequency distribution of the predicted number of local extinction (a) and colonization (b) events from 1996 to 1997 for the best-fitting modified model of Red-browed Treecreepers. The observed number based on field surveys is indicated by the asterisk.

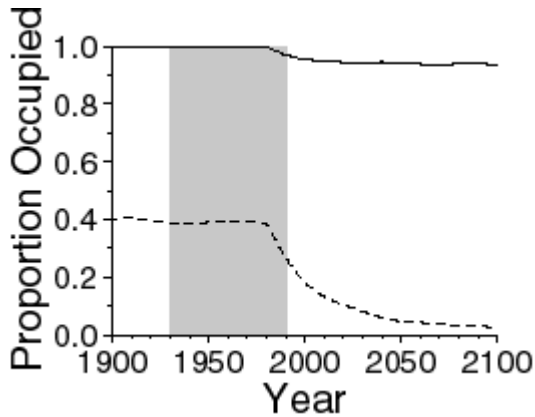


FIG. 5. The mean proportion of the 39 patches in the BSF that were predicted to be occupied by White-throated Treecreepers (solid line) and Red-browed Treecreepers (dashed line). The shaded area represents the period of fragmentation during which the original native forest was cleared.

#### DISCUSSION

The present study is one of few that attempts to test the predictions of a spatially explicit population model where the model was parameterized with data from areas other than the study site. This is the situation most often faced when trying to manage an area with limited data. The initial model is equivalent to what would have been predicted prior to the impact of fragmentation. In our study, the predictions of the initial metapopulation models were significantly different from observations. For both species of treecreeper, a relatively small change in a single aspect of the model was sufficient to improve the fit to the field data, illustrating that the models are quite sensitive to minor errors. This is consistent with previous studies demonstrating that the absolute predictions of stochastic population models are often subject to considerable uncertainty (Taylor 1995, McCarthy et al. 1996). Unless tested, the absolute predictions of PVA models will remain uncertain. Given all the difficulties of parameterizing PVA models with limited amounts of data, an iterative process of model development and testing appears to be essential if the models are to be useful management tools. Sensible modifications should be made in the light of ecological intuition, because any number of changes may improve the fit of the model to the observed data. In our examples, we tested whether increasing dispersal distances, increasing population growth rates, or allowing foraging in the matrix (in the case of the White-throated Treecreeper) could increase the occupancy rates to those observed. The results suggested that allowing birds to forage in the matrix adjacent to the patches would improve the predictions for the White-throated Treecreeper. Increasing the population growth rate of Red-browed Treecreepers improved the predictions for this species. Additional simulations

indicated that increasing the population growth rate by modifying fecundity had almost identical effects on the predictions as increasing the survival rate of adults (results not shown).

Even without modifying the models, there was a significant positive relationship between the predicted patch occupancy and the observed occupancy, suggesting that the models can predict the relative occupancy of patches. Such relative predictions may be useful (Possingham et al. 1993), especially because the probability of patch occupancy may be correlated with its contribution to metapopulation persistence (Lindenmayer and Possingham 1996). The models also predicted the correct relative impact of fragmentation on the two species, with the Red-browed Treecreeper being most adversely affected, apparently because of its requirement for larger areas of habitat and inability to utilize the pine matrix. Therefore, the results suggest that the relative predictions of PVA models may still be useful, even when their absolute predictions are shown incorrect. However, this will not necessarily be the case for models of other taxa.

The initial models were developed without data on the two species of treecreeper in the eucalypt patch system at BSF, so the comparisons with occupancy data in 1996 were independent tests of the models. However, the subsequent modifications of the models were made in the light of the statistical tests of the initial models. Therefore, comparing the modified models to data on patch occupancy in 1996 and 1997 was not equivalent to testing the model against independent data (Lacy 1993). Data on occupancy in 1996 were used to change the model in an effort to obtain a better fit, making the comparisons similar to calibration rather than validation. Occupancy data in 1997 was correlated with occupancy data in 1996, so a good fit to the 1997 data was likely given a good fit to the data in 1996. In contrast, the comparisons of the number of transition events were independent tests of the models, because these data were not analyzed until after the modifications were made, and were not conditional on the fit of the model in 1996.

The modified models tended to underestimate the observed transition (extinction and colonization) rates, especially in the case of Red-browed Treecreepers (Figs 3 and 4). This may arise due to errors in the model, or because of errors in the observations of the birds. False absences may be recorded where there is a chance of birds remaining undetected during the field surveys when they are in fact present in a patch. Additionally, the model predicts the distribution of territorial (not necessarily breeding) adults, but field surveys may record birds that are moving between areas while dispersing or foraging. Such observations may produce false presences. If false

absences or false presences were recorded in patches, the number of transitions would be over estimated by the field data. Even when the probability of recording false absences or false presences is low, false transitions would be recorded when numerous patches are surveyed. This tendency to overestimate the number of transition events has implications for empirical studies of metapopulation dynamics. We are unsure about the probability of recording false presences or false absences, but we believe that these probabilities are small, especially for the White-throated Treecreeper, which is the more common species. Nevertheless, there is some uncertainty about whether imperfect sampling of patches or model error has contributed to the under-prediction of the observed transition rates. If the model was the source of the error, then dispersal, birth and death rates would all need to be significantly higher to provide predictions that more closely matched the observed transitions.

The tests of patch occupancy using logistic regression were based on the assumption that the samples (occupancy in each patch) were independent. This is not true because the patches are linked by dispersal and are subject to the same environmental fluctuations. Spatial correlation will tend to result in population sizes fluctuating in synchrony. This reduces the effective degrees of freedom of the statistical tests, with the result that the calculated *P*-values will tend to be too small, and tests for differences between the observations and predictions will reject the model too frequently. Nevertheless, the predictions of patch occupancy by the modified models were not significantly different from the field data, despite the lack of independence between patches. In any event, the correlations between the predicted occupancy in patches were relatively small, with all pair-wise correlations less than 0.11 for the modified Red-browed Treecreeper model, and less than 0.34 for the modified White-throated Treecreeper model. Many of the patches were relatively remote from each other (> 1 km), which would tend to reduce the correlations.

We believe the modified models provide the best possible predictions about the fate of the two treecreepers in the patch system at BSF given the available data on the species. The modified model of Red-browed Treecreepers predicted that this species will continue to decline in the eucalypt patch system (Fig. 5), with the predicted rate of local extinction greater than the predicted rate of colonization (Fig. 4). The model predicts that several decades will elapse before the full impact of fragmentation will occur (Fig. 5), a prediction that is consistent with delayed effects in other fragmented systems (Suckling 1982, Bennet 1987, Loyn 1987, Saunders et al. 1993, McCarthy et al. 1997). In contrast, occupancy of patches by White-throated Treecreepers is predicted to remain relatively stable (Fig. 5), with the number of extinctions

being approximately equal to the number of colonization events (Fig. 3). These are important predictions for the purposes of conservation biology, because metapopulation models are often used to determine whether species will persist in particular fragmented systems. Planned fieldwork using repeated sampling of patches in future decades will determine the accuracy of these predictions.

The tests of metapopulation models of Red-browed Treecreepers and White-throated Treecreepers demonstrated that there was a significant positive relationship between the predictions of patch occupancy and actual patch occupancy determined from field surveys. Testing of the models facilitated modifications that improved their fit. Model testing is a little used but important aspect of population viability analysis. The aim of model testing is not to prove the truth of a model because, by definition, no model is a perfect representation of reality. Testing a model increases confidence in its use, and helps improve its predictions by identifying its weakest aspects.

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