Modelling The Impacts Of Wildfire On The Viability Of Metapopulations Of The Endangered Australian Species Of Arboreal Marsupial, Leadbeater's Possum

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Abstract

Catastrophic events such as intensive wildfires have a major effect on the dynamics of some wildlife populations. In this investigation, the computer package ALEX (Analysis of the Likelihood of Extinction), was used to simulate the impacts of wildfires on the persistence of metapopulations of the endangered species Leadbeater's possum (*Gymnobelideus leadbeateri*) which is restricted to the montane ash forests of the Central Highlands of Victoria. A range of scenarios was examined. First, the response of *G. leadbeateri* to tires in hypothetical patches of old growth forest of varying size was modelled. Metapopulation dynamics were then modelled in four existing forest management areas: the O'Shannassy Water Catchment and the Steavenson, Ada and Murrindindi Forest Blocks using GIS-derived forest inventory data on complex spatial arrangements of potentially suitable old growth habitat patches. The impacts of different fire frequencies and the proportion of forest area that was burnt in the Steavenson Forest Block and the O'Shannassy Water Catchment were examined. Finally, the combined impacts of both wildfires and post-fire salvage logging operations on the persistence of populations of *G. leadbeateri* were assessed. Our analyses indicated that, even in the absence of wildfires, populations of *G. leadbeateri* are very susceptible to extinction within single isolated habitat patches of 20 ha or less. The probability of persistence approached 100% in patches of 250 ha. The incorporation of the effects of wildfire was predicted to have a major negative impact on isolated populations of *G. leadbeateri*. In these cases, the probability of population extinction remained above 60%, even when a single patch of 1200 ha of old growth forest was modelled. In the absence of wildfires, there was a low probability of extinction of *G. leadbeateri* in the O'Shannassy Water Catchment where very large patches of old growth forest presently exist. The risk of extinction of the species was significantly higher in the Murrindindi and Ada Forest Blocks where there are lower total areas of, and significantly smaller, suitable habitat patches. Wildfires resulted in an increase in the predicted probability of metapopulation extinction in the four areas that were targeted for study. An investigation of the Steavenson Forest Block and the O'Shannassy Water Catchment revealed that the predicted values for the probability of extinction were sensitive to inter-relationships between the frequency of fires and the proportion of habitat patches that were burnt during a given fire event. The probability of extinction of *G. leadbeateri* was predicted to be lowest when there were frequent fires that burnt only relatively small areas of a given forest block. Conversely, the results of our analyses suggested that populations of the species are vulnerable to infrequent but intensive conflagrations that burnt a large proportion of the forest. The results of the suite of analyses completed in this study suggest hat four management strategies will be important for the long-term conservation of *G. leadbeateri*. (1) Attempts to suppress wildfires should be maintained as even the largest remaining areas of old growth forest may be susceptible to being burnt by repeated widespread wildfires that could result in localised and/or global extinction of the species. (2) Because the probability of population persistence is greatest in those areas that support more extensive stands of old growth forest, it will be important to grow relatively large patches of existing regrowth forest (over 50 ha) through to ecological maturity. This will be particularly important in some wood production forest blocks where there are only limited areas of old growth forest. (3) Patches that are set aside for the conservation of *G. leadbeateri* should be spatially separated to minimise the risk that all of the reserved areas in a region are destroyed in a single major fire event. (4) Salvage logging operations should be excluded from stands of old growth forest and reserved areas that are burnt in a wildfire. This is because such activities can have a major negative impact of the development of suitable habitat for *G. leadbeateri*.

1. Introduction

Catastrophes such as diseases, floods and fires are extreme events which occur randomly and may have a major impact on wildlife populations (Soulé and Simberloff, 1986; Lacy and Clark, 1990; Catling, 1991; Durant and Harwood, 1992). They can result in a direct reduction in animal abundance (Clark, 1989) and/or produce significant long-term changes in habitat suitability with corresponding implications for population dynamics (Menges, 1990; Possingham et al., 1994). The published literature contains many cases where catastrophes have influenced the processes of species decline and/or extinction. For example, fires and windstorms were two of a plethora of interacting factors that contributed to the demise of the Heath Hen, *Tympanuchus cupido cupido* (Simberloff, 1986, 1988). Given the potentially important effects of catastrophes on population persistence, modelling and predicting the impacts of such events is valuable for attempts to conserve and manage endangered species (Ewens et al., 1987; Lacy et al., 1989; Burgman et al., 1993). For example, studies of the viability of the Puerto Rican Parrot, *Amazona vitatta*, indicated that a hurricane was likely to have a significant negative impact on the remaining population (Lacy et al., 1989). A hurricane struck Puerto Rico soon after the completion of the study and killed many individuals from the small population of *A.vitatta* (Lacy and Clark, 1990). Management recommendations that were made on the basis of the results of population viability analysis (PVA) (Lacy et al., 1989), such as the provision of protected captive-breeding pens, may have enhanced attempts to conserve this species.

In this paper, a computer model was used to simulate the impacts of wildfires on metapopulations of the endangered forest-dependent arboreal marsupial, Leadbeater's Possum, *Gymnobelideus leadbeateri* McCoy in the Central Highlands of Victoria, southeastern Australia, There have been several major fires in the region over the past 150 years (Noble, 1977; Lindenmayer et al., 1991a), and they have had a significant effect on vegetation structure in the area (Griffiths, 1992). They have also significantly influenced the suitability of these forests as habitat for *G. leadbeateri* (Lindenmayer et al., 1991b), as well as the spatial arrangement of habitat patches (e.g. areas of old growth forest) (Lindenmayer et al., 1993b). This investigation examined the relationship between the risk of the extinction of the species and: (1) the size of patches of suitable habitat that are burnt; (2) interactions between the frequency of wildfires and the proportion of habitat patches that are burnt in a fire; (3) disturbance regimes where there are recurrent wildfires; (4) a combination of wildfires and salvage 1ogging operations. To do this we used a range of key types of data that included: (1) detailed information on the habitat requirements and life history attributes of *G. leadbeateri*; (2) GIS-derived forest inventory data on the spatial distribution of potentially suitable habitat patches; (3) a suite of dynamic habitat models that tracked temporal changes in the suitability of habitat patches. The integration of this array of data, particularly the information on the spatial arrangement of patches and temporal changes in their habitat suitability for *G. leadbeateri*, sets this study apart from many others where PVA has been applied to endangered species management. This approach was used in studies of one water catchment and three wood production forest blocks that were characterised by different amounts of suitable remaining old growth forest habitat. The implications of our findings for the development of wildlife conservation strategies are discussed.

2. Methods
2. I. Study areas

Our study focused on the montane ash forests of the Central Highlands of Victoria, southeastern Australia. These forest types in the region contain virtually the entire known distribution of *G. leadbeateri* (Lindenmayer et al., 1989, 1991a). The four areas within the Central Highlands of Victoria that were selected for detailed analysis were the O'Shannassy Water Catchment and the Murrindindi, Ada and Steavenson Forest Blocks (Fig. 1) . The total area of these study sites is approximately 13 290 ha, 3800 ha, 6700 ha and 4490 ha respectively. These areas are dominated by

montane ash forest. The three Forest Blocks are managed for multiple uses including wood and water production, wildlife conservation, recreation, historical values and landscape aesthetics by the Department of Conservation and Natural Resources (Government of Victoria, 1986; Jeremiah and Roob, 1992). The major form of land use in the O'Shannassy Water Catchment is the production of water for the city of Melbourne and timber harvesting has been excluded from the area since 1910 (Land Conservation Council, 1993).
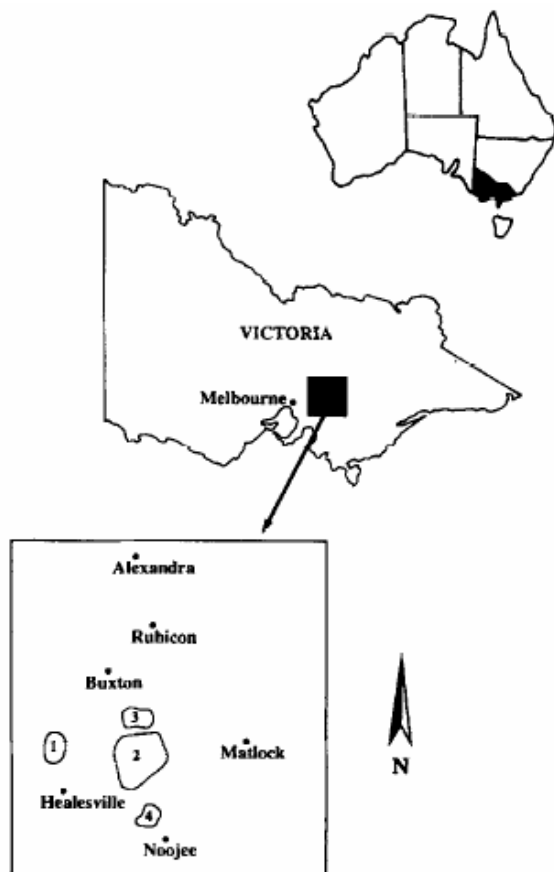

Fig. 1. The location of the three forest blocks and the water catchment that were targeted for detailed analysis. The numbers correspond to a particular study area: (1) Murrindindi Forest Block, (2) O'Shannassy Water Catchment; (3) Steavenson Forest Block; (4) Ada Forest Block.

2.2. Modelling patches of old growth forest

Our investigation focused on the persistence of *G. leadbeateri* within patches of old growth montane ash forest as such areas will become increasingly important refugia for remnant populations of *G. leadbeateri* (Lindenmayer et al., 1990a; Smith and Lindenmayer, 1992; Lindenmayer and Norton, 1993). This is because past wildfires and logging operations have created extensive areas of young, predominantly even-aged forest that are less than 55 years old (Squire et al., 1991). Large trees with hollows provide nest sites for *G. leadbeateri* (Smith and Lindenmayer, et al., 1991c). Most such trees within regrowth forest are large mature stems that were killed or badly damaged by the catastrophic 1939 wildfires. Many are now severely decayed and they are collapsing at a rapid rate (Lindenmayer et al., 1990b, D.B. Lindenmayer et al., unpublished data, 1994). Stands of regrowth forest are predicted to be almost devoid of suitable nest sites within the next 10-30 years (Lindenmayer et al., 1990b, D.B. Lindenmayer et al., unpublished data, 1994).

Table 1
The number of patches of old growth montane ash forest in various size classes in three forest blocks (Murrindindi, Ada and Steavenson Forest Blocks) and the O'Shannassy Water Catchment within the Central Highlands of Victoria, southeastern Australia

	Patch size[a] (ha)	No. of patches
Murrindindi Block	0–1	38
	1–3	6
	Total area (ha)	24
Ada Forest Block	1–3	14
	4–6	4
	7–10	3
	11–14	3
	>14	3
	Total area (ha)	162
Steavenson Forest Block	0–3	141
	3–6	10
	6–9	3
	9–12	2
	12–24	2
	>25	2
	Total area (ha)	264
O'Shannassy Catchment	1–5	6
	6–10	1
	11–15	2
	16–20	5
	21–50	3
	51–100	5
	101–200	2
	201–500	1
	500–1500	2
	>1501[b]	1
	Total area (ha)	6420

[a] Different patch size intervals are given owing to differences in the amount of old growth forest between the various study areas.

[b] The size of this hugest patch is approximately 3530 ha.

There will be a prolonged shortage of nest sites for *G. leadbeateri* until existing 55-year-old trees in regrowth forests reach an age of approximately 200-500 years and become potentially suitable nest sites for the species (Lindenmayer et al., 1991c, 1993a). Given these factors, existing stands of old growth montane ash forest will be those most likely to support sufficient nest sites to meet the habitat and nest tree requirements of *G. leadbeateri* during the next 150 years (see Lindenmayer et al., 1990b, 1991b; Lindenmayer and Gilmore, 1994).

Fig. 2. The old growth patch structure that was used for analyses of the persistence of populations of *G. leadbeateri* in the Murrindindi Forest Block. The solid block polygons correspond to stands of old growth forest. The solid lines are movement corridors that allow animals to 'diffuse' between habitat patches (see text). Each patch of potentially suitable habitat has been assigned a unique identifying number.
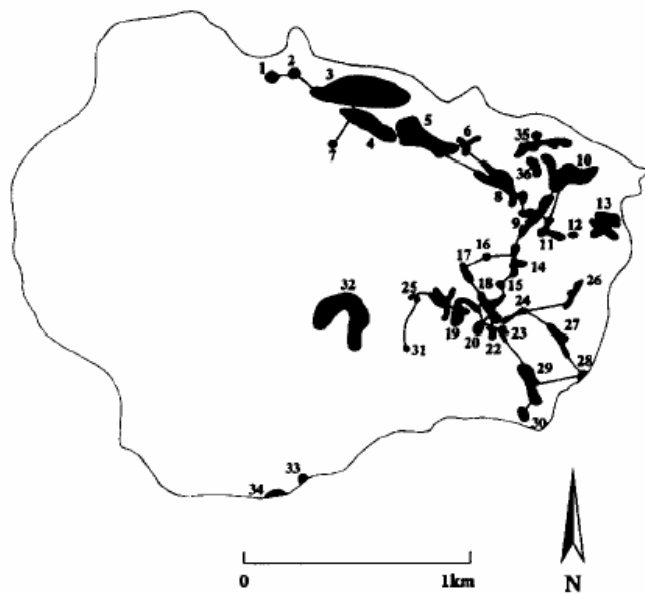

Fig. 3. The old growth patch structure that was used for analyses of the persistence of populations of *G. leadbeateri* in the Steavenson Forest Block. The solid lines are movement corridors that allow animals to 'diffuse' between habitat patches (see text). Each patch of potentially suitable habitat has been assigned a unique identifying number.

Fig. 4. The patch structure that was used for analyses of the persistence of populations of *G. leadbeateri* in the Ada Forest Block. The solid lines are movement corridors that allow animals to 'diffuse' between habitat patches (see text). Each patch of potentially suitable habitat has been assigned a unique identifying number.
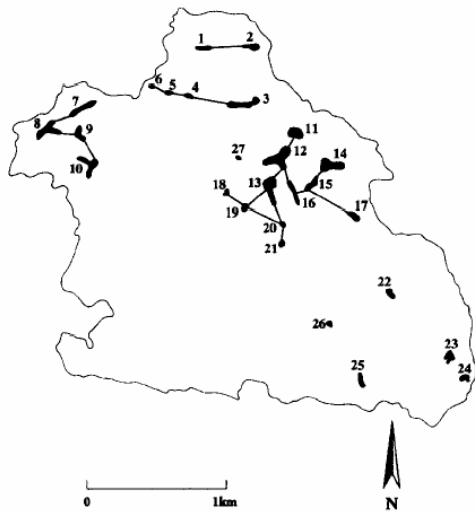

Fig. 5. The patch structure that was used for analyses of the persistence of populations of *G. leadbeateri* persistence of populations of *G. leadbeateri* in the O'Shannassy Water Catchment. Areas of old growth forest are represented by solid black polygons. The blank areas on the map are stands of regrowth montane ash forest or areas that do not support ash-type eucalypt forest.

The amount of old growth montane ash forest in the four study areas varies from approximately 24 ha (Murrindindi Forest Block), 162 ha (Ada Forest Block), 264 ha (Steavenson Forest Block), and over 6420 ha (O'Shannassy Water Catchment) (Table 1, Figs. 2-5). The spatial distribution of various forest age classes has been mapped from field surveys and aerial photography of forest

resources by the Department of Conservation and Natural Resources (e.g. Smith and Woodgate, 1985) and the Melbourne Water Corporation. These data have been stored in a Geographic Information System (GIS) (ARCINFO, ESRI, California) that was developed by the Department of Conservation and Natural Resources. The GIS database was interrogated to derive information on the location and size of patches of old growth montane ash forest. The mapped results of these procedures are presented in Figs. 2-5. A grid was overlaid on the maps of old growth forest and a set of x,y co-ordinates were calculated for the centre of each patch. These co-ordinates, together with the accompanying data on the size of each patch, formed part of the dataset for subsequent analyses. Very small fragments of old growth forest (less than 1 ha) that were adjacent to larger, more contiguous stands, were merged and modelled as a larger connected unit. In addition, we connected pairs of patches that were less than 200 m apart with a 'corridor' that enabled animals to 'diffuse' between such areas (see below). The location of corridors coincided with the spatial location of areas of forest on steep and rocky terrain or in streamside reserves that are typically unavailable for timber harvesting (Department of Conservation, Forest and Lands, 1989; Macfarlane and Seebeck, 1991). These areas were simulated as facilitating dispersal if they connected existing patches of old growth forest but they did not provide sites for animals to inhabit or breed. Extremely small patches (less than 1 ha) that were remote (over 200 m) from other areas of old growth were excluded from the analysis. This was because such areas were assumed to make only a negligible contribution to metapopulation persistence. This assumption was later vindicated by our analyses.

2.3. Computer package used in metapopulation viability analysis

The program ALEX (Version 2.2b) (Analysis of the Likelihood of EXtinction) (Possingham et al., 1992, 1994; Possingham and Davies, 1995) was used in this study. The structure of the program enabled us to model: (1) the complex network of habitat patches that presently exist within blocks of montane ash forests of the Central Highlands of Victoria and (2) temporal changes in vegetation structure and thus habitat patch quality for *G. leadbeateri* in response to wildfires (Appendix 1).

3. Parameters input to ALEX
3. 1. Life history parameters and initial population density estimates

During the past 15 years there have been a number of detailed studies of the biology and ecology of *G. leadbeateri* (Smith, 1980, 1984a,b; Smith and Lindenmayer, 1988, 1992; Lindenmayer, 1989, 1992a,b; Thomas, 1989; Lindenmayer et al., 1990a,b, 1991a-f, 1993c,d). Values for parameters such as the number of female offspring, age at sexual maturity and death, age specific rates of mortality and metapopulation growth rate have been derived from these studies and they were input to ALEX (Table 2). Individuals were assigned to one of three age classes: (1) newborn (under 1 year); sub-adults (1-2 years old): (3) adults (over 2 years old) (Table 2). Detailed surveys of more than 200 field sites (Lindenmayer, 1989; Lindenmayer et al., 1994a) have indicated that there is approximately one reproductively active female *G. leadbeateri* per 6 ha of old growth forest. Because ash-type eucalypts within old-growth forest are predominantly large living stems, there would be only minimal rates of collapse of hollow-bearing trees in such areas (Lindenmayer et al., 1990b). Thus, we incorporated no temporal changes in habitat suitability within old growth patches for the duration of the time horizon used in the analysis.

3.2. Frequency and intensity of wildfires

During the past 250 years there have been many wildfires in the Central Highlands of Victoria including those in 1730 (approximately), 1824, 1851, 1905,1909, 1919, 1926, 1932, 1939, 1948 and 1983 (Noble, 1977; Lindenmayer et al.,1991a; Griffiths, 1992). The impacts of these events have been variable (Banks, 1993) and some have been extensive (e.g. 1939 wildfires; Noble, 1977) whereas others have been limited to relatively small areas (e.g. 1983 fires; Smith and Woodgate, 1985). On this basis, we investigated a wide range of values for fire extent and frequency.

Table 2
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	2 females ha^{-1}
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	2 years
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	2km
Population density before migration (% of maximum)	20%
Migration probability of subadults	70%
Population density before diffusion (% of maximum)	10%
Diffusion probability for subadults	20%

### 3.3 The direct impacts of wildfire on *G. leadbeateri*

The direct impacts of wildfire on populations of *G. leadbeateri* are unknown but they may vary with fire intensity. Inions (1985) found that low intensity fires had a minimal effect on populations of arboreal marsupials in south-western Australia and that some individuals nesting in trees not destroyed by wildfire may survive. Newsome et al. (1975) reported similar findings from studies of forest vertebrates in south-east- New South Wales. However, in such cases animals probably die soon after because of a shortage of food or increased levels of predation. Given this, we assumed that all animals inhabiting patches that were burnt by a wildfire were killed.

3.4. Inter-relationships between wildfires, vegetation structure and habitat suitability

The vegetation structure of montane ash forest is a major factor influencing habitat suitability for *G. leadbeateri* (Lindenmayer, 1989). Lindenmayer et al. (1991b, 1994a,c) derived a logistic regression model of the habitat requirements of *G. leadbeateri* that was based on surveys for the species at more than 200 sites. This model contained two significant explanatory variables: the basal area of *Acacia* spp. in the forest understorey and the abundance of trees with hollows. *Acacia* spp. trees exude gum which is a major source of food for *G. leadbeateri* (Smith, 1984b; Lindenmayer et al., 1994b) and trees with hollows provide den and nest sites for the species (Lindenmayer et al., 1991c). Wildfires influence the suitability of habitat components for *G. leadbeateri* (Smith and Lindenmayer, 1992; Lindenmayer et al., 1993a) and their impact on key stand characteristics is, in part, related to the age of the forest when it is burnt (Lindenmayer et al, 1991a, 1993a). If a fire occurs in a patch of old growth forest, then large ash-type eucalypt trees with hollows that are several hundred years old may be killed or fire-scarred. Such trees are likely to develop cavities that are suitable for use by *G. leadbeateri*. However, the colonisation of the area would be delayed

approximately 20 years until the development of a suitable foraging substrate comprised of an understorey of *Acacia* spp. Most large trees with hollows become highly decayed and eventually collapse within 70 years (Lindenmayer et al., 1990b; D.B. Lindenmayer et al., unpublished data, 1993). Regrowth montane ash forests would then remain virtually devoid of nest sites until new trees are recruited that contain cavities suitable for occupation by *G. leadbeateri*. This process takes 200 or more years (Smith and Lindenmayer, 1988; Lindenmayer et al., 1993a). If areas of young regrowth are burnt by high intensity fires, the damaged or killed stems within the stand will be too small to become suitable trees with hollows. This occurred in 1983 within the Powelltown State Forest when 45-year-old trees were burnt (D.B. Lindenmayer et al., unpublished data, 1993). Thus, if high intensity wildfires recur at intervals of less than 150 years, stands of ash-type trees may never attain a stage that would support stems with hollows. Furthermore, a fire frequency of less than 25-30 years may totally eliminate stands of montane ash forest (Ashton, 1981a,b) because the trees would be killed before they reach sexual maturity (Mount, 1979). In such circumstances, they would be replaced by extensive areas of *Acacia* spp. Low intensity fires in stands of old growth may create multi-aged stands comprised of dense regenerating *Acacia* spp. overtopped by a combination of living fire-scarred and dead hollow-bearing trees. Notably, the extremely wet climatic regimes which characterise montane ash forests (Ashton, 1981a,b; Lindenmayer et al., 1991d) prevents the ignition of fires under most weather conditions. This precludes the prescribed burning as a method to actively create multi-aged stands and promote the development of habitat for *G. leadbeateri*.

 Acacia spp. trees are usually killed by wildfire which eliminates a major food source for *G. leadbeateri*. However, stands of such types of trees quickly regenerate (Adams and Attiwill, 1984) and form a suitable foraging substrate for the species within approximately 20 years. There is a decline in the suitability of the understorey after 60-80 years when most *Acacia* spp. die, although some trees persist in older undisturbed stands of montane ash forest (Adams and Attiwill, 1984).
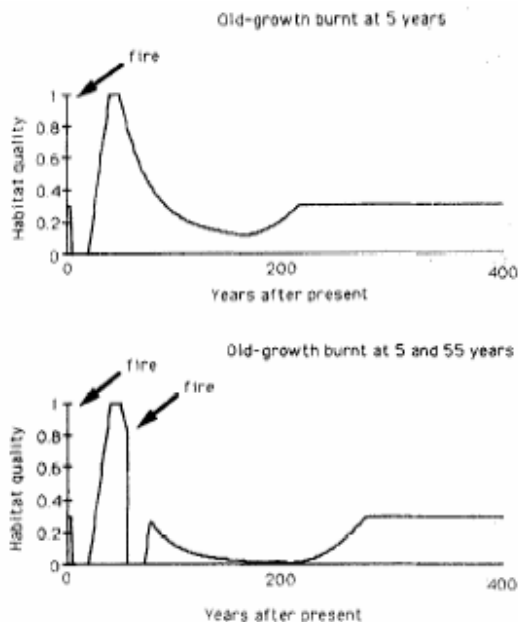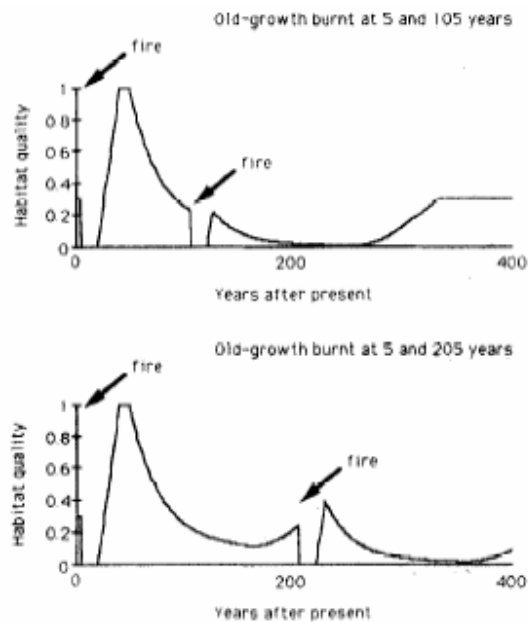
Fig. 6. The response curves for temporal variations in habitat suitability following a wildfire within stands of different ages. The line in each case represents the habitat quality value and corresponds to the maximum abundance of adult breeding female animals per hectare that could occur in the patch (see text and Appendix 1) .

Post-fire salvage logging operations have followed past wildfires in the montane ash forests of the Central Highlands of Victoria (Smith and Woodgate, 1985; McHugh, 1991). Such operations typically result in the clearfelling of all, or nearly all, stems in a burnt stand to produce for timber and pulpwood. Thus, the structure of vegetation that is produced after salvage logging operations is different from that which occurs following disturbance by wildfire alone, particularly with respect to the number of trees with hollows that remain. Indeed, the removal of stems during salvage harvesting operations results in a prolonged period of over 150 years before the recruitment of new trees with hollows that provide potentially suitable nest sites for *G. leadbeateri* (Lindenmayer and Gilmore, 1994). For almost all of the scenarios that were completed in this study, we assumed that patches of old growth forest and other areas of potentially suitable habitat were not salvage logged if they were burnt in a wildfire. In the case of old growth forest, we assumed that approximately 15% of large mature trees in a stand would survive the impacts of a wildfire.

We developed a number of sub-models that describe the inter-relationships between wildfires, vegetation structure, the age of a stand and the abundance of *G. leadbeateri* (Appendix 1, Fig. 6). An additional sub-model was constructed for one of the scenarios where we tested the impacts of post-fire salvage logging operations on the persistence of populations of the species. We have based these relationships on: (1) the response of ash-type eucalypt trees to fire (Noble and Slatyer, 1980; Ashton, 1981a,b; Lindenmayer et al., 1991a,e, 1993a); (2) the time required for montane ash trees to develop cavities suitable for occupation by arboreal marsupials such as G. leadbeateri (Ambrose, 1982; Smith and Lindenmayer, 1988; Lindenmayer et al., 1993a); (3) measured rates of the decay and collapse of trees with hollows in montane ash forests (Lindenmayer, 1989; Lindenmayer et al., 1990b; D.B. Lindenmayer et al., unpublished data, 1993); (4) the dynamics of populations of *Acacia* spp. in response to disturbance (Adams and Attiwill, 1984; Smith and Lindenmayer, 1992). The series of sub-models that was used in our analyses is presented in Appendix 1 and they were incorporated within the sequence of program flow of ALEX to enable us to simulate temporal and spatial variations in habitat suitability for G. leadbeateri. These sub-models tracked the temporal dynamics of key habitat components for the species particularly: (1) the abundance of living trees with hollows; (2) the abundance of dead hollow-bearing trees; (3) the suitability of foraging substrates (i.e. the basal area of *Acacia* spp.). An index

of overall habitat quality with a value between 0 and 1 was derived from the application of the various sub-models (see Appendix 1, Fig. 6) . The reciprocal of this value was the home range required for a *G. leadbeateri* breeding female. For example, if the habitat quality index is 0.2, each adult breeding female requires at least 5 ha of forest.

3.5. Movement between habitat patches
The movement of *G. leadbeateri* between habitat patches was simulated by invoking both the diffusion and migration sub-models within ALEX (see Possingham et al., 1994; Possingham and Davies, 1995). There are limited data on patterns of movement in *G. leadbeateri* and the values used in our study are estimates based on demographic and radio-telemetry studies (Smith, 1980, 1984a; D.B. Lindenmayer et al., unpublished data, 1992). Migration simulated the movement of animals between patches of habitat that were separated by more than 200 m of unsuitable forest. This minimum distance was used because the home range of *G. leadbeateri* is approximately 1-3 ha (Smith, 1980; D.B. Lindenmayer et al., unpublished data, 1992) . Each migrating animal moved from its source patch in a straight line and a random direction. There was an exponential decline in the probability of survival as the inter-patch distance increased. Thus, the probability of survival of any given individual was a function of the size of, and distance to, other suitable patches of habitat. Animals were capable of moving an average of 2 km before they died. This is approximately twice the maximum distance recorded for movements by the species (D.B. Lindenmayer et al., unpublished data, 1992). We limited migration to the sub-adult cohort and the maximum value for the annual probability of migration diffusion was set to 70%. We used these values because Smith (1980, 1984a) found that adult female *G. leadbeateri* enforced the dispersal of their female offspring when they were approximately 12 months old. Migration occurred when the abundance of individuals in a particular patch exceeded 20% of its maximum carrying capacity. For lower population densities, animals would tend to disperse to adjacent unoccupied forest located within the same habitat patch. Our values for the relationship between maximum carrying capacity and migration were based on studies of the mating system and social structure of the species which shows that adult female *G. leadbeateri* are intolerant of adult conspecifics of the same sex (Smith, 1980, 1984a).

The diffusion sub-model in ALEX simulated the movement of animals between neighbouring patches that were less than 200 m apart. It was invoked to model the movement of animals to suitable unoccupied habitat in an adjacent patch. There was no mortality associated with this form of movement and animals were able to diffuse to one new patch in any given year. The maximum number of animals diffusing in any given year was limited by the length of the common boundary of adjacent areas of suitable habitat. The probability of 'diffusion' was set to 20% for subadult females and this accounted for the movement of those animals that did not undergo migration (see above). A value of 10% was used for the adult age cohort to allow some animals to make minor adjustments to location of their territories.

Notably, we completed extensive sensitivity analyses for each of the parameters associated with the simulation of animals moving between habitat patches. A wide range of analyses, incorporating values of plus or minus 50% for the various migration and diffusion parameters, was undertaken, The results of these simulations indicated that for the patch structures examined in this study, our values for the predicted probabilities of extinction were insensitive to variations in migration and diffusion parameters.

3.6. The impacts of environmental variability on *G. leadbeateri*
Environmental variation was modelled in ALEX by sampling a random number from a normal distribution with a specified mean and standard deviation. Environmental variation influenced the probability of reproduction ins any given year but we assumed that it had no effect on other aspects of population dynamics such as rates of mortality. We set the mean value for environmental variation to 0.68 with an associated standard deviation of 0.1. These values corresponded to a failure of *G. leadbeateri* to reproduce in 1 out of 6 years. Such levels of environmental variability

appear to be appropriate given that regular climatic factors such as drought limit the abundance of arthropod prey for *G. leadbeateri*, and result in a major decline in fecundity (Smith, 1980, 1984b).

3.7. Time horizon used in PVA

In several scenarios, the behaviour of metapopulations of *G. leadbeateri* was simulated for a period of 150 years. This is the minimum expected duration of the shortage of nest sites for the species in regrowth montane ash forests (Lindenmayer et al., 1990b; Smith and Lindenmayer, 1992) and the time required for the development of cavities within regrowth trees that are presently 55 years old (Lindenmayer et al., 1991c, 1993a). However, many simulations were run for a period of over 300 years to test the impacts of repeated fire events on the persistence of populations of *G. leadbeateri*. In these cases, we assumed that areas that currently support stands of regrowth forest within wood production forests would be clearfelled at least twice during the next 200-300 years and continue to be unsuitable as habitat for the species. For the O'Shannassy Water Catchment, we assumed that existing areas of regrowth forest, if undisturbed by fire, would eventually provide suitable habitat for *G. leadbeateri*. This was because logging is presently excluded from the water catchments.

3.8. Output data derived from computer simulation modelling

Three measures of extinction risk were generated: the median time to extinction, the probability of quasi-extinction (sensu Ginzburg et al., 1982), and the incremental or 'steady state' probability of extinction. Quasi-extinction is a threshold population size which must be maintained to ensure the long term persistence of the species (Ferson and Burgman, 1990). We considered quasi-extinction to occur when a population was comprised of just two females. This criteria was adopted because: (1) only females are modelled using ALEX and the program is not appropriately equipped to track the dynamics of very small populations, and (2) the impacts of genetic factors were not examined in the analysis and these processes are likely to have a significant effect on populations of this size (Lacy, 1993).

The incremental or steady state probability of extinction was a measure of the likelihood of extinction during a given length of time (usually 150 years) and it was derived by the following method. A value for the probability of extinction was generated for each 150 year time interval of a simulation. This value was a function of amount of population viability (%) lost during that time step relative to the proportion of population viability that had remained at the end of previous time step. The values for 150-300, 300-450 and 450-600 year time steps were then averaged. We used this approach to overcome: (1) the dependence of measures of extinction probability on the corresponding value from the previous time step, and (2) an 'initialization effect' where the results derived in the early parts of a simulation were heavily biased by the patch structure that was used at the start of the analyses. Standard deviations were generated for estimates of the predicted and incremental probabilities of extinction using the formula

$$SD = \sqrt{np(1-p)}$$

where *n* is the number of simulations, and *p* is the probability of extinction during a given time frame (typically 150 years in this study). Thus, for scenarios with 300 runs which was the minimum number that we completed for each scenario, the standard deviation in the extinction probability would be plus or minus 3% or less. Notably, the completion of many runs for each scenario is important to stabilise the output that is derived from computer simulation modelling (see Harris et al., 1987; Maguire and Shaffer, 1988).

4. Scenarios examined in this study

Our study was limited to six scenarios and these were as follows.

4.1. Scenario 1: No wildfire in single isolated old growth patches

In this scenario, estimates of population persistence were derived for hypothetical isolated old growth patches of varying size that were not subjected to wildfires. This phase of the analysis was

completed to give a set of values from which we could subsequently estimate the relative contribution of wildfires to the likelihood of metapopulation extinction.

4.2. Scenario 2: Examining the impacts of wildfire on single isolated patches of old growth forest
Here, the analyses were the same as those in Scenario 1, but the impacts of wildfire were incorporated. The annual probability of a fire was 1% and there was a 75% chance that any given patch was burnt during the fire. These values were equivalent to a wildfire occurring in each habitat patch on average every 133 years. Information from this scenario allowed us to compare the impacts of fire in a single isolated patch with those of subsequent analyses where an ensemble of spatially distributed patches was burnt.

4.3. Scenario 3: The impacts of fire in the four study areas
The impacts of wildfire in the four study areas was examined. These impacts were simulated using the GIS derived old growth patch structures that presently occur in each management area. The frequency of fires and the area of forest that was burnt was the same as applied in Scenario 2.

4.4. Scenario 4: Variations in there frequency and the proportion of patches that were burnt
The relationship between different fire regimes and the probability of species persistence was examined using the existing old growth patch structures in the Steavenson Forest Block. These analyses enabled comparisons to be made between the impacts of a range of different lire regimes where the overall probability that any given old growth patch is burnt in any year remained constant. For this scenario, we varied the annual probability of wildfires from l%, 2% and 4%, giving an average of one conflagration every 100 years, 50 years and 25 years respectively. These rates of fire frequency were modelled in combination with different values for the proportion of patches that were burnt in any given fire event. This was represented as-an annual probability of a fire in a given habitat patch, and the values examined ranged from 0.04 to 0.0002 (see Table 3) . These values corresponded to a mean fire interval in a given patch of 25-5000 years.

4.5. Scenario 5: Modelling the combined impacts of wildfires and post-fire salvage logging operations
In Scenarios 1-4, we assumed that stands of old growth forest that were burnt were both (1) exempt from salvage logging and (2) excluded permanently from timber harvesting and not added to the part of the forest that was generally available for wood production. These conditions were modified in Scenario 5 where we simulated the effects on populations of *G. leadbeateri* of post-fire salvage logging in areas of burnt old growth forest within the Steavenson Forest Block. Some examples of the types of habitat response curves that would associated with this form of perturbation are described in Appendix 1. The annual probability of fire in this scenario was set to 1% and the number of old growth patches burnt in any given wildfire event was 50% and 75%.

4.6. Scenario 6: The impacts of various fire regimes in the O'Shannassy Water Catchment
The impacts of a range of fire regimes were simulated for a mixture of patches of old growth and regrowth forest in the O'Shannassy Water Catchment. We completed detailed analyses for this area because it presently contains the largest remaining patches of old growth forest in the Central Highlands of Victoria. Indeed, most of the old growth forest in the region occurs within this water catchment (Lindenmayer and Gilmore, 1994). Therefore, estimates of the probability of extinction of *G. leadbeateri* in O'Shannassy Water Catchment may provide a good indication of the species overall chances of persistence per se, and hence throughout its known range.

In this scenario, the annual probability of a wildfire was varied from 0-67%, 1% and 1.33%. Values for the proportion of patches burnt in any given fire event ranged from 50%, 75% and 100%. Because salvage harvesting is presently precluded from the O'Shannassy Water Catchment, we modified the sequence of program flow of ALEX to simulate the maturation of existing stands regrowth forest over a period of more than 150 years (see Appendix 1). We excluded the impacts of salvage logging operations from our simulations of the O'Shannassy Water Catchment because recently proposed management strategies have recommended that such

activities should be excluded from the area (Land Conservation Council, 1993). Thus, the patch structure that formed the basis of the analyses completed in this scenario was comprised of 38 patches of old growth forest giving a total of 6420 ha (Table 1) and an additional 35 patches comprising 4920 ha of regrowth ash-type eucalypt forest (Fig. 5).

Table 3
The estimated probability of extinction (%) of populations of *G. leadbeateri* in response to wildfire[a] in the four forest management areas that were targeted for detailed study. For those scenarios where the impacts of wildfires were modelled, there was no added impact of post-tire 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)
Murrindindi Forest Block			
No fire	100	100	10
With fire	100	100	10
Ada Forest Block			
No fire	34	48	--
With fire	18	98	87
Steavenson Forest Block			
No fire	2	5	--
With fire	48	84	162
O'Shannassy Water Catchment			
No fire	0	0	--
With fire	4	15	--

[a] The annual probability of a fire was 1% and 75% of patches were burnt in any given fire event.

5. Results

5.1. Scenario 1: No wildfire in isolated old growth patches

Table 4 contains the results of analyses of populations of *G. leadbeateri* inhabiting single isolated patches of 3-500 ha of old growth montane ash forest. These findings demonstrated that the probability of extinction declined with an increase in the size of forest patches. When a patch was more than 250 ha, the predicted probability of extinction was almost zero (Table 4). There was a sigmoidal relationship between the probability of extinction and the size of habitat patches (Fig. 7). Populations inhabiting patches of 20 ha or less were predicted to suffer rapid rates of extinction and none persisted longer than 150 years (Table 4). However, the predicted probability of extinction declined to 60% for patches of 40 ha and less than 10% where the patch size was over 90 ha (Table 4). These findings reflect a type of threshold relationship where an increase in the size of a patch beyond a minimum of 20 ha made a significant positive contribution to the probability of population persistence (Fig. 7).

5.2. Scenario 2: The impacts of wildfire on isolated patches of old growth forest

The effects of a wildfire on populations of *G. leadbeateri* in hypothetical patches of old growth are presented in Table 3 and Fig. 8. There were a number of trends in the data that were similar to those obtained from Scenario 1. In particular, there was an increase in the probability of population persistence associated with an increase in the size of patches of old growth forest. Populations of *G. leadbeateri* in patches of 20 ha or less were predicted to be highly vulnerable to extinction (Table 4) (P[*E*] = 100%). However, unlike the findings of Scenario 1, there was a high probability of extinction (over 60%), even in large isolated patches of forest (over 600-1200 ha).

Table 4
The estimated probability of extinction of populations of *G. leadbeateri* during a 150 year time period within single isolated patches of old growth forest in response to a wildfire and in the absence of fires. The annual probability of fires was 1% and 75% of patches were burnt in any given fire event (see text for further explanation). The impacts of post-fire salvage logging operations were not included in the analyses.

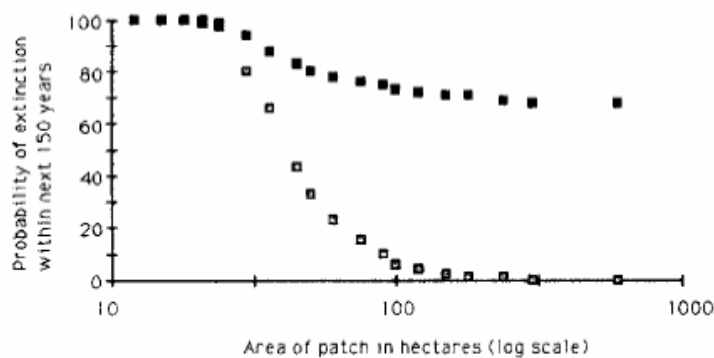| Patch size (ha)	Log patch size	$P(E)_{150}$ fire absent	$P(E)_{150}$ with fire
3	0.48	100	100
6	0.78	100	100
9	0.95	100	100
I2	1.08	100	100
15	1.18	100	100
18	1.26	100	100
21	1.32	99	100
24	1.38	98	99
30	1.48	80	94
36	1.56	66	88
45	1.65	43	83
50	1.70	33	80
60	1.78	23	78
75	1.88	15	76
90	1.95	10	75
100	2.00	6	73
120	2.08	4	72
150	2.18	2	71
180	2.26	1	71
240	2.38	1	69
300	2.48	0	68
600	2.78	0	68
1200	3.08	0	68

Fig. 7. The relationships between the probability of extinction of *G. leadbeateri* and the size of single hypothetical patches of old growth forest when a fire was and was not modelled. An annual probability of a fire of 1% was used in these analyses, and 750h of patches were burnt in any given fire event (see text). The open squares represent the results of simulations where the impacts of wildfires were incorporated in the analyses. The solid squares correspond to simulations completed without such effects.
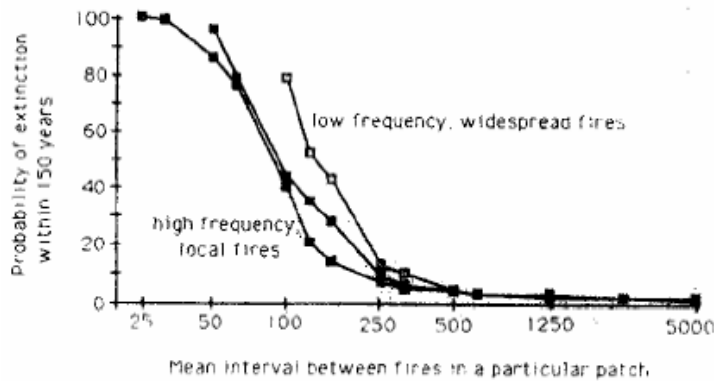
Fig. 8. The impacts on the probability of extinction of the inter-relationships between fire frequency, the extent of a wildfire and the interval between a fire in any given habitat patch.

5.3. Scenario 3: The impacts of fire in each of the four management areas

A comparison of the outcomes of scenarios with and without wildfires in each of the four study areas is presented in Table 3. Even in the absence of fire there was a high probability of extinction in the Murrindindi and Ada Forest Blocks (100% and 43% respectively). The corresponding values for the Steavenson Forest Block and the O'Shannassy Water Catchment were much lower (2% and 0%, Table 3). The inclusion of wildfires significantly elevated the predicted probabilities of, and median time to, metapopulation extinction, except for the Murrindindi Forest Block where higher values were not possible (i.e. $P(E)_{150} = 100\%$). General trends from our analyses showed that the amount of old growth forest in a given forest block had a significant effect on metapopulation persistence. Thus, the lowest values for $P(E)_{150}$ and $P(E)_{300}$ were from the O'Shannassy Water Catchment where there are presently large areas of old growth forest including several patches that exceed 500 ha in size (Table 1).

The probability of metapopulation extinction in the Steavenson Forest Block increased from 48% during the first 150 years of our simulations to 84% after 300 years (Table 3). The corresponding values for $P(E)_{150}$ and $P(E)_{300}$ in the Ada Forest Block were 78% and 97% respectively. Thus, for the case of the Steavenson Forest Block, populations were predicted to persist for 150 years in 52% of our simulations. However, the probability of extinction within the following 150 year period rose to approximately 69%, resulting in only a 16% probability of persistence for a 300 year period. Similar trends were observed for the Ada Forest Block. Hence, there were proportionally greater rates of extinction in the second 150 year time component of our simulations than were recorded in the earlier phase of the modelling.

5.4. Scenario 4: The impacts of variations in fire frequency and the proportion of patches that were burnt

Table 5 and Fig. 8 contain the results of simulations from the Steavenson Forest Block where we modelled the interacting effects of fire frequency and the number of old growth patches that were burnt on the dynamics of populations of *G. leadbeateri*. As expected, the probability of population persistence declined in response to an increase in the amount of an area that was burnt (Table 3). However, a more interesting result was that fires which occurred more frequently and burnt a smaller proportion of the total number of habitat patches, led to a lower probability of extinction than less frequent but more extensive conflagrations (Table 5, Fig. 8).

5.5. Scenario 5: Modelling the impacts of wildfires and post-fire salvage logging operations

There was a significant increase in the predicted and incremental probabilities of extinction of metapopulations of *G. leadbeateri* when the combined impacts of both wildfires and salvage logging operations were modelled than where the effects of fires alone were simulated (Table 6).

This trend was consistent irrespective of the fire regimes that were employed (i.e. 50% and 75% of patches burnt in a wildfire). Indeed, for the simulations where the fire regime resulted in 50% of patches being burnt, the incremental probability of extinction declined from 61 to 42% when we excluded salvage logging from our analyses. The predicted probability of extinction after 150 years was reduced from 83 to 66% in this case (Table 6).

Table 5
The predicted probability of extinction (%) during 150 years of *G. Ieadbeateri* in the Steavenson Forest Block in response to the frequency of wildfires and the proportion of old growth areas that are burnt (see text for further explanation of the scenarios examined). The dashes highlight those combinations of fire frequency that cannot occur. These analyses were completed without the impacts of post-fire salvage logging operations

Annual probability of fire in a given patch	Average time between fires (years)	Annual probability of any fire in Steavenson Block		
		0.01	0.02	0.04
0.0002	5000	3	3	3
0.0004	2500	3	3	3
0.0005	2000	3	3	3
0.001	1000	4	3	3
0.002	500	5	4	3
0.004	250	12	11	7
0.005	200	16	13	11
0.0075	133	48	32	25
0.008	125	53	34	24
0.01	100	77	47	40
0.016	63	--	--	73
0.012	50	--	96	88
0.04	25	--	--	99

Table 6
The estimated probability of extinction (%) of populations of *G. leadbeuteri* in the Steavenson Forest Block. For these analyses we set the annual probability of a fire to 1% and the number of patches that were burnt in a conflagration was either 50% or 75%

Proportion of patches burnt in a wildfire (%)	Extinction probability at various times					Mean[a]
	P_{150}	P_{300}	P_{450}	P_{600}	P_{750}	
Without salvage logging						
50	17	49	72	82	91	42
75	42	79	91	97	99	60
With salvage logging						
50	34	71	89	95	99	58
75	58	86	96	99	100	69

[a]Values for the incremental probability of extinction. The methods used to calculate this measure are outlined in the text.

5.6. Scenario 6: The impacts of various fire regimes in the O'Shannassy Water Catchment
The results of computer simulations of various fire regimes in the O'Shannassy Water Catchment are presented in Table 7. As in the other scenarios that were modelled, the predicted probability of extinction increased with an increase in both the annual probability of fire and the proportion of patches that were burnt during any given conflagration. Thus, we predicted that

metapopulations of *G. leadbeateri* were most likely to persist when the annual fire frequency was 0.67% and only 50% of patches are burnt in any given wildfire event (Table 6). This was the only fire regime where the probability of extinction of populations of *G. leadbeateri* remained at 1% or less when our simulations were run for a prolonged period (e.g. over 450 years) (Table 6).

Table 7
Predicted probabilities of extinction for simulated populations of G. leadbeateri in the O'Shannassy Water Catchment in response to a range of wildfire regimes. These analyses were completed without the impacts of post-fire salvage logging operations

Time horizon (years)	Annual probability of fire			Percent of patches burnt in fire		
	1.33% 100 years	1% 133 years	0.67% 200 years	100 100 years	75 133 years	50 200 years
Patches of old growth only						
150	6	3	2	69	3	0
300	26	15	6	91	15	0
450	46	29	12	97	29	1
600	63	42	17	99	42	3
750	75	49	23	100	49	5
Combination of old growth and existing regrowth patches						
150	8	3	1	76	3	0
300	24	13	3	95	13	0
450	40	26	7	99	26	0
600	58	35	9	100	35	1
750	68	46	11	100	46	1

[a]Interval between fires in a patch.

As expected, the probability of extinction was lower when patches of both old growth and regrowth were modelled than for the analyses of old growth alone. The exception to this trend was for the most extreme fire regime, where the addition of stands of regrowth forest did not significantly reduce the predicted probability of population extinction (Table 6). For the other simulations, a significant reduction in extinction probability was observed only when we ran our simulations for more than 150 years. This occurred because this was the time required for existing stands of regrowth forest to eventually become suitable for *G. leadbeateri* (see above). Furthermore, stands that were burnt before they reached this age would not contain suitable large old fire-damaged trees with hollows to meet the habitat requirements of the species.

6. Discussion
6.1. General findings
Wildfires resulted in an increased probability of extinction of populations of *G. leadbeateri*. This was readily demonstrated by a comparison of the findings for hypothetical populations in isolated patches of old growth that were burnt and where the effects of fire were excluded (see Fig. 7). For small patches of old growth forest, the incorporation of the effects of wildfire increased the already very high values for the predicted probability of extinction (Fig. 7). The results for larger patches highlighted the impacts of fire on the likelihood of persistence of *G. leadbeateri*. In the absence of fire, the probability of extinction amongst isolated populations in areas of 100 ha or more was less than 10%. In contrast, the probability of extinction in simulations of patches of equivalent size that were subjected to wildfire did not decline below 60%. However, our results for large patches require some qualification. In this part of our analysis, we assumed that all of a patch would be burnt in a fire.

However, the larger an area, the lower the probability that a patch would be completely destroyed by a given catastrophic event (Bronmark, I 985; Seagle and Shugart, 1985; Weiss et al., 1988). Within large patches of montane ash forest there would be considerable environmental and topographic heterogeneity, and such areas would incorporate forest that varies in slope, aspect, topographic position (e.g. midslopes and gullies) and a number of other parameters (Lindenmayer et al., 1991a). These factors, in turn, influence the intensity of fire and the area that is burnt (Ashton, 1981a,b), leaving a mosaic of patches that exhibit differences in the extent of fire damage (see Smith and Woodgate, 1985). The relationship between the size of a remnant area and variations in the degree of damage resulting from a fire, highlights the importance of the very large remaining areas of old growth forest as key refugia for the long-term conservation of G. leadbeateri (e.g. those of more than 3000 ha within the O'Shannassy Water Catchment; Table 1). Indeed, populations of *G. leadbeateri* were predicted to have a higher probability of persistence in the O'Shannassy Water Catchment than in any other area that was modelled. This trend would hold when comparing this area with any other in the Central Highlands of Victoria, because it contains significantly more old growth forest than elsewhere in the region. However, even in the O'Shannassy Water Catchment, our analyses revealed that there was a finite probability of extinction for populations of *G. leadbeateri* (Table 7).

These findings emphasise the need for strategies for the management of *G. leadbeateri* to aim to conserve the species not only in the O'Shannassy Water Catchment, but in many other parts of the species distribution including the 75% of its range which occurs in wood production areas. Notably, only when we modelled the O'Shannassy Water Catchment and employed a moderate fire regime (45% of patches burnt), did our predictions for metapopulation extinction approach those typically specified for long-term viability by other authors (i.e. a value of 1% chance of extinction during a 1000 year period; see Shaffer, 1981; Shaffer and Samson, 1985). However, the predicted values for the probability of extinction were much higher than this for all the other scenarios completed for the O'Shannassy Water Catchment (Table 6), suggesting that populations of the species are susceptible to the impacts of fire in the area. On this basis, it will be important to continue attempts to exclude fire from the O'Shannassy Water Catchment and we consider that it should remain closed to public access to minimise the risk of fires being started by campers and walkers.

6.2. The predicted impacts of recurrent fires on population persistence

The potentially detrimental impacts of wildfires on populations of *G. leadbeateri* are a cause for concern. More than one high-intensity wildfire within a 150 year period would result in major changes to the structure of montane ash forests such as a significant reduction in the abundance of trees with hollows (see above) (Lindenmayer et al., 1991a, 1993a); with a corresponding negative effect on populations of the species. Notably, unlike the conflagration that occurred in 1939, major wildfires that may occur over the next 100 years would not create large areas of suitable habitat for *G. leadbeateri*. This is because the 1939 wildfires burnt stands supporting large old growth stems which contained, or subsequently developed, cavities suitable for use by the species. These types of trees with hollows would not be created by burning 55-year old regrowth forest (Lindenmayer et al., 1993a).

Our results for the various forest management areas highlight the potentially detrimental impacts of recurrent wildfires on population persistence. For example, a comparison of the values for $P(E)_{150}$ and $P(E)_{300}$ in the Steavenson Forest Block indicated there were proportionally greater rates of extinction in the second time component of our simulations (i.e. for the interval 150-300 years) than were recorded in the earlier phases of the modelling (from now until 150 years in the future) (Table 3). These results can be attributed to two inter-related factors. (1) Our analyses were initialised using a patch structure comprised of existing areas of old growth that may not persist in a fire regime where there are recurrent wildfires. (2) When several fires occur within a 300 year interval, there is a considerably increased chance that the areas which are being burnt would be patches of regrowth forest that are regenerating after a previous conflagration. In the simulations of

the Steavenson Forest Block, the annual probability of fire was set to 1% and the proportion of patches that were burnt in any conflagration was 75%, yielding a mean interval of 133 years between fires in any given patch (Table 3). Under this fire regime there would typically be only one fire in any given patch during a 150 year period. There would be an increased probability of at least two or more tires occurring over a 300 year time horizon. The cumulative impacts of several fires would substantially reduce the likelihood that lire-damaged areas would develop suitable habitat for G. leadbeateri before they were burnt again. Thus, the elimination of key habitat components as a result of recurrent intensive wildfires could lead to the loss of *G. leadbeateri* from large areas of montane ash forest.

Several key questions for wildlife management arise from the observation that wildfires have the potential to eliminate networks of suitable old growth habitat patches. In particular: how much forest needs to be reserved to ensure that there will still be sufficient suitable habitat for *G. leadbeateri* remaining after a wildfire; or put another way, given that catastrophic fires can damage or eliminate some areas of suitable habitat, how can we sustain a suitable patch structure that will maintain a reasonable chance of metapopulation persistence in the long term? We are not able to answer this question. However, one of the implications of the impacts of recurrent wildfires is the need to have several large reserves in an attempt to guarantee both (1) a perpetual supply of sufficient suitable habitat to ensure the persistence of *G. leadbeateri* and (2) minimise the risk that all reserves would be burnt in a single fire event.

6.3. Implications for fire management strategies

The results of our studies have indicated that strategies designed for the conservation of *G. leadbeateri* need to consider methods that both (1) reduce the frequency and number of wildfires and (2) mitigate the potential impacts of, and the area burnt by, wildfires. This may involve developing additional methods for the rapid suppression of forest fires as well as the more careful application of high intensity bums that are used to promote the regeneration of logged areas. In some cases, it may be appropriate to replace high intensity regeneration fires with other methods such as low intensity bums or mechanical disturbance to stimulate the revegetation of cut-over areas, particularly where logging coupes are located near large stands of existing old growth forest (e.g. those at the edge of the O'Shannassy Water Catchment). Indeed, the identification of alternative stand regeneration methods should be a target for future silvicultural research in montane ash forests. We believe that the potentially detrimental impacts of high intensity regeneration fires that could bum out of control should be a factor that is considered in the formulation of regional fire protection plans.

The implementation of upgraded fire management strategies could have many additional economic and social benefits such as enhancing the protection of very valuable stands of timber and reducing losses of human life. The successful suppression of wildfire would also assist the transition of areas of regrowth forest to more advanced successional stages. The importance of additional areas of old growth in contributing to the long-term conservation of *G. leadbeateri* is discussed further by Lindenmayer and Norton (1993) and Lindenmayer and Gilmore (1994). Notably, our conclusions about the importance of more vigilant fire protection procedures is in marked contrast with earlier management recommendations for the conservation of *G. leadbeateri* that called for a 'let-burn' policy amongst existing areas of old growth forest, particularly those extensive stands within the O'Shannassy Water Catchment (Smith et al., 1985).

Our analyses indicated that for a fixed per patch mean fire interval, the probability of persistence of populations of *G. leadbeateri* was highest when fires were frequent but only a proportion of habitat patches were burnt. Conversely, infrequent extensive fires resulted in very high rates of extinction (Table 5, Fig. 7). These findings appear to support the ideas of Smith et al. (1985) who believed that prior to the arrival of Europeans, suitable habitat for *G. leadbeateri* may have typically been stands of multi-aged forest created by low intensity fires that were patchy and frequent. Our results also have important implications for fire management strategies as they

highlight a need to limit the spread of wildfires and attempt to prevent widespread high intensity conflagrations such as those which occurred in 1939 when more than 65% of the montane ash of the Central Highlands of Victoria was burnt.

6.4. Spreading the risk: catastrophic wildfire events and reserve design

The results of our investigation indicated that small patches of forest will not support populations of *G. leadbeateri* that are viable in the long term. This may be particularly true within wood production forests where existing areas of old growth forest are typically very small (less than 3 ha). Given this, an aim of forest management in these areas should be to attempt to grow larger areas of existing regrowth montane ash forest to ecological maturity. However, attempts to set aside reserved areas within forest blocks that are broadly designated for timber production need to take account of the potential effects of catastrophes such as wildfires. There is a possibility that much of a single contiguous reserved area could be destroyed by one wildfire. A better strategy may be to reserve several areas from timber harvesting in any given wood production forest block. The importance of 'spreading the risk' and avoiding potential problems associated with the spatial correlation of catastrophes between reserved areas is more thoroughly discussed by Gilpin (1987), Simberloff and Cox (1987), Quinn and Hastings (1987) and Quinn et al. (1989). Examples of taxa where a lack of environmental correlation between habitat patches has benefited species persistence are given by Berger (1990), Murphy et al. (1990) and Stacey and Taper (1992) . The impact of this effect is highlighted by comparing the results of simulations completed for the Steavenson Forest Block and those of a single patch of old growth forest. Our analyses revealed that the predicted probability of extinction for a population of *G. leadbeateri* occupying a hypothetical single habitat patch of 250 ha was 67% (Table 3). When the same fire regime (one fire per 100 years and 75% of patches burnt) was applied to the Steavenson Forest Block which contains approximately 260.ha of old growth montane ash forest, the resulting probability of extinction was 42% (Table 3). The most parsimonious explanation for this result was that the spatial dispersion of habitat patches within the Steavenson Forest Block resulted in some of them escaping the impacts of the wildfire. In addition, dispersing animals from unburnt areas could have recolonised burnt patches which also may, in turn, have made a positive contribution to population persistence.

The impacts of wildfires also need to be considered in determining the best places to locate reserves for *G. leadbeateri* within wood production areas. For example, it could be valuable to position reserved areas in the most mesic and sheltered parts of the landscape. These include areas in deep valleys and on southern slopes where there may be a smaller chance of them being burnt and/or the fire-intensity is likely to be lower (Ashton, 1981a,b). The spatial location of existing stands of old growth forest may be a useful guide in identifying forest for reservation because they are areas that have escaped past fires. However, more information is urgently required to assist a reserve selection process within montane ash forests. This will require research on modelling the behaviour and spread of fires in the region. Studies of the O'Shannassy Water Catchment could be particularly instructive in this regard, as the patterns of fire damage in this area are not complicated by other types of disturbance such as logging operations.

6.5. Post-fire salvage .logging and population persistence

Salvage logging operations have followed several of the major wildfires in the Central Highlands of Victoria (Noble, 1977; Smith and Woodgate, 1985; Griffiths, 1992; Smith and Lindenmayer, 1992). These have involved the removal of large dead and fire-scarred trees for sawlogs and pulpwood. For most of our analyses of the various wood production forest blocks, we assumed that burnt patches of old growth forest were not salvage logged. The analyses completed in Scenario 5 indicated that future post-fire salvage harvesting will have a significant negative impact on populations of *G. leadbeateri* (Table 6). Such types of operations impede the process of habitat development after wildfires, particularly in areas of old growth forest where dead and living burnt trees may eventually provide nest sites for hollow-dependent fauna such as *G. leadbeateri*. Indeed,

past salvage logging operations have contributed to the present and future shortage of trees with hollows for the species (Smith and Lindenmayer, 1992; Lindenmayer and Gilmore, 1994).

7. Assumptions and limitations of the study

There are a range of assumptions and limitations that underpin the use of PVA, and an understanding of these is fundamental to any valid application of the approach (Boyce, 1992; Lindenmayer et al., 1994a). Possingham and Noble (1991) and Possingham et al. (1992,1994) have discussed the assumptions and limitations associated with ALEX. The particular assumptions that were pertinent to this study are outlined briefly below.

We assumed that sub-divided populations of *G. leadbeateri* were linked by a regular exchanges of individuals. There are only limited data on the movement patterns of the species. However, the results of extensive sensitivity analyses of a range of key dispersal parameters indicated that the movement capability of *G. leadbeateri* would have to be very poor to alter to the major conclusions drawn from our study. Despite this, there is considerable merit in completing additional field studies to examine the movement patterns and dispersal capabilities of *G. leadbeateri*. For the purposes of our analyses, we assumed that only old growth and multi-aged forests would support populations of *G. leadbeateri*. This was considered appropriate because: (1) areas of regrowth forest that presently support numerous potential nesting sites are unlikely to remain suitable for more than another 15-20 years owing to very rapid rates of decay amongst existing trees with hollows (Lindenmayer et al., 1990b; D.B. Lindenmayer et al., unpublished data, 1994); (2) the species is absent or extremely rare within forests that are excluded from logging such as stands on steep and rocky areas, retained linear strips and reserves of streamside forest (Lindenmayer, 1989; Lindenmayer et al., 199lb, 1993d; Lindenmayer and Nix, 1993). Notably, we completed a number of additional simulations for the Murrindindi, Ada and Steavenson Forest Blocks that incorporated the patch structures comprised of a combination of old growth patches and areas that were presently unavailable for timber harvesting. When the excluded areas were added to the patch structure and they were assigned a highly optimistic habitat suitability value to allow them to support some breeding animals, the incremental probability of extinction declined by <10%. The exception to this was for the Murrindindi Forest Block where the values PE_{150} and PE_{300} remained constant at 100%, irrespective of the network of patches that was modelled.

Wildfires were the only type of catastrophic events that were modelled in this investigation. Others were omitted such as clearfelling operations that are known to have a highly detrimental impact on populations of *G. leadbeateri* (Lindenmayer et al., 1990a; 1991e; Lindenmayer, 1992a,b; Smith and Lindenmayer, 1992). Logging is presently excluded from most areas of old growth and multi-aged forest (Macfarlane and Seebeck, 1991). However, there may be important interactions between the prevalence of timber harvesting operations and the frequency and intensity of wildfires. For example, high intensity fires that are used to regenerate logged forest (Squire et al., 1991) may ignite surrounding areas of uncut forest and instigate a major conflagration. The combined effects of habitat losses both from fires and logging may have an important cumulative impact on populations of *G. leadbeateri*. These factors, and those described above may mean that we have underestimated the risk of extinction of populations of *G. leadbeateri*, particularly those that occur in areas of wood production forest. An important assumption underlying our study was that patches of burnt and subsequently salvage logged old growth forest were not treated in the same way as the rest of the production forest and added to the area of the forest estate that was harvested on a 50-l 20 year rotation. Hence, we assumed that burnt old growth patches had the capacity to revert to mature forest. If this did not occur and all fire-damaged areas become available for timber production, there would be no potential for the development of new and/or additional stands of old growth forest and the extinction of populations of *G. leadbeateri* within wood production areas would be virtually assured.

8. Conclusions

(1) Wildfires are predicted to have a significant negative effect on the persistence of populations of *G. leadbeateri*. Strategies that attempt to ensure the long-term conservation of *G. leadbeateri* should include approaches that mitigate the impacts of wildfire on the species.

(2) The relationships between wildfires and extinction risk varied significantly between the forest management areas that were targeted for study. Metapopulations of *G. leadbeateri* were predicted to have the highest probability of persistence in the O'Shannassy Water Catchment which is characterised by relatively large contiguous areas of old growth forest. Thus, wildlife management strategies in timber production areas should attempt to grow some large areas of regrowth forest through to ecological maturity.

(3) Post-fire salvage logging operations have a highly detrimental impact on metapopulations of *G. leadbeateri*. As a result, we strongly recommend that existing stands of old growth forest and other reserved areas should not be available for salvage harvesting if they are burnt.

(4) A risk-spreading strategy should underpin the design of a network of spatially dispersed reserves for the conservation of *G. leadbeateri*. This would minimise the chance that all of the reserved area would burnt in a single wildfire.

Appendix 1: A description of the various submodels within ALEX that were used to track temporal variations in habitat sustainability for G. leadbeateri

Baseline sub-models

Two factors affect the quality for *G. leadbeateri*, the availability of food and the abundance of trees with hollows. 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. The model 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 hectare.

Habitat variable one, $H_1(t)$, is a measure of food availability, in particular *Acacia* spp., t years after a fire. After each fire it follows the trajectory described by the equation

$$H_1(t+1) = 0$$
$$0 < t \le 15$$
$$= (t-15)/20$$
$$15 < t \le 35$$
$$= 1$$
$$35 < t \le 60$$
$$= 1 - 0.7(H_1(t) - 60)/40$$
$$60 < t \le 100$$
$$= 0.3$$
$$t > 100 \qquad\qquad (A1)$$

Habitat variable two, $H_2(t)$, is a measure of the availability of hollows in mature living trees t years after a fire. We assume that $H_2(t)$ is capped at a value of 100. After a fire and salvage logging its dynamics are given by the equation

$$H_2(1) = 0$$
$$H_2(t+1) = 0.995 H_2(t)$$
$$1 < t \le 150$$
$$= 0.995 H_2(t) + 1.6((t) - 150)/150$$
$$150 < t \le 300$$
$$= 0.995 H_2(t) + 1.6$$
$$t > 300 \qquad\qquad (A2)$$

This equation indicates that there will be no mature trees with hollows in an area until 150 years after it was burnt and salvage logged. After this time, the availability of mature trees with hollows increases at an increasing rate until it reaches a maximum value of 100. Habitat variable three, $H_3(t)$, reflects the availability of hollows in senescent or dead trees t years after a fire. After a fire and salvage logging, its dynamics are

$$H_3(1) = 0$$
$$H_3(t+1) = 0.96 H_3(t)$$
$$+ 0.02 H_2(t) \quad \text{for } t > 0 \quad (A3)$$

This equation indicates that dead trees with hollows only occur after there has been recruitment of mature living trees with hollows. At equilibrium, $H_2(t) = 100$ and $H_3(t) = 50$.

If there are no post-fire salvage logging operations, then we assumed that the density of living trees with hollows is 15% of what it was before the wildfire, viz

$$H_2(1)=0.15H_2(0)$$

The abundance of dead trees with hollows is five times what it was in an old growth forest before a fire event.

$$H_3(1)= 5H_2(0)$$

The total habitat quality value

The value for habitat quality t years after a fire was the minimum of $H_1(t)$ and $(H_2(t)+H_3(t))/100$. This means that either food or hollows limit the minimum breeding territory size. Fig. 6 contains a series of response curves that highlight temporal fluctuations in the habitat suitability index in burnt stands of old growth forest. In existing stands of old-growth habitat we assumed the time since fire was sufficient to ensure that hollows were not limiting but the availability of food had fallen to 0.3 (Eq. (Al), Fig. 6).

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