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Modelling the inter-relationships between habitat patchiness, dispersal capability and metapopulation persistence of the endangered species, Leadbeater's possum, in south-eastern Australia

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Abstract

A computer simulation model was used to derive estimates of the probability of extinction of populations of the endangered species, Leadbeater's Possum (*Gymnobelideus leadbeuteri),* inhabiting ensembles of habitat patches within two wood production forest blocks in central Victoria, south-eastern Australia. Data on the habitat patches were extracted from forest inventory information that had been captured in the database of a Geographic Information System (GIS). Our analyses focussed on a range of issues associated with the size, number and spatial configuration of patches of potentially suitable habitat that occur within the Ada and Steavenson Forest Blocks. The sensitivity of extinction risks in these two areas to variations in the movement capability of G. *leadbeateri* was also examined.

Our analyses highlighted major differences in the likelihood of persistence of populations of G. *leadbeuteri* between the Ada and Steavenson Forest Blocks. These were attributed to differences in the spatial distribution and size of remnant old growth habitat patches as well as the impacts of wildfires. In addition, simulation modelling revealed a different relative contribution of various individual patches, and ensembles of patches, to metapopulation persistence in the two study areas. In those scenarios for the Ada Forest Block in which the impacts of wildfires were not modelled, our analyses indicated that a few relatively large, linked patches were crucial for the persistence of the species and their loss elevated estimates of the probability of extinction to almost 100%. A different outcome was recorded from simulations of the Steavenson Forest Block which, in comparison with the Ada Forest Block, is characterized by larger and more numerous areas of well connected patches of old growth forest and where we included the impacts of wildfires in the analysis. In this case, metapopulation persistence was not reliant on any single patch, or small set of patches, of old growth forest. We found that in some circumstances the probability that a patch is occupied whilst the metapopulation is extant may be a good measure of its value for metapopulation viability. Another important outcome from our analyses was that estimates of extinction probability were influenced both by the size and the spatial arrangement of habitat patches. This result emphasizes the importance for modelling metapopulation dynamics of accurate spatial information on habitat patchiness, such as the data used in this study which were derived from a GIS.

The values for the predicted probability of extinction were significantly influenced by a range of complex interacting factors including: (1) the occurrence and extent of wildfires, (2) the addition of logging exclusion areas such as forest on steep and rocky terrain to create a larger and more complex patch structure, (3) estimates of the quality of the habitat within the logging exclusion areas, and (4) the movement capability of *G. leadbeuteri.* Very high values for the probability of extinction of populations of G. *leadbeateri* were recorded from many of the simulations of the Ada and Steavenson Forest Blocks. This finding is the result of the limited areas of suitable old growth forest habitat for the species in the two areas that were targeted for analysis. Hence, there appears to be insufficient old growth forest in either of the two forest blocks to be confident that they will support populations of *G. leadbeateri* in the long-term, particularly if a wildfire were to occur in the next 150 years.

The results of sensitivity analyses indicated that estimates of the probability of extinction of G. *leadbeuteri* varied considerably in response to differences in the values for movement capability modelled. This highlighted the need for data on the dispersal behaviour of the species.

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1. Introduction

The destruction of temperate and tropical forests and the fragmentation of the remaining forested areas is a major problem world-wide (Harris 1984; Wilcox and Murphy 1984; Wilcove ***et al.*** 1986). These changes to forest landscapes can lead to the sub-division of populations of some forest-dependent organisms which may not be viable in the long-term (Pahl ***et al.*** 1988; Temple and Carey 1988; Laurance 1990; Thomas ***et al.*** 1990; Lamberson ***et al.*** 1992, 1994; Possingham ***et al.*** 1994). Connectivity ***(sensu*** Noss 1991) between remnant patches of habitat may assist the reversal of localised extinctions (Henderson ***et al.*** 1985; Fahrig and Merriam 1985; Lovejoy ***et al.*** 1986) or create larger connected sub-populations that have a greater probability of persistence (Forney and Gilpin 1989; Bennett 1990; Merriam and Lanoue 1990; Bennett ***et al.*** 1994).

Issues associated with aspects of habitat patchiness and landscape modification are fundamentally important to the long-term conservation of Leadbeater's Possum, ***Gymnobelideus leadbeateri,*** an endangered species of arboreal marsupial that is virtually restricted to a 80 km x 60 km area of montane ash forest in the Central Highlands of Victoria, south-eastern Australia (Lindenmayer ***et al.*** 1991a). There are several reasons for this. First, approximately 75% of the distribution of the species is restricted to forests that are clearfelled extensively to produce timber and pulpwood (Macfarlane and Seebeck 1991). The use of these types of silvicultural operations creates extensive areas of regrowth forest that are generally unsuitable for occupation by the species (Lindenmayer ***et al.*** 1990a; Lindenmayer 1992a, 1992b, 1994a; Smith and Lindenmayer 1992; Lindenmayer and Norton 1993). Second, within this matrix of unsuitable forest, patches of old growth and multi-aged forest that are presently not available for logging provide key areas of potentially suitable habitat for the species within wood production forests. However, the majority of habitat patches are very limited in size (< ten ha) and are spatially dispersed (Lindenmayer ***et*** *al.* 1993a, 1993b; Possingham ***et al.*** 1994). This range of factors lead to a number of questions. Some of these include: (1) What is the relationship between the predicted probability of extinction of populations of G. ***leadbeateri*** and the number and spatial arrangement of habitat patches in various wood production forest blocks where the species presently occurs? (2) What is the contribution of individual patches and ensembles of patches to estimates of metapopulation persistence? (3) What will be the contribution to population persistence of areas of unlogged forest ***(e.g.*** wildlife corridors)? Given there are few data on the movement of G. ***leadbeateri,*** an important additional question is: (4) How sensitive are estimates of extinction probability to variations in dispersal capability?

We have tackled these questions by integrating data on: (1) the known habitat requirements of the species using information derived from detailed field studies coupled with subsequent statistical analyses (Lindenmayer 1989; Lindenmayer ***et al.*** 1991b; Lindenmayer ***et al.*** 1994a); (2) the spatial distribution of real patches of suitable habitat within two timber production forest blocks that was derived from forest inventory information (Department of Conservation and Natural Resources unpublished data); (3) temporal dynamics of the suitability of habitat for ***G. leadbeateri*** in response to disturbances like fire and logging (Lindenmayer 1994a, 1995); (4) the known life history parameters of G. ***leadbeateri*** (Smith 1980, 1984a; Lindenmayer ***et*** *al.* 1993b); (5) the use of retained linear strips (wildlife corridors) as ***habitat*** by the species (Lindenmayer ***et*** *al.* 1993c; Lindenmayer ***et al.*** 1994c; Lindenmayer and Nix 1993), and (6) Victorian State Government forest management strategies for habitat retention and logging exclusion zones with wood production areas (Government of Victoria 1986; Department of Conservation, Forests and Lands 1989; Macfarlane and Seebeck 1991). This information was input to a computer model for Population Viability Analysis (PVA) ***(sensu*** Shaffer 1990; Boyce 1992), to simulate the influence of varying levels of habitat patchiness on the dynamics of metapopulations of G. ***leadbeateri.***

2. Methods

2.1. ***Background – the biology and ecology of G. leadbeateri***

G. ***leadbeateri*** is a small (< 160 g), cryptic species of arboreal marsupial that was thought to be extinct for the first half of this century before it was "re-discovered" in 1961 (Wilkinson 1961). G. ***leadbeateri*** is the only species of native mammal that is restricted to Victoria and it is one of the faunal emblems of that State (Government of Victoria 1971). The conservation of G. ***leadbeateri*** is controversial because a significant proportion of its distribution overlaps with

Fig. 1. The location of the Central Highlands region of Victoria, south-eastern Australia (shown as a black square in the middle map). The Ada Forest Block (marked as Area 1) and the Steavenson Forest Block (marked as Area 2) are depicted in the bottom figure.

some of the most valuable and productive areas of forest for timber harvesting in Australia (Lindenmayer and Norton 1993). A draft plan of management for the conservation of G. *leadbeateri* within wood production areas has been released by the Department of Conservation and Natural Resources (Macfarlane and Seebeck 1991). One of the key initiatives of this document was the exclusion of timber harvesting from existing stands of old growth montane ash forest. These are in addition to stands of forest on steep slopes and riparian areas that are unavailable for logging under environmental guidelines in timber harvesting zones (Department of Conservation, Forests and Lands 1989).

There have been a number of studies of G. *leadbeateri* and these have examined various aspects of the biology and ecology of the species including its distribution (Lindenmayer *et al.* 1989, 1991a), life history (Smith 1980, 1984a; Thomas 1989), habitat requirements (Smith and Lindenmayer 1988, 1992; Lindenmayer 1989; Lindenmayer *et al.* 1991b; Lindenmayer *et al.* 1994a), diet (Smith 1984; Lindenmayer *et al.* 1994b), nest tree use and requirements (Smith and Lindenmayer 1988; Lindenmayer *et al.* 1990b, 1991c, 1991d); the use of retained strips or wildlife corridors (Lindenmayer *et al.* 1993c; Lindenmayer and Nix 1993), response to logging operations (Lindenmayer *et al.* 1990a; Lindenmayer 1992a, 1992b, 1994a) and the climatic conditions which characterise those areas inhabited by the species (Lindenmayer *et al.* 1991a). The values for the parameters used in computer simulation modelling have been drawn from this array of studies. The rationale for the values that were used in PVA is outlined below.

2.2. *Wood production forest blocks targeted for detailed study*

Two areas were selected for this study. These were the Ada and the Steavenson Forest Blocks (Figs. 1–3). Our study was based on forest blocks because this is the scale used for detailed forest and wildlife management planning by the Victorian Department of Conservation and Natural Resources. In addition, a key aim of forest management strategies is to attempt to conserve native biota throughout their natural ranges (Government of Victoria 1992), and maintain populations of animals and plants in each forest block (Loyn 1985).

The Ada and Steavenson Forest Blocks cover approximately 6700 ha and 5500 ha respectively, and they are dominated by stands of Mountain Ash, *Eucalyptus regnans* forest. Old growth montane ash forest covers approximately 2.5% (= 160 ha) of the Ada Forest Block. A similar amount of forest occurs on steep terrain and in streamside reserves that is unavailable for timber harvesting. About 10% (= 550 ha) of the Steavenson Forest Block is either: (1) old growth forest, or (2) within streamside reserves and on steep terrain. A similar amount of forest occurs in each type of area.

Parts of the boundary of the Steavenson Forest Block, together with areas in the neighbouring forest blocks are dominated by non ash-type or dry mixed

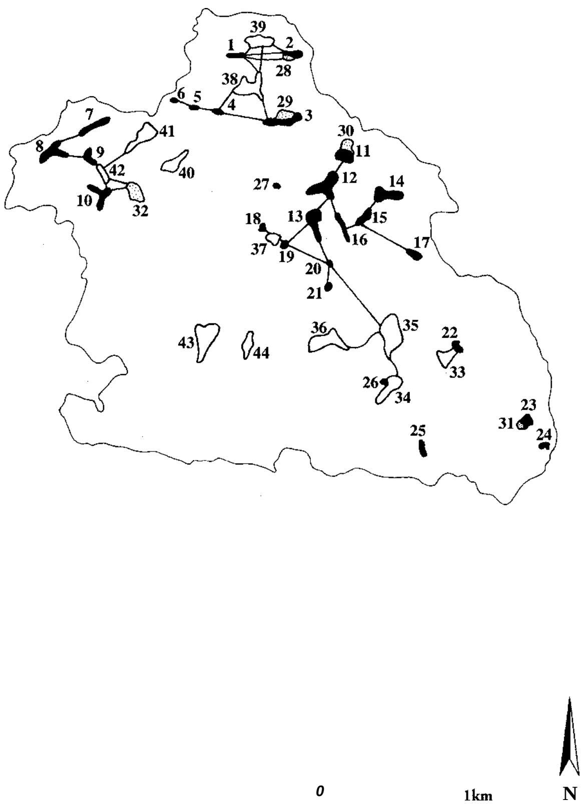

Fig. 2. The patch structure that was used in simulations of the persistence of populations of G. ***leadbeateri*** in the Ada Forest Block. The solid black polygons (***e.g.*** Patch #14) correspond to stands of old growth forest, the lightly stippled polygons (***e.g.*** Patch #32) represent areas of regrowth forest that support numerous trees with hollows and are temporarily reserved from logging operations, and the open polygons and (***e.g.*** Patch #43) are patches of forest that are excluded from timber harvesting. Each patch of potentially suitable habitat has been assigned a unique identifying number. The solid lines are movement corridors that allow animals to "diffuse" between habitat patches (see text). The total area of the forest block is approximately 6700 ha.

Fig. 3. The patch structure that was used for analyses of the persistence of populations of G. ***leadbeateri*** in the Steavenson Forest Block. The total area of the forest block is approximately 5500 ha. The solid black polygons (*e.g.* Patch #32) correspond to stands of old growth forest, the densely stippled patches (*e.g.* Patch #38) represent areas of regrowth forest that support numerous trees with hollows and are temporarily reserved from logging operations, and the lightly stippled polygons (***e.g.*** Patch #57) are patches of forest that are excluded from timber harvesting. Each patch of potentially suitable habitat has been assigned a unique identifying number. The solid lines are movement corridors that allow animals to "'diffuse" between habitat patches (see text).

species eucalypt forest. *G.* ***leadbeuteri*** does not occur on stands of regrowth forest. However, the O'Shannassy Water Catchment occurs directly south of the Steavenson Forest Block and this area is notable within Central Highlands region because it supports the large areas of old growth montane ash forest (Land Conservation Council 1993). Conversely, the Ada Forest Block contains more old growth forest than the surrounding forest blocks, although detailed mapping of old growth forest in the area has yet to be completed (J. Smith personal communication). For the purposes of our analyses we assumed that each forest block was modelled as a "closed system''. Thus, there was no migration into the forest blocks from surrounding areas, and animals moving beyond the boundaries of each block died.

2.3. Model used in computer simulation analyses

The computer program ALEX (Possingham *et al.* 1992; Possingham and Davies 1995) was used in this study. A detailed account of the structure of the model is provided by Possingham and Davies (1995). Other examples where the package has been applied are outlined by Norton and Possingham (1991), Possingham *et al.* (1993, 1994), Goldingay and Possingham (1993), Lindenmayer *et al.* (1993a), and Possingham and Gepp (1993).

ALEX is a spatially-explicit demographic population simulation package in which only the fate of female animals is modelled and the impacts of genetic factors on population dynamics are ignored (see Possingham and Davies 1995). The model has a number of special features which made it useful for this study, including its ability to model: (1) complex spatial arrangements of forest patches, and (2) temporal variations in the suitability of areas of habitat in response to forest succession that result from wildfires. The structure of ALEX is also particularly valuable as it enables numerous scenarios, and simulations within scenarios, to be completed rapidly. This, in turn, allows many permutations of potentially significant factors to be examined (Possingham *et al.* 1992).

2.4. Patch structures used in the analyses

Detailed forest inventory information on the forest types within the Ada and Steavenson Forest Blocks have been digitised by the Victorian Department of Conservation and Natural Resources and stored in a GIS database (ARCINFO, ESRI, California). These data include information on the size and spatial location of patches of potentially suitable habitat for G. *leadbeateri*. These data were input to ALEX. Maps of the patches are presented in Figures 2 and 3.

The patch structure used in our analyses was comprised of three types of areas that may provide potentially suitable habitat for G. *leadbeateri*. These were: (1) stands of old growth forest, (2) areas of regrowth montane ash forest that support numerous large old trees with hollows and are temporarily excluded from timber harvesting, and (3) areas of forest that are excluded from wood production including streamside reserves and stands on steep and rocky sites (Figs. 2 and 3). The part of each forest block that was not assigned to these types of habitat patches was assumed to be available for clearfelling and unlikely to support suitable habitat for G. *leadbeateri*.

2.5. Temporal variations in habitat suitability values for different patch types

We derived a habitat quality index to track temporal changes in the suitability of the different types of habitat patches for G. *leadbeuteri*. The values for this index were based on information from detailed studies of the habitat requirements of the species (Lindenmayer *et al.* 1991b, 1994a). These studies have been based on extensive field studies in which data on the presence and abundance of animals, as well as the structural and floristic characteristics of the forest, were gathered at many sites throughout the Central Highlands of Victoria. Statistical modelling was then used to identify key components of the habitat requirements of G. *leadbeateri* (Lindenmayer *et al.* 1991b). Importantly, the validity of these models were subsequently confirmed from further field surveys and statistical analyses specifically designed to assess the performance of the habitat models (Lindenmayer *et al.* 1994a).

The habitat quality index used in ALEX was based on the temporal availability of three key habitat resources for G. *leadbeateri:* (1) the abundance of large dead trees with hollows that provide potential nest sites for the species (Lindenmayer *et al.* 1991c), (2) the abundance of large living trees with hollows that is indicative of the future availability of nest tree resources (Lindenmayer *et al.* 1990b) and which is also a reflection of available den sites (Lindenmayer *et al.* 1991c), and (3) the basal area of *Acacia* spp. which reflects the suitability of the foraging substrate for G. *leadbeateri* (Smith and Lindenmayer 1992; Lindenmayer *et al.* 1994b). The values for these three measures were combined to give a value between zero and one for each patch that represents the overall quality of the habitat for G. *leadbeateri* (Appendix 1). The reciprocal of the habitat quality value is the minimum home range size for a breeding animal. For example, a total of 12 adult female G. *leadbeuteri* can breed within a 60 ha patch assigned a habitat quality value of 0.2

We set the habitat quality index to 0.3 for stands of old growth forest. This value allowed for a maximum of two reproductively active females per six ha of old growth forest. However, a detailed examination of our simulations revealed that there were typically half this number of animals. This corresponds with field

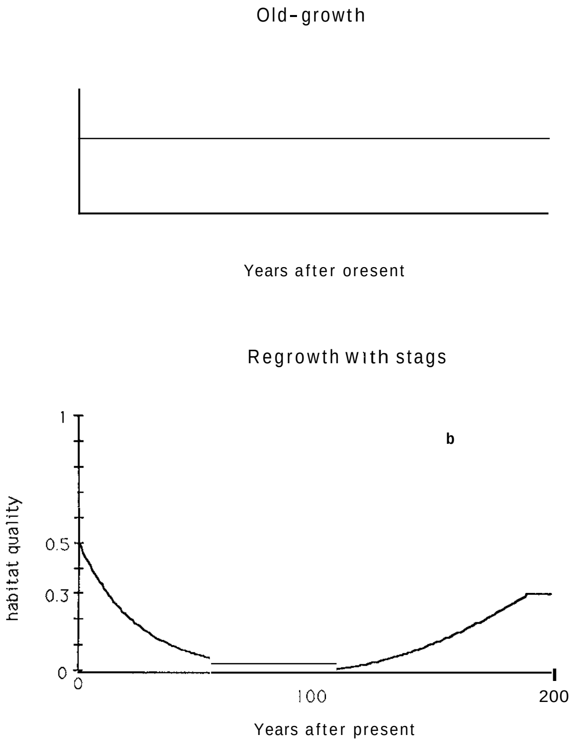

Fig. 4. The response curves for temporal variations in habitat suitability in the areas of old growth forest (part a), and, areas excluded from logging (*e.g.* steep slopes and streamside reserved) (part b). The line in each case represents the habitat quality value and corresponds to the maximum abundance of adult breeding female animals per ha that could occur in a given type of patch (see text and Appendix 1).

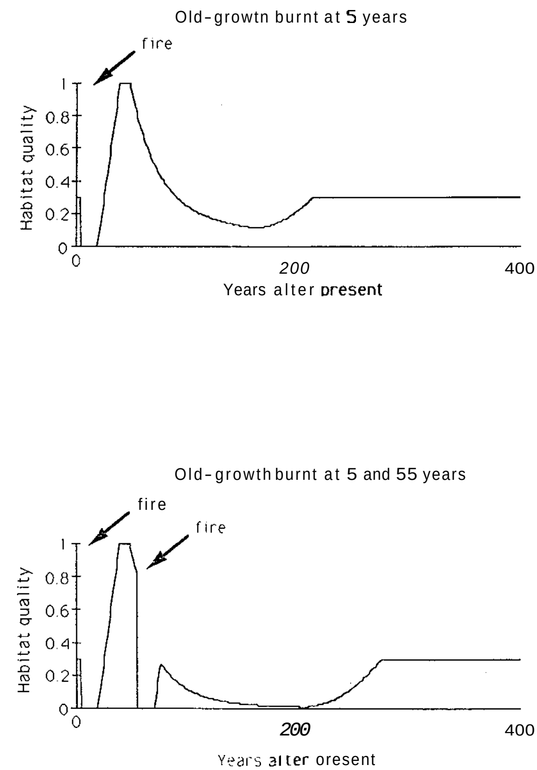

Fig. **5.** The response curve for temporal variations in habitat suitability following a wildfire within a stand of old growth montane ash forest burnt five years from now (part a), and, burnt by successive wildfires that occur at an interval of 50 years (part b). The line in each case represents the habitat quality value and it corresponds to the maximum abundance of adult breeding female animals per ha that could occur in the patch (see text and Appendix 1).

observations from patches of old growth montane ash which have indicated that in this type of forest there is typically only approximately one adult breeding female per six ha (Lindenmayer ***et*** *al.* 1993b).

Because factors such as the abundance of potential nest sites remain relatively constant within stands of old growth forest, we fixed the habitat suitability index at 0.3 for the duration of most of our simulations (Fig. 4, Appendix 1). However, the temporal changes in the habitat suitability index were more complex for those scenarios where the impacts of wildfires were simulated, with the response being a function of the fire history in a patch (***e.g.*** age of the stand when it was burnt) (see below; Figs. 5 and 6; Appendix 1).

Patches of forest confined to streamside reserves and steep and rocky areas were assigned a maximum habitat quality value of 0.15. A relatively low value was used because the results of a range of field surveys have indicated that: (1) G. ***leadbeateri*** only rarely inhabits strips of forests that are set aside as streamside reserves (Lindenmayer ***et*** *al.* 1993c; Lindenmayer and Nix 1993), and, (2) the abundance of the species is significantly lower in forests on steep slopes (Lindenmayer ***et*** *al.* 1991b, 1994a). Most areas in streamside areas and on steep slopes contain areas of regrowth montane ash forest and the majority of trees with hollows in these areas are large dead or fire-damaged mature stems that were burnt in the 1939 wildfires. These trees are becoming increasingly decayed and are collapsing at a rapid rate (Lindenmayer ***et*** *al.* 1990b, unpublished data). Thus, there will be a rapid and significant decline in the availabil-

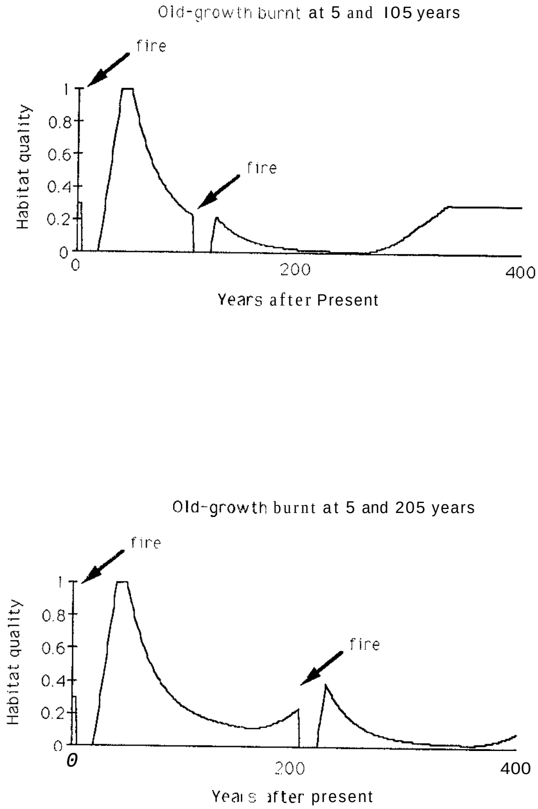

Fig. 6. The response curves for temporal variations in the habitat suitability index for *G.* ***leadbeuteri*** in a stand of old growth montane ash burnt by successive wildfires that occur at different frequencies. The line in each diagram represents the habitat quality value and it corresponds to the maximum abundance of adult breeding female animals per ha that could occur in the patch (see text and Appendix 1).

ity of nest sites for C. *leadbeuteri* in these areas, with a corresponding reduction in habitat suitability and animal abundance (Lindenmayer *et al.* 1990a, 1993b). Given these factors, we set the habitat suitability value of such areas so that it gradually declined to 0.05 over the next 100 years in response to the collapse of trees with hollows (Fig. 4; Appendix 1). After this time there would be recruitment of new potential nest sites as a result of the maturation of the existing regrowth trees with hollows. Accordingly the habitat index was specified so that it gradually returned to a value of 0.15 (Fig. 4; Appendix 1).

Regrowth montane ash forests with numerous large trees with hollows typically provide both suitable nesting resources and foraging substrates for *G. leadbeuteri* (Smith and Lindenmayer 1988; Lindenmayer *et al.* 1991b). We specified a value of 0.5 for habitat quality in these areas because the species typically occurs in greater numbers than within old montane ash forest (Lindenmayer *et al.* 1989, 1993b). However, there was a rapid rate of decline in habitat quality in regrowth forest. These types of areas are only temporarily reserved and they become available for timber harvesting when the abundance of trees with hollows drops below a given threshold (four trees with hollows per ha) (Macfarlane and Seebeck 1991). Based on long-term studies of the rate of decay and collapse of trees with hollows within regrowth montane ash forests, patches of regrowth forest are likely to support very few potential nest sites for G. *leadbeateri* within 20–30 years (Lindenmayer *et al.* 1990b; unpublished data), after which they will be clearfelled and be unsuitable for the species. Hence, we assigned a habitat quality value of zero for patches of this type of forest after a period of 30 years.

There were more complex temporal changes in habitat suitability index in those scenarios where the impacts of wildfires were incorporated in our analyses and these are outlined in the following section.

2.6. Simulating the impacts of wildfires

Wildfire has been an important factor influencing both the structure of montane ash forests (Lindenmayer *et al.* 1991e) and the spatial location of remaining areas of old growth forest. Given this, we incorporated the impacts of fires in some of the scenarios completed in this study. In such simulations, we set the annual probability of wildfires to 1% and the proportion of patches burnt in a conflagration was either 50% or 75%. These values for fire frequency and distribution were based on information on the occurrence of wildfires in the Central Highlands of Victoria since European settlement. We recognise that a much wider range of fire regimes could have been examined. However, this warrants a major investigation in its own right and it has been reserved for another study (Lindenmayer and Possingham 1995). Notably, because very little is known about the behaviour, spread and response to stand age structure of fires in montane ash forests, we did not include spatial contagion in our simulations of wildfires, or differential burning patterns between the various types of habitat patches.

Fire damaged stands of montane ash forest are usually salvage harvested after a major conflagration

(Noble 1977; Smith and Woodgate 1985; McHugh 1991), and these activities involve the clearfelling of burnt forests. Such operations have a major negative impact on the suitability of forest habitat for G. *leadbeateri* (Smith and Lindenmayer 1992). However, we did not include the added impacts of post-fire salvage logging operations in our analyses.

For the purposes of this investigation, wildfires were modelled as having both a direct impact upon populations of animals that inhabit stands of forest at the time they are burnt, and a longer term effect by changing the vegetation structure. Because G. *leadbeateri* is a territorial species with strong site affinity (Smith 1980), animals are unlikely to move far during a wildfire. Given this, we assumed that no animals would survive a wildfire in a given patch. This was because even if some animals were not killed directly in a fire (*e.g.* by sheltering within a large unburnt stem), there is a very high probability of them dying soon after because of elevated predation rates and/or a shortage of food.

The impact of wildfires on vegetation structure, and hence the suitability of burnt forest patches as habitat for G. *leadbeateri*, depended upon: (1) the amount of time since the previous fire, and, (2) the habitat characteristics of a given patch. For example, stands of old growth forest, if burnt, would contain numerous burnt or killed large trees with hollows that would provide potential nest sites for G. *leadbeateri* (Lindenmayer *et al.* 1991f, 1993d). Such post-fire stand conditions characterise many areas where the species has been detected (Lindenmayer *et al.* 1991a). Conversely, a wildfire in stands of young forest has a markedly different effect (Ashton 1981), and it typically does not result in the creation of large trees with hollows (Lindenmayer *et al.* 1993d). Notably, this has occurred in the Ada Forest Block within stands of 50 year old regrowth forest that were burnt in the 1983 "Ash Wednesday" fires (Lindenmayer, unpublished data). We have incorporated a number of sub-models within the sequence of program flow of ALEX to simulate the impacts of wildfires on the suitability of forest habitats for G. *leadbeateri*. These are represented as temporal changes in the habitat suitability index (Appendix 1). Figures 5 and 6 contain a number of typical habitat response curves that characterised simulations where the effects of wildfires were incorporated in the analysis.

2.7. Life history attributes of G. leadbeateri

Information from several studies of the life history of G. *leadbeateri* (Smith 1980, 1982, 1984a; Thomas 1989; Lindenmayer *et al.* unpublished data) was used to parameterise ALEX (Table 1). The basis for these values is only briefly summarised here because it has been outlined in a previous study (see Lindenmayer *et al.* 1993b).

Smith (1980, 1982, 1984a) completed a detailed examination of the basic biology and life history of G. *leadbeateri*. These studies revealed that the species has a matriarchal social structure in which colonies of animals are typically comprised of a monogamously-mated breeding pair, pre-dispersal aged offspring and unrelated non-breeding adult males.

Although the sex ratio of G. *leadbeateri* at birth is 1:1, higher rates of mortality amongst sub-adult females, together with the social structure of colonies of animals, typically results in a 3:1 male-biased sex ratio (Smith 1980). This results in the abundance of breeding animals being limited by the number of adult females (Smith 1984a). ALEX is well suited to modelling taxa with this type of mating system and social structure because the fate of only one sex (usually females) is simulated by the package (Possingham *et al.* 1992; Possingham and Davies 1995).

Adult female G. *leadbeateri* become reproductively-active at approximately two years old (Smith 1980) and can produce up to four young per year (Smith 1980, 1984a). Table 1 contains the estimated probabilities of different numbers of female young being produced per year. Survivorship varied between the three age-classes modelled in ALEX; *viz.*: newborn (< one year old); sub-adults (1–2 years old) and adults (> two years old) (Table 1). We based our values on: (1) the high rates of mortality amongst juvenile females when they disperse from the natal territory (Smith 1980, 1984a), and, (2) estimates of the longevity of adult animals derived from capture-recapture studies of a marked population (Meggs *et al.* 1991; Lindenmayer *et al.* unpublished data).

2.8. Incorporating the impacts of environmental variability

We included a parameter in ALEX to model the impacts of environmental variability on breeding success in G. *leadbeateri*. The model was parameterised so that there would be, on average, a complete failure

Table 1. Values for the life history attributes of ***G.*** *leadbeateri* that were input to ALEX for metapopulation viability of the species. Further explanation of the population parameters and methods used to derive them are provided in the text.

Min. home range of females in highest quality habitat	1.0 ha
Min. home range size of breeding females in old-growth	3.3 ha
Max. population density (females per ha)	2
Reproduction	
Annual probability of 0 female young per female	0.45
Annual probability of 1 female young per female	0.30
Annual probability of 2 female young per female	0.18
Annual probability of 3 female young per female	0.06
Annual probability of 4 female young per female	0.01
Age at sexual maturity (years)	2
Mortality	
Annual probability of death	
newborn	0.0
juvenile	0.3
adult	0.3
Population growth	
Population growth rate under ideal conditions	1.21
Population threshold for quasi extinction	2
Movement	
Mean migration distance of juveniles	2 km
Population density before migration (% of maximum)	20%
Migrtion probability of subadults	70%
Population density before diffusion (% of maximum)	10%
Diffusion probability for subadults	20%

to reproduce every six years. This value was based on field studies of G. *leadbeateri* which have indicated that climatic fluctuations (*e.g.* droughts or prolonged wet weather during summer) can lead to a major reduction in the abundance of food such as arthropods (Smith 1980, 1984a) and the availability of the exudates from *Acacia* trees (Lindenmayer unpublished data). These factors can, in turn, significantly influence the fecundity of the species. For example, Smith (1980, 1984a) found that during a drought in 1978, no young survived to weaning age (approximately three months of age) and the overall population size declined by about 45%. Because the distribution of G. *leadbeateri* is confined to such a small area within a single region, the effects of environmental variability are likely to be consistent throughout the species' highly restricted distribution.

2.9. *Simulating the dispersal capability and movement patterns of G. leadbeateri*

The movement of G. *leadbeateri* between habitat patches was simulated using two sub-models that are available within ALEX. These are called "migration" and "diffusion" and they correspond to different types of movement that may be expected to occur in a landscape where there are varying distances between ensembles of habitat patches (see Possingham *et al.* 1992; Possingham and Davies 1995). The parameterisation of the migration and diffusion sub-models was based on the life history of ***G.*** *leadbeateri* (Smith 1980, 1984a), as well as information on the home range and movement patterns of the species (Smith 1980; Lindenmayer *et al.* unpublished data).

The migration sub-model simulated the movement of G. *leadbeateri* between spatially separated habitat patches that were > 200 m apart. Migrating animals moved away from the source patch in a random direction. There was an exponential decline in the probability of survival as the inter-patch distance increased. The probability of successful migration from a source patch to a target patch was calculated using the formula: $\exp[-da/m]$ where d is the distance between the two patches, a is the probability that a line drawn in a random direction from the centre of the source patch will strike the target patch, and m is the mean expected migration distance (see below). The value of a is calculated using the formula:

$$a = \arctan(r/d)/\pi \quad \text{for } d > \pi$$
$$= 0.5 \quad \text{for } d < r,$$

where r is the radius of the target patch. Although this measure is an approximation, it reflects the general concept that migrants are more likely to contact large adjacent patches than smaller, more remotely located ones (A.T. Smith 1980; Fahrig and Merriam 1985; Van Dorp and Opdam 1987; Kindvall and Ahlen 1992; see Hanski 1994 for a review). The mean migration distance (m) is the average distance that a migrating animal can travel from its source patch before it dies. A value of two km was employed for most scenarios examined in this study. This is twice the maximum known distance individual G. *leadbeateri* have moved during radiotracking studies (Lindenmayer *et al.* unpublished data). However, there is considerable uncertainty about this aspect of the biology of the species and the sensitivity of our results to a range of values for mean migration distance was examined.

Only sub-adult females migrated (*i.e.,* those animals aged 1–2 years old). Migration occurred when the abundance of animals in a given patch exceeded 20% of habitat carrying capacity. We assumed that animals would disperse into unoccupied habitat within the same habitat patch when the carrying capacity was lower. The maximum value for the annual probability of migration was set to 70%. A number of findings from field studies were used to guide the selection of these values. The most important of these were: (1) the home range of G. *leadbeateri* is approximately 1.5–3 ha (Smith 1980); (2) adult female animals are intolerant of their daughters and enforce their dispersal when they become sub-adults, and, (3) there are rarely more than two adult conspecifics in the same territory (Smith 1980).

When habitat patches were located < 200 m apart or were joined by riparian vegetation along a streamline, we connected them with a corridor and invoked the diffusion sub-model in ALEX to simulate the movement of animals into unoccupied habitat in adjacent patches. Unlike the migration sub-model, there was no mortality associated with this form of movement. The number of diffusing animals in any given year was limited by the length of the common boundary between adjacent areas of suitable habitat. A given animal was allowed to "diffuse" to only one new patch in any year. We set the probability of "diffusion" for sub-adult females to 20% and this accounted for the movement of those animals that did not undergo migration (see above). A value of 10% was used for adult age animals (> two years old) to allow some individuals to make relatively small changes in the location of their territories.

2.10. *Output data used in the interpretation of the results*

Four kinds of information were derived from the application of ALEX and were used to assist in the interpretation of our results. These were: (1) the median time to extinction, (2) the predicted probability of extinction, (3) the "steady state" probability of extinction, and, (4) proportion of the time a particular patch remained occupied while the metapopulation was extant.

The steady state probability of extinction is a measure of the likelihood of extinction averaged over a series of 150 year intervals following the initial 150 year period of the simulations. It was used to overcome problems associated with the "initialisation effect", where the results derived in the early parts of a simulation were heavily biased by the initial state of the patch system. The steady state probability of extinction was calculated using the following method. A value for the extinction probability was derived for each of the following time intervals: 150–300 years, 300–450 years, 450–600 years and 600–750 years. These values were then averaged to give an estimate of the steady state probability of extinction.

It is important to complete many simulations of each scenario tested with computer simulation modelling to stabilize the output (see Harris *et al.* 1987; Maguire and Shaffer 1988). Standard deviations were generated for many of the values derived from the application of ALEX. These were calculated using the formula: **SD** = $\sqrt{np(1-p)}$ where n = the number of simulations, and p is the probability of extinction during the time horizon of interest. As we completed a minimum of 300 simulations for each scenario, the standard deviation in output values (*e.g.* for the probability of extinction) would be a *maximum* of ±3%. The values for standard deviations tend to peak when the estimates for extinction probability approach 50%.

3. Scenarios examined in this study

This study focussed on a number of questions associated with habitat patchiness, the spatial arrangement of patches and metapopulation persistence. The analyses were categorised into a number of scenarios and they are described below.

3.1. *Scenario 1 – The estimation of metapopulation persistence in the study areas*

In this scenario, we estimated the probability of persistence of G. *leadbeateri* in both the Ada and Steavenson Forest Blocks. These simulations were completed initially without the impacts of wildfires. The analyses were then repeated with the effects of wildfires being incorporated in the model. In these cases, the annual probability of fire was set to 1% with 75% of habitat patches burnt in any given conflagration. This combination of fire frequency and fire extent meant that, on average, a given patch would be burnt every 133 years.

3.2. Scenario 2 – The contribution of particular old growth habitat patches to metapopulation persistence in the Ada Block

Here, we completed a detailed examination of the contribution of individual patches and groups of patches of old growth habitat to the persistence of G. *leadbeateri* in the Ada Forest Block. These simulations were completed to assess the impacts of the loss of particular patches on the likelihood of extinction of the species. This may parallel situations in the field where particular patches are logged or burnt.

We commenced our analyses with a patch structure that was comprised of 27 individual areas of old growth forest (see Fig. 2). Each patch of old growth forest that occurred in Ada Forest Block was individually removed from the array of patches and the viability analysis was repeated to determine the effect of its loss on metapopulation persistence. At least 300 simulations were completed for each iteration. Thus, changes of about 3% in the predicted probability of extinction indicated that there was a significant impact resulting from the loss of a particular patch.

Further analyses of the Ada Forest Block focussed on the impact of removing groups of patches from the habitat patch structure. This involved deleting: (1) sets of patches belonging to given size classes (*e.g.* all patches < three ha, and all patches < six ha), and, *(2)* ensembles of connected and/or neighbouring patches. The approach used to model the impact of such procedures was identical to that described for the removal of individual areas and it allowed a comparison between the results of simulations that were completed with, and without, a particular set of patches. All of the simulations in Scenario *2* were completed without the impacts of wildfires.

3.3. Scenario 3 – The contribution of particular old growth habitat patches to metapopulation persistence in the Steavenson Forest Block

The analyses of the Steavenson Forest Block that were undertaken in Scenario 3 were similar to those described in Scenario 2 for the Ada Forest Block. The only major difference was that we included a fire regime in which there was a 1% annual probability of wildfires and 75% of patches were burnt in a given fire event.

3.4. Scenario 4 – The contribution to population persistence of areas of forest excluded from timber harvesting

In this scenario, values for the predicted and steady state probabilities of extinction in the Ada Forest Block and the Steavenson Forest Block were derived from simulations where the patch structures were comprised only of old growth forest. The analysis was then repeated using more complex patch structures comprised of patches of old growth forest, together with other areas that are presently excluded from timber harvesting such as forest on steep and rocky terrain and in streamside reserves. For these simulations we varied the suitability as habitat for G. *leadbeateri* of areas of excluded forest. The maximum values for habitat quality that were used for excluded areas were equivalent to 20% and 50% of that of old growth montane ash forest (= 0.03 and 0.15 respectively). We used this range of values in our analyses because of uncertainty about the long-term value of retained strips and other logging exclusions as habitat for G. *leadbeateri* (Lindenmayer *et al.* 1993c; Lindenmayer and Nix 1993). Finally, the analyses were completed with, and without, the impacts of wildfires. The fire regime that was invoked was the same as described in Scenario 3 (*i.e.*, a 1% annual probability of a fire with 75% of patches burnt).

3.5. Scenario 5 – The impact of the dispersal capability on estimates of extinction probability

Scenario 5 focussed on various aspects of the movement of G. *leadbeateri.* In previous scenarios, the value for the mean migration distance was set to 2 km. However, there are only limited data on the movement capabilities of G. *leadbeateri.* Given this, we varied the mean distance that animals travelled before they died from 100 m, 500 m, 1 km, 2 km and 100 km. These analyses obviously included some extreme values for movement (*i.e.,* 100 m and 100 km). However, they were invoked to test the sensitivity of our results to the dispersal capability of the species. The other parameters associated with the movement of animals remained the same as in other scenarios. These included the proportion of animals in a given age cohort that moved, and the relationship between habitat carrying capacity and the incidence of animal movement (see above).

Two different patch structures were modelled in analyses of the Ada Forest Block: (1) areas of old growth forest only, and, (2) patches of old growth plus other areas that are excluded from timber harvesting (*e.g.* stands of forest on steep and rocky terrain and in streamside reserves). The same range of patch structures was employed in simulations of the Steavenson Forest Block, but the analyses included the impacts of fire: an annual probability of wildfire of 1% with the proportion of patches burnt being either 50% or 75%.

3.6. Scenario 6 – The relationships between migration, diffusion and population persistence

In Scenario 6 we examined the relationship between the persistence of populations of G. *leadbeateri* and the impacts of migration and diffusion. Here, we completed a series of pairwise simulations where the migration and diffusion sub-models in ALEX were, and were not, invoked. Their effects were examined using a patch structure comprised solely of areas of old growth forest. As in most other parts of the study, modelling of the Ada Forest Block was undertaken in the absence of wildfires. In the case of the Steavenson Forest Block, the same fire regimes were employed as outlined in Scenario 5.

4. Results

4.1. Scenario 1 – The estimation of metapopulation persistence in the study areas

The results of simulations of the behaviour of populations of G. *leadbeateri* in the old growth patch structures within the Ada and Steavenson Forest Block are presented in Table 2. There were significant differences in the extinction probabilities between the two study areas, irrespective of whether fires were, or were not, included in the simulations (Table 2). In all cases, the values for the extinction probabilities were significantly greater in the Ada Forest Block than those derived from simulations of the Steavenson Forest Block (Table 2). Not surprisingly, we recorded higher values for the predicted probability of extinction when wildfires were more frequent or more extensive.

4.2. Scenario 2 – The deletion of individual patches of old growth habitat patches in the Ada ***Block***

Table 3 contains the results of simulations where individuals patches of old growth forest were removed from the patch structure in the Ada Forest Block. The results of our analyses indicated that no single patch was always occupied when the metapopulation was extant (Table 3). The values for patch occupancy ranged from 2%–82% and they were influenced by a range of factors. Big patches (*e.g.* > 12 ha) were occupied for a greater amount of time those of a smaller size, particularly if they were connected and/or adjacent to other large patches. Small patches located near larger ones were typically occupied for more of the time than areas of similar size that were spatially isolated from other patches of suitable habitat. For example, patch #24 and patch #18 were both two ha in size, but there were significant differences in the proportion of the time they remained occupied (3% and 11% respectively; see Table 3). Patch #24 was isolated from relatively large areas of old growth forest, whereas patch #18 was part of an ensemble of areas that included the biggest patches in the Ada Forest Block (see Fig. 2; Table 3).

The contribution of each habitat patch to metapopulation persistence was assessed by comparing the extinction probability derived when a given patch was removed, with that recorded when all 27 patches of old growth forest were included in the patch structure. We were unable to detect a significant increase in extinction probability when 19 of the 27 patches were deleted individually (Table 3). These patches were typically those that were either small (< five ha) and/or connected to other small patches. Conversely, we identified a number of patches that, if lost, would have a major negative impact on the likelihood of population persistence. For example, the deletion of patch #12 resulted in an increase in the predicted probability of extinction from 34% to 74% (Table 3).

The spatial location of habitat patches that were deleted also influenced our results. This is illustrated by a comparison of the outcomes of removing patches #3 and #15 from the patch structure. Patch #3 is twice the size of patch #15 but its loss had significantly less impact on the extinction probability (Table 3). It is likely that this outcome was due to the proximity of patch #15 to a network of relatively large patches. In comparison, patch #3 was part of an ensemble comprised of only a few, small patches of old growth forest (Fig. 2).

Table 2. The estimated probability of extinction (%) of populations of G. *leadbeuteri* in response to wildfire in the Ada and Steavenson Forest Blocks. The analyses were completed using a patch structure limited to stands of old growth forest only. The annual probability of fires was set to 1% and 75% of patches burnt in a given fire event (see text for further explanation). For those scenarios where the impacts of wildfires were modelled, there was no added impact of post-fire salvage logging operations incorporated in the analysis.

Study area	Predicted probability of extinction after 150 years	Predicted probability of extinction after 300 years	Median time to extinction (years)
Ada Forest Block			
(no fire)	34	48	> 300
(with fire)	78	98	87
Steavenson Forest Block			
(no fire)	2	5	> 300
(with fire)	48	84	162

4.3. *Scenario 2 – The deletion of groups of patches of old growth habitat patches in the Ada Block*

The results of simulations where groups of patches of old growth forest were deleted from the patch structure in the Ada Forest Block are given in Table 4. The loss of all patches that were < three ha in size made no significant change to the predicted probability of extinction. This finding corroborates those where single, very small areas of old growth forest were deleted without significantly impacting upon metapopulation persistence (Table 3). The decline in population viability was more pronounced with an increase both in the size classes of patches that were deleted and, concomitantly, the total area of forest that was removed from the patch structure (Table 4). However, there was not a simple relationship between the size cohort of deleted patches and the corresponding change in the extinction probability. Indeed, a major increase in the amount of lost viability occurred when the size of the deleted areas was increased from all patches ≤ 9 ha to all of those of 12 ha or smaller (Table 4).

Our analyses indicated that the loss of a group of key patches resulted in a major elevation in the probability of extinction. For example, no populations of G. *leadbeateri* were predicted to persist when patches #8, #12, #13 and #14 were removed from the habitat

Table 3. The relationship between the proportion of the time patches **of** different sizes and spatial locations in the Ada Forest Block were occupied by G. *leadbeuteri*. The number assigned to each patch corresponds to that given in Figure 2. This value is the increase above the value generated for the predicted probability of extinction after 150 years (= $P[E]_{150}$) when all old growth patches were included in the patch structure ($P[E]_{150}$ = 34%; see Table 2). A minimum of 300 simulations were completed in each case where a given patch was deleted from the patch structure. No impacts of wildfires were incorporated in our analyses. A dash indicates that no significant change was detected (*i.e.* < 3%) in the predicted probability of extinction following the deletion of a given habitat patch.

Patch no.	Patch size (ha)	Identity of other patches to which patch is connected	Proportion of time occupied	Decline (%) in viability from deletion*
1	3	2	11	–
2	4	1	15	–
3	11	4	53	8
4	5	3, 5	22	–
5	2	4, 6	6	–
6	2	5	5	–
7	8	8	32	–
8	14	7, 9	48	11
9	5	8, 10	25	–
10	8	9	28	12
11	12	12	66	24
12	16	11, 13, 16	82	61
13	16	12, 19, 20	82	26
14	16	15	74	29
15	6	14, 16, 17	51	26
16	7	12, 15	57	23
17	3	15	16	–
18	2	19	11	–
19	2	13, 18, 20	13	–
20	1	13, 19, 21	8	–
21	2	20	9	–
22	2	–	4	–
23	3	–	7	–
24	2	–	3	–
25	2	–	3	–
26	1	–	2	–
27	1	–	8	–

*These values correspond to the increase in $P[E]_{150}$ relative to the scenario with all old growth patches were included in the patch structure ($P[E]_{150}$ = 34%; see Table 2). The % of the viability that was lost was calculated from the equation $(P[E]_{150[new]} - P[E]_{150[old]})/(1-P[E]_{150[old]})$.

Table 4. The change in the predicted probability of extinction of metapopulations of G. *leadbeareri* in the Ada Forest Block in response to the deletion of constellations of various habitat patches. Patch numbers given in column 1 correspond to those shown in Figure 2. A minimum of 300 runs were completed for each part of the analysis and a dash in column 3 indicates that there was no significant change (*i.e.* < 4%) in the predicted probability of extinction. The analyses were completed without the impacts of wildfires and the patch deletions were limited only to stands of old growth forest.

Identifying number of patches	Area (ha) of deleted system	Decline of viability due to patch deletion (%)*
Deletion of areas by patch size classes		
All patches ≤ 3 ha	28	–
All patches ≤ 6 ha	48	11
All patches ≤ 9 ha	71	18
All patches ≤ 12 ha	94	61
All patches ≤ 15 ha	108	67
Deletion of ensembles of patches		
1 & 2	7	–
3, 4 & 5	18	
7, 8, 9 & 10	35	20
12 & 13	32	73
12 & 14	32	86
13 & 14	32	53
12, 13 & 14	48	91
8 & 12, 13, 14	62	100
11–21 (inclusive)	73	91
22, 23, 24, 25 & 26	10	–

Denotes the increase in $P[E]_{150}$ relative to the scenario with all old growth patches were included in the patch structure ($P[E]_{150}$ = 34%; see Table 2). For example, if the value for $P[E]_{150}$ following the deletion of a patch is 70% then the loss of remaining viability is (70–34)/(100–34) = 55%.

patch structure (Table 4). Indeed, there was an 86% loss of population viability when only two of these patches (#12 and #14) were removed. Here, the deletion impact was significantly bigger than in cases where other ensembles of more patches were lost and a greater area of forest was removed (*e.g.* the deletion of patches #7, #8, #9 and #10; see Table 4).

4.4. Scenario 3 – The contribution of particular old growth habitat patches to metapopulation persistence in the Steavenson Forest Block

Some trends in our data from the Steavenson Forest Block were similar to those derived from the analyses of the Ada Forest Block that were described in Scenario 2. For example, the highest levels of patch occupancy occurred in larger patches, and in large areas connected to other relatively big patches. However, in this forest block, some of the small patches, such as those measuring only one ha, were predicted to have relatively high occupancy rates (*e.g.* patches #11 and #16 were occupied 34% and 27% of the time; see Table 5). Indeed, only two patches contained G. *leadbeateri* for less than 25% of the time (Table 5). Spatially isolated small patches were occupied for a lower proportion of the time than areas of similar size that were connected or adjacent to larger patches (Table 5). As with the Ada Forest Block, no patches were constantly occupied while the metapopulation was extant, although several were occupied more than 90% of the time (Table 5).

Unlike the Ada Forest Block, no single habitat patch or small set of patches in the Steavenson Forest Block was predicted to be crucial for the persistence of G. *leadbeateri*. This was highlighted by the results of simulations were individual patches were deleted from the patch structure in the forest block (see Table 5). Indeed, for 23 of the 36 individual patches of old growth forest, we did not detect a significant change (*i.e.,* > 3%) in the extinction probability when they were deleted. The loss of the larger patches in the Steavenson Forest Block often resulted in a significant increase in the predicted probability of extinction. However, the increase in the probability of extinction did not exceed 12% for the removal of any one patch (Table 5).

Table 6 contains the results of analyses where we examined the relationships between the extinction of G. *leadbeateri* and the removal of groups of patches in the Steavenson Forest Block. A diagrammatic representation of the deletion of constellations of patches is presented in Figure 7. As expected, the extinction probability increased with the size of the area that was deleted. The loss of small groups of patches (< 20 ha) did not elevate the predicted probability of extinction above that recorded when the present patch structure remained intact (*i.e.,* $P[E]_{150}$ = 48%). Conversely, the most substantial impact was recorded ($P[E]_{150}$ = 74%) when the largest area (111 ha) was deleted (Table 6). The loss of some areas that were somewhat smaller than this also resulted in a significant increase in extinction probability. For example, a value for $P[E]_{150}$ = 68% was obtained from simulations where different ensembles of patches measuring 55 ha and 60 ha respectively, were erased from the

Table **5.** The relationship between the proportion of the time patches of different sizes and spatial locations in the Steavenson Forest Block were occupied by ***G.*** *leadbeateri*. For these analyses, the annual probability of a wildfire was set to 1% and the 75% of patches were, burnt in a fire. The number assigned to each patch corresponds to that given in Figure 3. Column 4 contains information on the change in the probability of metapopulation extinction in response to the deletion of a given patch. This value is the increase above the value generated for the predicted probability of extinction after 150 years (= $P[E]_{150}$) when there were no deletions and all old growth patches were included in the patch structure $P[E]_{150}$ = 48%; see Table 2). A dash in column 4 signifies that there was no significant change (*i.e.* < 3%) in the predicted probability of extinction when a total of 300 simulations were completed.

Patch number	Patch size (ha)	Proportion of time occupied (%)	% decline in viability from patch deletion
1	5	60	–
2	5	74	–
3	38	91	8
4	20	91	–
5	22	56	10
6	4	81	–
7	1	31	–
8	16	91	10
9	6	84	10
10	21	89	6
11	4	69	–
12	1	34	–
13	14	68	6
14	5	60	6
15	2	40	–
16	1	21	–
17	3	45	–
18	7	68	–
19	9	72	10
20	8	67	8
21	3	51	–
22	2	32	–
23	3	47	–
24	3	46	–
25	2	28	–
26	6	49	–
21	6	41	–
28	1	20	–
29	13	53	–
30	4	31	–
31	1	13	–
32	21	84	12
33	1	2	–
34	1	1	–
35	10	77	–
36	5	79	–

Table 6. The change in the predicted probability of extinction of metapopulations of *G. leadbeateri* in the Steavenson Forest Block in response to the deletion of constellation of various habitat patches. The identity of the various patches that were deleted is given in Figure 3. **A** number of the constellations have been assigned an identifying code (lettered A–E) which correspond to the ensembles of patches that are highlighted in Fig. 6.

Identity of patches deleted	Area deleted (ha)	Extinction probability after 150 years
No deletions	0	48
Deletions of patches by size classes		
Patches I 3 ha	25	49
Patches I 6 ha	75	52
Patches ≤ 9 ha	99	51
Patches **I** 12 ha	109	59
Patches **I** 13 ha	I22	60
Patches ≤ 15 ha	136	60
Patches **I** 18 ha	152	61
Patches **I** 20 ha	172	72
Patches ≤ 21 ha	193	74
Patches ≤ 22 ha	215	80
Patches ≤ 30 ha	242	86
Deletions of spatial arrangements of patch constellations		
1–8 (inclusive) *A*	111	74
9–13, 35 & 36B	61	61
14–18 *C*	18	50
24, 26–30 *D*	33	56
19–23, 25, 31 & 32E	55	68
3, 5	60	68
9, 18, 23	16	48

patch system (Table **6).** In one of these cases, the patch deletion procedure resulted in two of the three largest patches in the block being removed; and in the other an array of areas in a central part of the study region was eliminated (see Table **6** and Fig. 7).

4.5. Scenario 4 – The contribution to population persistence of areas of forest excluded from timber harvesting

The various estimates of extinction probability derived from the simulations completed in Scenario 4 are presented in Table 7. The results of our analyses indicated that the addition of areas of excluded forest to the patch structure (*i.e.*, steep and rocky areas and forest in streamside reserves) typically did not make a significant contribution to population persistence until the simulations had been run for **a** prolonged period

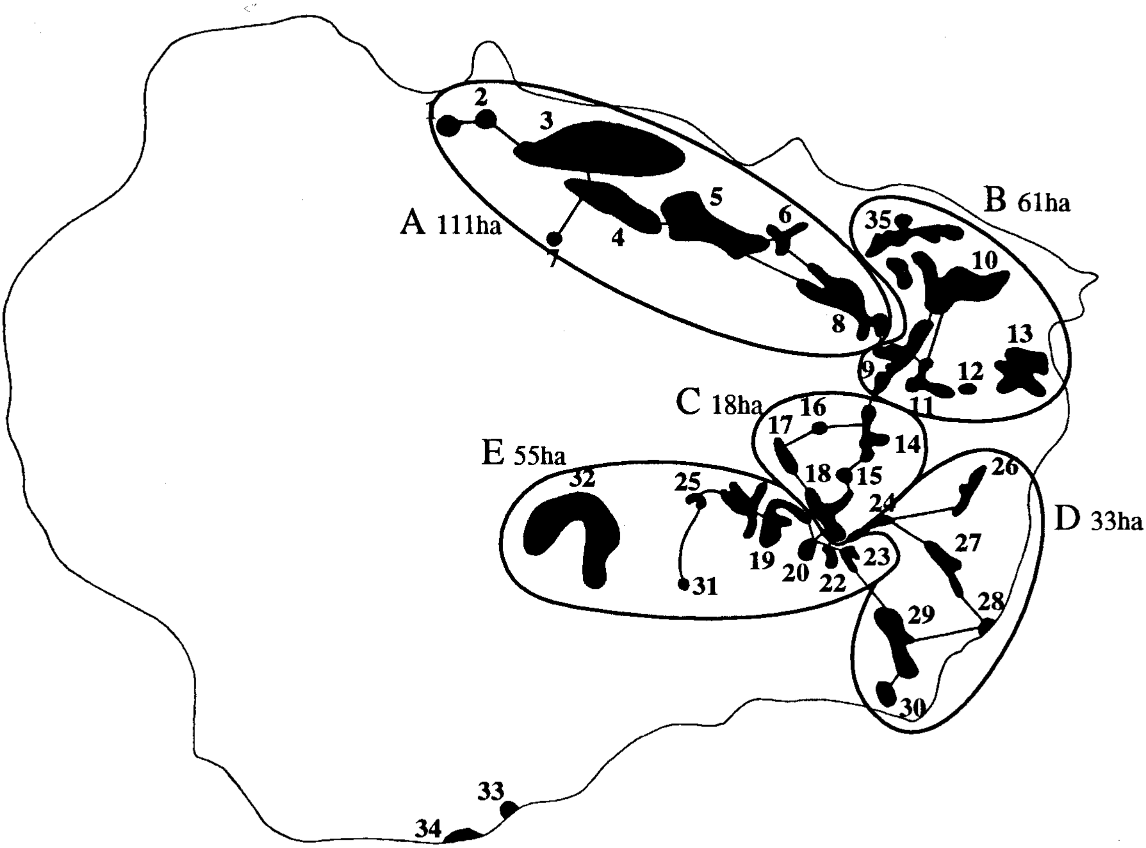

Fig. 7. The constellations of areas of old growth forest that were deleted from the patch structure in simulations of the persistence of populations of G. *leadbeateri* in the Steavenson Forest Block (see Scenario *3).* The letters correspond to a particular group of patches that were deleted from the old growth patch structure and are the same as those given in Table 6.

(300 years or longer). In these cases, the range of values for the extinction probability was usually lower in simulations where the habitat quality of the excluded areas was highest and the impacts of fires were excluded from the analyses (Table 7).

4.6. *Scenario 5 – **The impact of the dispersal capability on estimates of extinction probability***

A number of trends in our data were common to the results of analyses of both the Ada and Steavenson Forest Blocks. In particular, the values for the predicted and steady state probabilities of extinction were significantly lower when animals could travel further before they died (Table 8 and Table 9). However, the results were also influenced by the extent of the patch structure that was modelled and the fire regimes that were invoked (Table 8, Table 9, Figs. 8 and 9). The largest reductions in extinction probability were recorded when wildfires were not modelled and high values for the mean migration were invoked (*e.g.* > I km). Under these conditions, the addition of the logging exclusions depressed the values for the predicted and steady state probabilities of extinction significantly below those generated from a patch structure comprised of areas of old growth forest alone (Table 8, Fig. 8).

4.7. *Scenario 6 – **The relationships between migration, diffusion and population persistence***

Table 10 contains the values for the predicted and steady state probabilities of extinction of G. ***leadbeateri*** within the Ada Forest Block in response to variations in migration and diffusion. As expected, the values for the extinction probability were lowest when both the mean migration distance was relatively long (*e.g.* > 1 km) and the diffusion sub-model within

Table 7. The predicted probability of extinction of populations of G. *leadbeateri* in the Ada and Steavenson Forest Blocks in response to differences in fire regimes and the quality of the habitat assigned to forest patches on steep and rocky areas and in streamside areas that were incorporated in the patch structure that was modelled. Values are presented for the predicted probability of extinction after 150 and 300 years (P_{150}; P_{300}) and the steady state probability of extinction ($P[S]_{150}$; see text for the methods used to calculate this measure). A different index of habitat quality has been used for each row of values in Sections 1–4. The patch structure was limited to stands of old growth in simulations where logging exclusions were not modelled. In the other rows the quality of the habitat in the logging exclusions was 20% and 50% of that of old growth forest (*i.e.* 0.03 and 0.15 respectively; see text). The fire regime that was applied was a 1% annual probability of a wildfire with 75% of patches burnt in a given conflaeration.

Habitat quality value	$P[E]_{150}$	$P[E]_{300}$	$PS_{[150]}$
Section 1 – Ada Forest Block, no fires			
Non exclusions not modelled	32	62	44
0.03	32	62	44
0.15	30	55	36
*Section 2 – Ada Forest Block, with fires**			
No exclusions	74	96	84
0.03	72	95	82
0.15	74	95	81
Section 3 – Steavenson Forest Block, no fires			
No exclusions	2	5	3
0.03	0	1	1
0.15	0	0	< 1
*Section 4 – Steavenson Forest Block, with fires**			
No exclusions	41	77	58
0.03	44	74	54
0.15	44	70	47

*The fire regime employed was an annual probability of a fire of 1% and 75% of patches burnt in a fire.

Table 8. Values for the steady probability of extinction ($P[S]_{150}$), and the predicted probability of extinction after 150 years ($P[E]_{150}$) and 300 years ($P[E]_{300}$) of populations of ***G.*** *leadbeuteri* in the Ada Forest Block in response to variations in the mean distance (km) that animals travel before they die during dispersal. The annual probability of wildfire in these simulations was 1%.

*Section **A** – only old growth patches modelled*

	Mean migration distance (km)				
	0.1	0.5	1.0	2.0	100
No fire					
$P[E]_{150}$	69	62	48	32	13
$P[E]_{300}$	94	90	81	62	26
$P[S]_{150}$	81	74	64	44	18
75% of patches burnt in a fire					
$P[E]_{150}$	91	88	83	78	61
$P[E]_{300}$	100	100	99	98	91
$P[S]_{150}$	100	100	93	85	77

Section B – old growth patches and exclusions modelled

	Mean migration distance (km)				
	0.1	0.5	1.0	2.0	100
No fire					
$P[E]_{150}$	69	63	48	32	12
$P[E]_{300}$	94	92	77	55	16
$P[S]_{150}$	81	77	56	34	5
75% of patches burnt in a fire					
$P[E]_{150}$	94	88	83	75	61
$P[E]_{300}$	100	100	98	95	87
$P[S]_{150}$	100	100	88	80	67

ALEX was applied (Table 10). **A** comparison of the extinction probability generated under these conditions with those recorded from the other simulations, highlighted the relative importance of migration and diffusion. There was a more substantial increase in the predicted and steady state probabilities of extinction associated with a reduction in the migration distance than if movement by diffusion was prevented. Thus, the results of analyses suggested that in our model, migration had a more significant impact on population persistence than diffusion.

Trends from simulations of the Steavenson Forest Block indicated that: (1) G. ***leadbeuteri*** was most likely to persist when both the migration and diffusion sub-models were invoked, (2) the highest extinction probabilities were recorded when neither form of movement was employed, and ***(3)*** the use of a more moderate fire regime resulted in lower values for the steady state probability of extinction, irrespective of the combination of movement parameters that was modelled (Table 11). Finally, as in the analysis of the Ada Forest Block, changes in migration had a greater impact on the likelihood of extinction than diffusion.

Table 9. Estimates of extinction vulnerability of populations of G. *leadbeateri* in the Steavenson Forest Block in response to variations in the mean distance (km) that animals travel before they die during dispersal. There are two rows of values associated with each set of simulations. The top row of numbers in each set of values corresponds to the predicted probability of extinction after 150 years. The second row contains the values for the steady state probability of extinction. The annual probability of fire for these simulations was 1%.

Fire regime patches burnt (%)	Mean migration distance (km)				
	0.1	0.5	1.0	2.0	100
Section A – Only old growth patches modelled					
	Predicted & steady state extinction probability				
50%	51	41	30	19	05
	68	63	48	38	27
75%	62	60	55	48	31
	68	73	70	66	54
Section B – Simulations with old growth patches and exclusions					
	Predicted & steady state extinction probability				
50%	44	38	26	13	06
	67	53	43	29	21
75%	66	57	54	39	28
	76	66	60	55	41

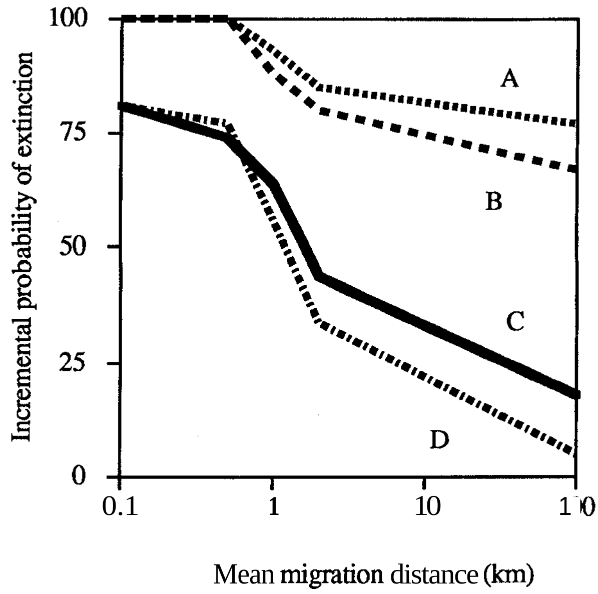

Fig. 8. The inter-relationships between estimates of the incremental probability of extinction of populations of G. *leadbeateri* in the Ada Forest Block and the distance travelled by juvenile females before they died (km). The values presented are for simulations where: (1) the patch structure was comprised only of areas of old growth forest and the annual probability of a wildfire was 1% with 75% of patches burnt (Line A); (2) a combination of areas of old growth forest and stands of excluded forest (see text) formed the patch structure and the annual probability of a wildfire was 1% with 75% of patches burnt (Line B); (3) the patch structure was comprised only of areas of old growth forest and there were no wildfires (Line *C*); and, (4) a combination of areas of old growth forest and stands of excluded forest formed the patch structure and there were no wildfires (Line D).

This can be seen from an inspection of Table 11. In simulations where an average of 50% of habitat patches were burnt in a wildfire, the steady state probability of extinction increased from 29% when both migration and diffusion were invoked, to 68% if migration was halted. However, when movement was limited to only diffusion, the corresponding increase in the steady state probability of extinction was 15% ($P[I]_{150} = 44\%$; see Table 11).

5. Discussion

5.1. Scenario 1 – The estimation of metapopulation persistence in the study areas

Our analyses revealed large differences in the probability of extinction between the two wood production forest blocks that were modelled (Table 2). This result was expected as there are major differences in the amount and spatial configuration of old growth patches in the two areas (compare Figs. 2 and *3*). The values for the predicted probability of extinction of G. *leadbeateri* in the Ada Forest Block over the next 150–300 years were substantial, even in the absence of the impacts of wildfires (Table 2). These findings highlight a concern for the long-term prospects for the survival of the species in many areas of its present distribution. This is because: (1) unpublished forest inventory information gathered by the Victorian Department of Conservation and Natural Resources indicates that the area of old growth montane ash forest which presently occurs within the Ada Forest Block is typical of the majority of other blocks in the Central Highlands of Victoria, and (2) the Steavenson Forest Block contains more old growth forest than other wood production forest blocks in the region.

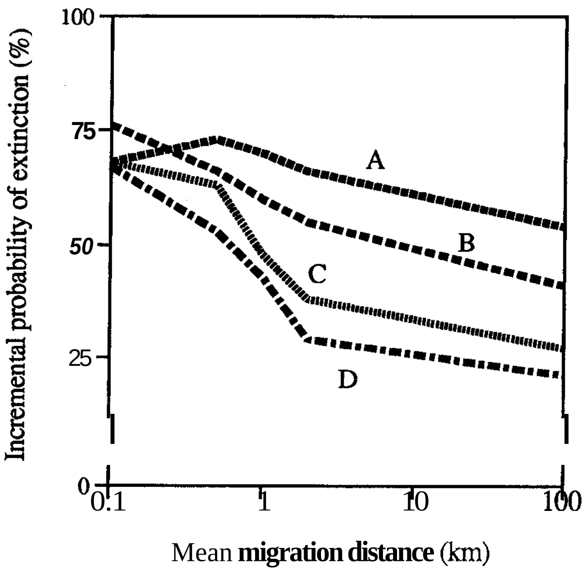

Fig. 9. The inter-relationships between estimates of the steady state probability of extinction of populations of G. *leadbeateri* in the Steavenson Forest Block and the distance travelled by juvenile females before they died (km). Lines A and B represent values where the annual probability of a wildfire was 1% and 75% of patches were burnt in each conflagration. Line A represents the values from simulations where the patch structure was limited to areas of old growth forest. Those from a more extensive patch structure comprised of areas of both logging exclusions and old growth forest are depicted in Line B. Lines *C* and D contain the values for the steady state probability of extinction resulting from a fire regime where the annual probability of a wildfire was 1% and 50% of patches were burnt in such catastrophic events. The results are presented for patches of old growth only (Line C) and a patch structure consisting of logging exclusions and areas of old growth forest (Line D).

Table 10. The impacts of diffusion coupled with different combinations of values of migration on the predicted and steady state probabilities of extinction of populations of G. *leadbeateri* in the Ada Forest Block. No impacts of wildfire were incorporated in the analyses. The patch structure used in the simulations was limited to stands of old growth forest.

		Diffusion	
		Yes	No
Probability of extinction after 150 years			
	2	28	43
Migration value (km)	0.2	70	92
Steady state probability of extinction			
	2	41	54
Migration value (km)	0.2	77	> 92

Table 11. The impacts of different combinations of values of migration and diffusion on the steady state probability of extinction of populations of G. *leadbeateri* in the Steavenson Forest Block. The mean migration distance was 2 km. The patch structure used in these simulations was comprised only of stands of old growth forest.

		Diffusion invoked	
		Yes	No
50% of habitat patches burnt			
	Yes	29	44
Migration invoked	No	68	79
75% of habitat patches burnt			
	Yes	55	62
Migration invoked	No	68	92

*5.2. Scenarios **2** and 3 – Patch deletion analyses and population persistence*

The results of Scenarios 2 and **3**, where areas of old growth forest were deleted from the patch structures in the Ada and Steavenson Forest Blocks, produced a number of interesting findings. An important outcome from these analyses was that both the size and spatial location of a patch significantly influenced the proportion of the time that it remained occupied, as well as the impacts on population persistence resulting from its deletion.

Although the Steavenson Forest Block contained more old growth forest than the Ada Forest Block (280 ha vs 160 ha), there were also significant differences in the spatial configuration of the habitat patches in the two areas (compare Figs. 2 and ***3)***. In the case of the Ada Forest Block, the mosaic of areas of suitable habitat was characterised by a number of loose, spatially isolated, constellations of patches (Fig. 2). Under this arrangement there were: (1) many patches which remained empty for a large proportion of the time, and, (2) a small number of patches that were crucial for population persistence, and when removed, significantly elevated the probability of extinction. In contrast, the patches of old growth forest in the Steavenson Forest Block were well connected and located relatively close together (Fig. 3). Here, we recorded high rates of patch occupancy and even the very small areas (*e.g.* those < one ha) were often occupied. Notably, the mean value for the occupancy of one ha areas in the Ada Forest Block was **6%** (n = 3), whereas the equivalent measure for such patches in Steavenson Forest Block was approximately 19% (n = 7). The differences between the two study blocks have added significance because we applied a wildfire regime in the analyses of the Steavenson Forest Block, but simulations Ada Forest Block were completed without the impacts of such events.

The results from the Steavenson Forest Block suggested the existence of a type of "rescue-effect'' (see Brown and Kodric-Brown 1978; A.T. Smith 1980; Hanski 1994) where dispersing animals reversed localised extinctions in particular habitat patches and/or supplemented populations of animals in such areas and reduced the incidence of localised extinction. Another important contrast in our results was the effect of patch deletion on the predicted probability of extinction. Unlike the Ada Forest Block, no single patch or suite of patches in the Steavenson Forest Block was pivotal to the persistence of populations of G. *leadbeateri*. This was because each given habitat patch was close to, or connected with, an array of other patches (Fig. 3). Thus, the removal of individual patches of old growth forest did not substantially disrupt the patch structure. As a result, there was no subsequent increase in the isolation of the remaining areas of habitat or a corresponding negative impact on extinction probability. This was highlighted by the results of our analyses which indicated that largest increase associated with the deletion of an individual patch of old growth forest was only 12% (Table 5). Indeed, the deletion impact associated with loss of the single largest patch in the Steavenson Forest Block (patch #3 [38 ha]) was < one-tenth of that resulting from the removal of the biggest patches in the Ada Forest Block (patch #12 and 14 = 32 ha).

5.3. *Scenarios 4, 5 and 6 – The inter-relationships between the extent of the patch structure, migration, diffusion and population persistence*

The results of our analyses indicated that stands of forest on steep and rocky terrain and in streamside reserves, when added to an old growth patch structure, had a significant positive impact on the persistence of populations of G. *leadbeateri,* particularly in the absence of catastrophic events like wildfire and when high values for movement capability were invoked (Tables 7, 8 and 9). As expected, the likelihood of extinction was reduced if the value of habitat quality index for logging exclusions was increased (Table 7). However, the benefits of a more extensive patch structure comprised of areas of higher quality habitat, were often not recorded until our simulations had run for a prolonged period (> 300 years). This was because areas of excluded forest presently support stands of regrowth montane ash forest that are < 55 years old and there will be a delay of at least 100 years until these stands begin to develop potentially suitable habitat for G. *leadbeateri* (Lindenmayer *et al*. 1991c). Thus, in the case of G. *leadbeateri,* and possibly other species which utilise old growth forest or structural elements characteristic of such stands, the greatest risks of extinction may occur *after* areas of forest have been set aside for their conservation. This is because of the extended period needed for appropriate stands structures (*e.g.* trees with hollows) to develop, and, in turn the prolonged interval until reserved habitat becomes suitable. In addition, wildfires will retard the recruitment of suitable habitat for G. *leadbeateri* by setting back the succesional stage of the forest (Lindenmayer *et al*. 1993d), particularly if they occur frequently (*e.g.* every 150 years or less). This was reflected by the significantly higher values for the predicted and steady state probabilities of extinction that were recorded from scenarios where wildfires were modelled in comparison with simulations in which such events were excluded from the analysis.

The results of our analyses indicated that changes in migration had a consideraby greater impact on population persistence than modifications in diffusion. The survival of migrating animals (juvenile females in the case of G. *leadbeateri)* was strongly influenced by the distance that can be travelled before animals die. This was highlighted by the results of analyses where we varied the mean migration distance (Tables 8–10). Thus, constraining migration would lead to a reduction in the probability that an animal would contact a suitable habitat patch, resulting in a concomitant increase in juvenile mortality, and, in turn, a weaker rescue effect. Conversely, changing the probability of diffusion has no impact on mortality (see above). This would account for the less pronounced effects on estimates of population persistence associated with variations in diffusion, than were observed with modifications to the migration sub-model in ALEX (Table 10 and Table 11).

There are important inter-relationships between the animal movement, habitat patchiness and the probability of extinction. This is because the mortality of dispersing animals is not only a function of movement capability, but also the number, size and distance between habitat patches (*e.g.* Lande 1988; Lamberson *et al.* 1992, 1994). This is illustrated by a comparison of the extinction probabilities from the two forest blocks. The Steavenson Forest Block was characterised by more patches of old growth forest that were larger and better connected than those in the Ada Forest Block (compare Figs. 2 and *3).* The effects of this are reflected by the fact that, although simulations of the Ada Forest Block were completed without the impacts of wildfires, the steady state probabilities of extinction were almost always higher than the corresponding values for the Steavenson Forest Block where fire regimes were applied.

Reductions in extinction probability associated with increasing migration distance were sensitive to the fire regime that was employed, and the change in these values were more pronounced when 50% of patches were burnt in a wildfire (see Table 9). Under more intensive fire regimes, the reduction in the predicted and steady state probabilities of extinction was less pronounced. It is likely that this outcome was due to temporal changes in habitat suitability resulting from repeated fire events. Where wildfires are less extensive, there is an increased probability that an area of forest will eventually provide suitable habitat for *G. leadbeuteri*. Migration will be important under such conditions as it will facilitate the re-colonisation of patches once they develop suitable habitat for the species. Conversely, it will be less effective when there is a high intensity fire regime because habitat patches will be unsuitable for a greater proportion of the time.

6. Some implications of the results for forest and wildlife management

The results of this study may have some important implications for the development of strategies for the conservation of G. *leadbeuteri* in wood production montane ash forests. We recorded high values for the probability of extinction of populations of the species in many of our simulations, even in those scenarios where unrealistically large distances for the dispersal capability were invoked (*e.g.* 100 km). These findings were related, in part, to the limited amount of suitable old growth habitat for G. *leadbeateri* which presently occurs in the forest blocks that were modelled. Hence, it is possible that there is insufficient suitable habitat in either area to support populations of G. *leadbeateri* in the long-term, particularly if a wildfire were to occur. Notably, the conservation problems created by the limited area of old growth forest within various wood production blocks is also likely to threaten the persistence of a number of other species of arboreal marsupials such as the Greater Glider *(Petauroides volans*) and the Mountain Brushtail Possum (*Trichosurus caninus*) that are reliant upon key attributes of old growth forest such as very trees with hollows (Lindenmayer and Lacy 1993, 1995; Lacy and Lindenmayer 1995; Possingham *et al.* 1994). Therefore, current prescriptions that reserve areas of old growth forest from logging should be maintained (Macfarlane and Seebeck 1991) to prevent any further decline in the amount of such important types of forest.

The results of our analyses highlight a need to create more extensive areas of suitable forest for G. *leadbeateri* to enhance the long-term survival prospects of the species in the various wood production forest blocks which comprise more than 75% of its distribution. This will be particularly important given that: (1) timber harvesting operations have the potential to create large areas of forest that are unsuitable for G. *leadbeateri* (Lindenmayer 1992a, 1992b, 1994a), and, (2) many wood production blocks in the montane ash forests of Victoria support a considerably smaller total area of old growth forest than presently occur in the two blocks that we investigated. The establishment of more areas of habitat will require the exclusion of wood production from existing stands of regrowth forest that are presently available for timber harvesting and allowing them to develop into potentially suitable old growth forest. Other strategies may be useful such as: (1) the reservation of forest that adjoins, and thus eventually increases the size of, existing old growth patches; and, (2) taking steps to ensure that habitat patches are not spatially isolated from each other.

The results of our analyses suggested that the persistence of populations of G. *leadbeateri* was enhanced when we added logging exclusions to the patch structure, particularly if such areas remain undisturbed and develop into old growth forest. These findings indicate that there is merit in continuing present strategies to set aside wildlife corridors and other retained areas within wood production areas (Department of Conservation, Forests and Lands 1989; Macfarlane and Seebeck 1991). However, such procedures should also consider other aspects of landscape patchiness because the effectiveness of retained systems is highly correlated with the size and status of habitat patches that are connected (Noss 1987, 1991; Lindenmayer 1994b), as was demonstrated by the differences between the results of our analyses of the two forest blocks in this investigation (see Scenario 1). In the case of G. *leadbeateri*, logging exclusions could have value in both facilitating movement and providing habitat for the species. The results of sensitivity analyses that were completed in this study indicated that estimates of the probability of extinction of G. *leadbeateri* varied considerably in response to differences in the values for movement capability that were modelled. This outcome has highlighted the need for data on the dispersal behaviour of the species. Indeed, such information will be valuable because it could influence the design of management strategies for G. *leadbeateri* (Lindenmayer 1994b). For example, if the species disperses in a random direction as occurs in some forest vertebrates (*e.g.* Northern Spotted Owl, *Strix occiddentalis caurina;* Simberloff *et al.* 1992), strips of retained habitat may only be of limited value in facilitating movement (Murphy and Noon 1992). Conversely, such areas may be important if the dispersal of G. *leadbeateri* is influenced by factors such as habitat suitability, as is believed to occur in several other species of mammals (*e.g.* Garrett and Franklin 1988; Lorenz and Barrett 1990; Nelson 1993). On this basis, we consider that there may be merit in completing an integrated study where the demographic and genetic status of subpopulations of G. *leadbeateri* occupying different habitat patches is assessed. This information could be used to monitor the prevalence of effective dispersal events and, in turn, determine if they are correlated with the spatial arrangement of, and connectivity between, habitat patches at a landscape scale. Such an approach may also be useful for investigating recolonization dynamics in habitat patches.

An important recurrent them arising from our study was that *both* the amount of remaining suitable habitat and how it was spatially arranged had a significant effect on the persistence of populations of G. *leadbeateri*. These types of anlyses can be most important for forest management as they can highlight the variation in value for species persistence of different habitat patches and help identify those which areas are important for wildlife conservation. The findings of our study also emphasize the importance for modelling metapopulation dynamics of obtaining accurate spatial information on the size and position of habitat patches and, in turn, demonstrates the potential value of GIs-generated data for estimating extinction risks (Akçakaya *et al.* 1995). They also highlight the need for a good understanding of the habitat requirements of the target taxon as a pre-requisite for defining what part of a landscape constitutes actual patches of suitable habitat.

Predictions of the dynamics of wildlife populations can be valuable as they can help managers anticipate, and plan proactively for, trends in population behaviour (Lindenmayer *et al.* 1993e). Unfortunately, to our knowledge, predictions from PVA are rarely, if ever, extensively tested in the field. Given this, it will be important to build on the findings of this study and test the predictions using field sampling. This will be a major task because field surveys for G. *leadbeateri* require considerable effort and expense (Lindenmayer 1989; Lindenmayer *et al.* 1991b). However, such an investigation will be valuable. For example, it will allow us to compare the actual field results for the occupancy by G. *leadbeateri* with predictions derived from simulation modelling.

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Appendix 1

A description of the sub-models in ALEX that were used to track temporal variations in habitat suitability within different types of habitat patches and in response to wildfires

1. Baseline models

Two factors influence the quality of habitat for G. *leadbeateri* – the availability of food and the abundance of trees with hollows (Lindenmayer *et al.* 1991b). We modelled the dynamics of three habitat variables, the first reflects food availability, the second corresponds to the abundance of living trees with hollows, and the third relates to the abundance of dead and/or senescent hollow-bearing trees. ALEX tracks the dynamics of all three habitat variables for each patch and integrates them into an overall measure of habitat quality. The reciprocal of habitat quality is the minimum area required for a breeding female, which in this study was a maximum of one adult breeding female G. *leadbeateri* per ha. For example, 12 females can breed in a 60 ha patch with a habitat quality value of 0.2

2. The dynamics of key habitat components (foraging substrates and nesting resources)

2.1. Habitat variable one – the availability of food for G. leadbeateri

Habitat variable one, $H_1(t)$ is a measure of the availability of food for G. *leadbeateri,* particularly the basal area of *Acacia* spp., t years after a fire. After each wildfire, the trajectory of this variable is described by the equation:

$$
\begin{aligned}
H_1(t+1) &= 0 && 0 \le t < 15\\
&= (t-15)/20 && 15 \le t < 35\\
&= 1 && 35 \le t < 60\\
&= 1-0.7(t-60)/40 && 60 \le t < 100\\
&= 0.3 && t \ge 100
\end{aligned}
\qquad \text{(A1)}
$$

2.2. Habitat variable two – the abundance of cavities in living trees

Habitat variable two, $H_2(t)$, is a measure of the availability of hollows in mature living trees, t years after a fire. We have assumed that $H_2(t)$ takes a maximum value of 100. Its dynamics after a fire are:

$$
\begin{aligned}
H_2(1) &= 0.15{*}H_2(0)\\
H_2(t+1) &= 0.995{*}H_2(t) && 1 \le t < 150\\
&= 0.995H_2(t) + 1.6(t-150)/150) && 150 \le t.
\end{aligned}
\qquad \text{(A2)}
$$

2.3. Habitat variable three – the abundance of hollows in highly senescent and dead trees

Habitat variable three, $H_3(t)$, is the availability of hollows in senescent or dead trees in year t. After a fire all existing dead and senescent trees are burnt and some may collapse. However, the number of hollows in this category of trees may increase substantially after a fire because mature living trees may be badly damaged or killed by such events. The dynamics of this variable can be described as follows:

$$
\begin{aligned}
H_3(1) &= 5{*}H_2(0)\\
H_3(t+1) &= 0.96H_3(t) + 0.02H_2(t) && t \ge 1.
\end{aligned}
\qquad \text{(A3)}
$$

At equilibrium, $H_2(t) = 100$ (*i.e.,* the abundance of hollows is capped at this value), and from equation **A3;** $H_3(t) = 50$.

2.4. Integrating the habitat variables to derive a habitat suitability index

The total habitat quality, t years after a fire, is the minimum of $H_1(t)$ and $(H_2(t) + H_3(t))/100$. Thus, either the availability of food or the abundance of hollows in trees may limit the minimum size of a breeding territory for G. *leadbeateri*. For patches of old-growth forest we have assumed that the time since the last fire is sufficient to ensure that the abundance of hollows is not a limiting factor but availability of food is; $H_1(t) = 0.3$.