

## The Conservation Of Arboreal Marsupials In The Montane Ash Forests Of The Central Highlands Of Victoria, South-Eastern Australia - VII. Modelling The Persistence Of Leadbeater's Possum In Response To Modified Timber Harvesting Practices

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### Abstract

A computer model for Population Viability Analysis (PVA) was used to simulate the relationship between the persistence of populations of the endangered species, Leadbeater's possum, *Gymnobelideus leadbeateri* and the implementation of a range of possible modified timber harvesting practices in two wood production blocks within the montane ash forests of the central highlands of Victoria, south-eastern Australia. The results of our analyses revealed that under the existing conservation strategies there was a high probability of extinction over the next 150 years in both blocks. Given that timber production areas comprise more than 75% of the distribution of *G. leadbeateri*, our findings highlight a need for additional conservation measures to enhance the survival prospects of the species. The range of upgraded conservation strategies that were examined included (1) extending the rotation time between logging operations; (2) modifying silvicultural practices to increase the amount of forest retained within each harvested coupe; and (3) permanently withdrawing areas from wood production. All of each of these approaches were found significantly to reduce the probability of extinction of populations of *G. leadbeateri*. However, when the relative merits of the various strategies were compared, the permanent withdrawal of potential logging coupes from timber harvesting was predicted to be the most efficient approach. Importantly, this strategy would have a number of practical advantages including that it overcomes both (1) the logistic difficulties of ensuring the long-term survival of retained trees within logged areas; and (2) human safety issues arising from implementing modified silvicultural practices. This practical application of PVA to compare the merits of different potential management options has provided new information that will enhance present efforts to conserve *G. leadbeateri* in wood production areas.

**Keywords:** Leadbeater's possum; population viability analysis; forest management; logging impacts; conservation strategies

### INTRODUCTION

Australian State and Federal Government policies aim to manage wood production forests on a multiple-use basis (*sensu* Behan, 1990) so they provide wood and paper products as well as support habitat for populations of native flora and fauna (e.g. Government of Victoria, 1986; Department of Conservation & Land Management, 1992; The Commonwealth of Australia, 1992). The challenge in managing multiple-use forests is to ensure that wood production is ecologically sustainable and does not compromise other values such as wildlife conservation (Ecologically Sustainable Forestry Working Group, 1991; Resource Assessment Commission, 1992). However, the management of species such as Leadbeater's possum *Gymnobelideus leadbeateri* that are sensitive to certain silvicultural practices may be a particular problem in timber production areas. *G. leadbeateri* occurs in the montane ash forests in the central highlands of Victoria, south-eastern Australia (Lindenmayer *et al.*, 1990a; Lindenmayer & Norton, 1993). Its highly restricted distribution overlaps extensively with some of the most economically valuable timber in Australia (Macfarlane & Seebeck, 1991; Squire *et al.*, 1991a).

Clearfelling on an 80-120 year rotation within montane ash forests is not compatible with the habitat requirements of *G. leadbeateri*, particularly nest sites in large trees > 200 years old (Lindenmayer *et al.*, 1990b, c, 1991a). The cessation of logging in large areas of wood production ash forest is not a realistic

management approach because the Victorian Government has agreed to provide Forest Industries with large quantities of timber and pulpwood from the central highlands of Victoria (Government of Victoria, 1983, 1986). However, the modification of present forest management practices has the potential to enhance the survival prospects of *G. leadbeateri* and better integrate the various uses of wood production areas. Such changes could include (1) increasing the rotation time between timber harvesting operations; (2) modifying existing clearfelling practices; (3) exempting areas from timber harvesting; and (4) a combination of these approaches (Loyn, 1985; Lindenmayer, 1994). In this study, we use a computer package for Population Viability Analysis (PVA) (*sensu* Shaffer, 1990; Boyce, 1992) to examine the first three of these possible management strategies and compare their relative merits in enhancing efforts to conserve the species.

### **Background -- the study region and existing conservation strategies for the conservation of *G. leadbeateri***

More than 80% of the central highlands of Victoria supports regrowth montane ash forest aged < 55 years old (Lindenmayer *et al.*, 1991b). The bias in the age class distribution in the region has arisen from several major wildfires, a prolonged history of post-fire logging to salvage timber from burnt trees, and, more recently, intensive and widespread clearfelling operations. The 1939 wildfires burnt stands of old growth montane ash forest (> 120-150 years old) producing extensive areas of regrowth forest interspersed with numerous large burnt trees (Lindenmayer *et al.*, 1990b). Areas of this type of regrowth forest have provided habitat for *G. leadbeateri* (Seebeck *et al.*, 1983; Lindenmayer *et al.*, 1989). However, the suitability of these regrowth forests for *G. leadbeateri* is declining rapidly because of the decay and collapse of the large mature trees with hollows which provide nest sites for the species (Lindenmayer *et al.*, 1990c). Within the next few decades, large areas of regrowth montane ash forest will support insufficient nest sites to meet the nest tree and habitat requirements of *G. leadbeateri* (Lindenmayer *et al.*, 1990c), and this is predicted to result in a major decline in populations of the species (Lindenmayer *et al.*, 1993a). The shortage of nest sites will persist for at least another 150 years until the existing 55 year-old stems begin to develop cavities that will be potentially suitable for use by *G. leadbeateri* (Lindenmayer *et al.*, 1990c).

Existing patches of old growth forest are predicted to be almost the only areas to support sufficient potential nest sites to provide suitable habitat for *G. leadbeateri* in the future (Lindenmayer *et al.*, 1990c). Old growth stands have been excluded from timber harvesting under recent strategies implemented for the conservation of *G. leadbeateri* in wood production forests (Macfarlane & Seebeck, 1991), although they are now confined to small remnant patches (Lindenmayer *et al.*, 1993c). Other areas that are unavailable for wood production include streamside reserves and stands of unmerchantable timber on steep and rocky areas (Department of Conservation, Forests & Lands, 1989), but these may be of limited conservation value for *G. leadbeateri* because (1) the abundance of the species is negatively correlated with slope steepness (Lindenmayer *et al.*, 1991a); (2) forests on steep topography (>20 °) support significantly fewer trees with hollows than stands on flatter areas (Lindenmayer *et al.*, 1991b); (3) *G. leadbeateri* is uncommon in strips of retained linear habitat 40-150 m wide such as those areas set aside in streamside reserves (Lindenmayer & Nix, 1993; Lindenmayer *et al.*, 1993d) and (4) riparian areas frequently contain patches of cool temperate rainforest (Ough & Ross, 1992) which rarely provide suitable habitat for *G. leadbeateri*.

A number of authors have drawn attention to the deficiencies in the present management strategies for the conservation of *G. leadbeateri* (e.g. Tanton & Norton, 1991; Smith & Lindenmayer, 1992; Lindenmayer & Norton, 1993). These workers have suggested that additional approaches will be required to enhance the species' prospects for survival within wood production forests. In this study, we analysed the relative contribution of some modified forest management practices to the persistence of populations of *G. leadbeateri*.

### **METHODS**

ALEX (Analysis of Likelihood of EXtinction), a generic computer model for PVA, was applied in this study. A detailed description of ALEX, its sequence of program flow, and other features of the model are given by Possingham *et al.* (1992) and Possingham and Davies (1995). Examples of other applications of the package are provided by Possingham *et al.* (1992, 1994), Goldingay and Possingham (1993), Lindenmayer *et al.* (1993c) and Possingham & Gepp (1993). The Murrindindi and Steavenson timber production Forest Blocks were targeted for detailed study (Fig. 1). This was because (1) there are presently extensive data on the spatial arrangement of existing suitable habitat patches and coupes proposed for logging in both areas; and (2) the area of old growth forest which occurs in these areas is close to the lower and upper amounts of such types of forest found in the various wood production forest blocks within the

central highlands of Victoria (J. Smith, Department of Conservation & Natural Resources, pers. comm.). Therefore, the trends in population dynamics in these forest blocks may be indicative of those in many other areas throughout the region. We chose to focus our analyses on forest blocks because they are the management unit in which planning for timber production and wildlife conservation takes place. Moreover, an important plank in State Government policies for multiple forest-use management is to ensure the conservation of forest-dependent taxa in each timber production block (see Loyn, 1985), and, in turn, throughout the known ranges of such species (Government of Victoria, 1988). Notably, larger areas could have been chosen for study and this would be appropriate for other species such as the sooty owl *Tyto tenebricosa* which have an extensive home range (> 800 ha) (Milledge *et al.*, 1991). However, in the case of *G. leadbeateri*, which has a much smaller home range (1-3 ha; Smith, 1980), analyses completed for forest blocks were those most likely to produce outcomes of greatest application for integrated forest planning and management and the conservation of the species.



**Fig. 1.** The location of the two forest blocks within the central highlands of Victoria, south-eastern Australia that were targeted for detailed analysis in this study. Area 1, Murrindindi Forest Block (total area approximately 3500 ha) area 2, Steavenson Forest Block (approximately 5500 ha).

The Murrindindi Forest Block measures approximately 3500 ha in area and about 25 ha of this is old growth. All of the patches of old growth forest are < 3 ha in size (Fig. 2). The Murrindindi Forest Block is adjacent to several forest blocks and the Maroondah Water Catchment which are also characterised by highly limited areas of old growth montane ash forest (Curry, 1981; J. Smith, pers. comm.). The southern boundary of the Murrindindi Forest Block abuts land that has been cleared for agriculture. Approximately 265 ha of the 5500 ha in the Steavenson Forest Block (= 2-5%) is old growth forest. There are five individual patches that exceed 20 ha in size and more than 20 which are 6 ha or smaller (Fig. 3). The southern part of the Steavenson Forest Block shares a common boundary with the O'Shannassy Water Catchment which contains some of the largest remaining areas of old growth montane ash forest in the central highlands of Victoria (Land Conservation Council, 1993). Other parts of the Steavenson Forest

Block abut areas characterised by dry mixed species eucalypt forest where *G. leadbeateri* does not occur or stands of regrowth ash-type forest. A range of types of data was input to ALEX to simulate the response of metapopulations of *G. leadbeateri* to various conservation strategies in the Murrindindi and Steavenson Forest Blocks. These data included (1) life history attributes of the species; (2) the size and spatial location of patches of different types of potentially suitable habitat within the two forest blocks that were targeted for detailed study; (3) the movement of animals between suitable habitat patches; (4) the response of populations of animals to vegetation disturbances resulting from wildfires and logging operations; (5) the spatial location of areas of forest that were cut for timber; and (6) temporal changes in the value of forest habitats for *G. leadbeateri* at various time intervals post-disturbance. The following sections contain a synthesis of the information used in ALEX, particularly the key input parameters and submodels.

Because of the range of assumptions associated with our application of PVA, it is likely that we have underestimated the probability of extinction of *G. leadbeateri*. However, it is unlikely that the results of our comparisons of the *relative* different management strategies would have changed, even if we were able fully to address all of the inadequacies of our data. Notably, several authors have highlighted that the comparison of options for conservation is a more appropriate use of PVA than attempts to identify a minimum population size that will be viable (e.g. Boyce, 1992; Burgman *et al.*, 1993; Possingham *et al.*, 1993).



**Fig. 2.** The patch structure that was used for analyses of the persistence of populations of *G. leadbeateri* in the Murrindindi Forest Block. The identity of the various patches are as follows: (1) solid black polygons (e.g. Patch No. 32) correspond to stands of old growth forest; (2) stippled patches (e.g. Patch No. 58) represent areas of forest that are unavailable for timber harvesting such as stands on steep and rocky terrain. The solid lines are movement corridors that allow animals to 'diffuse' between habitat patches (see text). Each patch has been assigned a unique identifying number. The open polygons correspond to potential logging coupes and where harvesting operations may take place. The blank areas within the block map are stands of non-ash type eucalypt forest or areas that have only recently been logged which would be unsuitable for reservation for *G. leadbeateri*.

## Parameterisation of variables input to ALEX

### *Habitat requirements and life history attributes of G. leadbeateri*

Forests with the highest probability of supporting *G. leadbeateri* contain numerous large hollow-bearing trees and a high basal area of *Acacia* spp. (Lindenmayer *et al.*, 1991a, 1994a). These two variables were the only ones shown to have statistically significant predictive power in explaining the presence of *G. leadbeateri* within areas of montane ash forest. Trees with hollows provide nest sites for *G. leadbeateri* (Lindenmayer *et al.*, 1991c). *Acacia* spp. provide food such as gum, and a dense connected understorey layer through which the species can move (Smith & Lindenmayer, 1988; Lindenmayer *et al.*, 1994b).

Values for the life history parameters of *G. leadbeateri* that were input to ALEX are presented in Table 1. They were based on the results of a wide range of field studies of the species (Smith, 1980, 1982, 1984a, b; Lindenmayer, 1989; Thomas, 1989; Lindenmayer *et al.* 1991a,b,c,d, 1993a, b,c,d). The rationale for these values has been outlined in a previous study (see Lindenmayer *et al.*, 1993a) and it is only briefly summarised here. *G. leadbeateri* has a matriarchal social structure in which colonies of animals are typically comprised of a monogamously-mated breeding pair, pre-dispersal aged subadult offspring, and unrelated non-breeding adult males. Members of a colony defend a territory of approximately 1-3 ha (Smith, 1980). The sex ratio of the species at birth is 1 : 1 but the mating system typically results in a 3 : 1 male-biased sex ratio (Smith, 1980), so the number of breeding animals is probably limited by the abundance of adult females (Smith, 1984a). This social structure facilitates the use of ALEX which models only the fates of female animals (Possingham *et al.*, 1992). We assigned female *G. leadbeateri* to one of three age classes: newborn (< one year); subadults (between one and two years old), and adults (> two years old) (Table 1).



**Fig. 3.** The patch structure that was used for analyses of the persistence of populations of *G. leadbeateri* in the Stevenson Forest Block. The identity of the various types of patches is the same as that described in Fig. 2.

Based on the studies completed by Smith (1980, 1984a) as a guide, we set the age of sexual maturity of females to two years. *G. leadbeateri* may reproduce twice a year and have up to two pouch young in each breeding season (Smith, 1980, 1984a). Table 1 contains the estimated probabilities of different numbers of female young being produced per year (maximum = four). Estimates for the rates of mortality used in ALEX were varied among the three age-classes that can be modelled (Table 1). They were based on: (1) the conclusions of Smith (1980) about high rates of mortality amongst subadult females when they leave the natal territory; 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). These values for fecundity and mortality allowed us to calculate a mean annual population growth rate ( $\lambda$ ) (= 1.21) (Table 1).

We included a parameter in ALEX to allow for temporal variations in breeding success. Field observations have shown that factors such as climate conditions may result in a major reduction in the availability of some types of food (Smith, 1980, 1984a). Breeding success in *G. leadbeateri* appears to be closely related to the abundance of protein-rich arthropods (Smith, 1980; Tyndale-Biscoe, 1984), the availability of which is sensitive to drought. In addition, an important source of carbohydrates for *G. leadbeateri* is derived from the gums from *Acacia* spp. (Smith, 1984b; Lindenmayer *et al.*, 1994b) that are produced in response to a range of factors (New, 1984), such as water stress (Smith & Montgomery, 1959). However, nodules of gum have been only very rarely observed on the stems of *Acacia* spp. trees in montane ash forests during the past two years (D. McDonald, pers. comm.; Lindenmayer, personal observations), possibly as a result of mild and wet summers in the central highlands of Victoria. Taking this limited information into account, we parameterised ALEX so that *G. leadbeateri* did not breed on average every six years. Notably, for the purposes of this investigation, we assumed that environmental variation did not affect other population parameters such as the rates of mortality.

**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.

Variable	Value	Reference <sup>a</sup>
Min. home range of females in highest quality habitat	1.0 ha	1,2,3,4
Min. home range size of breeding females in old growth forest	3.3 ha	1,2,3,4
Max. population density (females per ha)	2	1,2,3,4
<b>Reproduction</b>		
No. breeding events per year	2	1,2,3
Age at sexual maturity (years)	2	1,2,3
Maximum litter size	2	1,2,3
Annual probability of producing 0 female young per female	0.45	5
Annual probability of producing 1 female young per female	0.30	5
Annual probability of producing 2 female young per female	0.18	5
Annual probability of producing 3 female young per female	0.06	5
Annual probability of producing 4 female per female	0.01	4
<b>Mortality</b>		
Annual probability of death		
Newborn	0.0	6
Subadults	0.3	6
Adults	0.3	6
<b>Population growth</b>		
Population growth rate under ideal conditions	1.21	7
Population threshold for quasi-extinction	2	8
<b>Movement</b>		
Mean migration distance of subadults	2 km	9
Population density before migration (% of maximum)	20%	1,2,3,10
Migration probability of subadults	70%	1,2,3,10
Population density before diffusion (% of maximum)	10%	1,2,3,10
Diffusion probability for subadults	20%	1,2,3,10

<sup>a</sup>1, Smith (1980); 3, Smith (1982); 3, Smith (1984a); 4, Lindenmayer *et al.* (unpublished data) derived from mark-recapture and radio-telemetry studies at Cambarville in the central highlands of Victoria (see also Meggs *et al.*, 1991); 5, Derived from the application of a subprogram within ALEX called BIRTHS (see Possingham & Davies, 1995) where the probability of a certain number of young is calculated using data on sex ratio at birth and the number and size of litters; 6, Values based on data summarised in Lindenmayer *et al.* (1993a) that have, in turn, been synthesised from studies by Smith (1980, 1982, 1984a) as well as records from captive animals and a recent recapture investigation (Lindenmayer *et al.*, unpublished data); 7, Calculated by ALEX from a synthesis of other input data; 8, Quasi-extinction threshold (*sensu* Ginzburg *et al.*, 1982) defined as two specifically

for the purposes of this study; 9, Derived from radio-telemetry studies (Lindenmayer *et al.*, unpublished data); 10, Estimates calculated from a synthesis of field studies by Smith (1980, 1982, 1984a) and Lindenmayer *et al.* (unpublished data).

#### *Simulating the movement of animals between habitat patches*

The migration and diffusion submodels within ALEX were applied to simulate the movement of *G. leadbeateri* between patches of suitable habitat. The values used to parameterise these submodels are based on investigations of the demography of the species (Smith, 1980, 1984a) and radio-tracking studies (Lindenmayer *et al.*, unpublished data). The migration submodel was employed to simulate the movement of animals among patches of habitat > 200 m apart. This minimum distance criterion was applied because the home range of *G. leadbeateri* is normally 1-3 ha (Smith, 1980; Lindenmayer *et al.*, unpublished data). The migration submodel was invoked for only subadult *G. leadbeateri* (animals aged 1-2 years) and the maximum value for the annual probability of migration was set to 70%. This value was based on studies by Smith (1980, 1984a), who found that adult female *G. leadbeateri* enforced the dispersal of their female offspring when they were approximately one year old. Migration occurred when the abundance of individuals in a particular patch exceeded 20% of its maximum carrying capacity. This value was selected because adult female *G. leadbeateri* are intolerant of adult conspecifics of the same sex (Smith, 1980, 1984a). When population densities were lower, animals were likely to disperse to adjacent unoccupied forest located within the same habitat patch. The probability of survival during dispersal declined exponentially with an increase in the inter-patch distance. Migrating *G. leadbeateri* moved in a straight line and a random direction from a source patch and were capable of travelling an average of 2 km before they died. Hence, the probability of survival of any given individual was related to the size of suitable habitat patches and the distance between them.

The movement of *G. leadbeateri* to suitable habitat in adjacent patches (i.e. those areas < 200 m apart) or between patches connected by streamside reserves was simulated using the diffusion submodel in ALEX. There was no additional mortality associated with diffusion. The probability of diffusion was set to 20% for subadult females. This accounted for the movement of those animals that did not undergo migration (see above). The probability of diffusion was set to 10% for the adult age cohort (> two years old) to allow some animals to make minor adjustments to the location of their territories or move to adjacent areas of forest that supported more suitable habitat.

#### *Patch structure used in the analysis*

Four types of patches were used in our analyses of the Murrindindi and Steavenson Forest Blocks: (1) existing stands of old growth forest that are presently excluded from logging; (2) forests on steep and rocky terrain and in riparian zones which are unavailable for timber harvesting; (3) a subset of logging coupes where changes in present silvicultural practices were simulated; and (4) the remainder of the forest landscape where clearfelling operations occurred. Maps of the patch structures in the Murrindindi and Steavenson Forest Blocks are presented in Figs 2 and 3. The patch arrangement constructed for the Murrindindi and Steavenson Forest Blocks was based on forest inventory information that had been gathered by Victorian Department of Conservation & Natural Resources. A GIS database of this information was interrogated to extract information on the size and spatial location of patches of old growth forest and other logging exclusion zones in the two study areas. Each patch was assigned a number and a set of x,y co-ordinates that corresponded to its location within a given forest block. Data on the type, size and location of the various patches were put into ALEX. For our analyses, those old growth patches which were 0.4 ha or smaller and which were located > 500 m from other areas of old growth were not included in the patch structure. In those scenarios where logging coupes were modelled as containing potentially suitable habitat, such areas were incorporated into the patch structure by assigning them x,y co-ordinates and importing them to ALEX in the same way as outlined above.

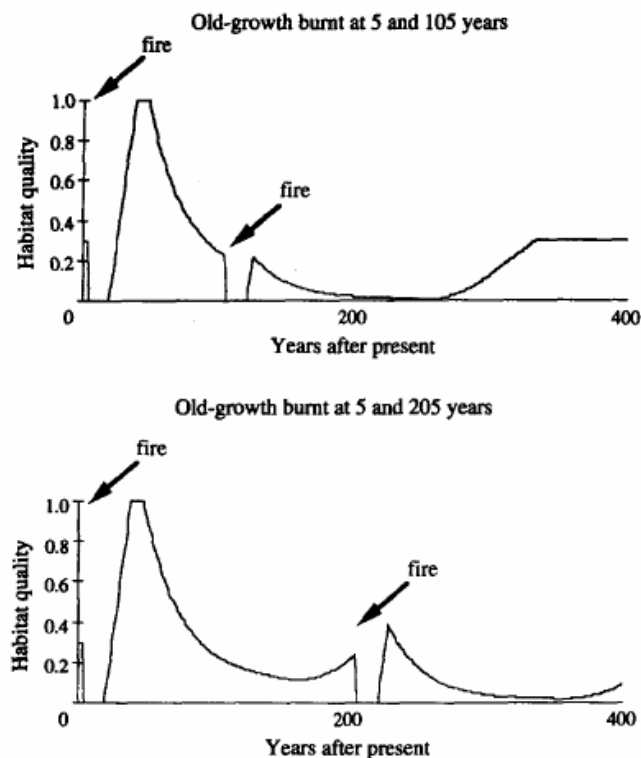
#### *Habitat quality indices for different types of patches*

We derived a habitat quality index with a value of between 0 and 1 for each of the four kinds of areas that comprised the patch structure used in our analyses. The reciprocal of this number corresponded to the maximum abundance of adult breeding female *G. leadbeateri* per ha. This habitat quality value was derived from a combination of measures of the suitability of the two key attributes of forest structure for the species: the foraging substrate and the availability of nest sites. The submodels that were used to calculate the various habitat suitability indices were, in turn, incorporated as part of the sequence of program flow within ALEX (see Appendices 1 & 2). We incorporated temporal variations in the suite of habitat indices to enable them to change in response to disturbances resulting from wildfires and logging operations (see

Appendices 1 & 2). The basis for the calculation of the various habitat suitability indices is outlined below, as well as in Appendices 1 and 2.

*Patch Type 1 -- OM growth forest.* Using the results of field surveys at 207 sites as a guide (Lindenmayer *et al.*, 1991a, 1994a), we estimated that old growth forests would support approximately one adult breeding female per 6 ha. The corresponding index for habitat quality was set to 0.3. Although this allowed for, at most, two reproductively active females per 6 ha of old growth forest, an examination of our simulations indicated that there were typically half this number of animals. This is equivalent to the values observed in field surveys. We incorporated no temporal changes in habitat suitability within old growth patches in the absence of wildfires (see Appendix 1). This was because (1) most trees with hollows within these types of forest are large living trees which suffer relatively minimal rates of collapse (Lindenmayer *et al.*, 1990c); and (2) studies to date have found no significant changes in the abundance of *G. leadbeateri* between stands of old growth forest of different age (Lindenmayer *et al.*, 1991a, 1994a).

*Patch Type 2 -- Forests on steep areas and in streamside reserves.* A habitat suitability value of 0.15 was specified for stands on steep and rocky areas and forest within streamside reserves. We used relatively low values for habitat quality in these areas because field observations have indicated that forests in these types of areas rarely support *G. leadbeateri* (Lindenmayer *et al.*, 1991a, 1993d). Because dead trees with hollows in these areas have a high probability of collapsing during the next two to three decades (Lindenmayer *et al.*, 1990c, unpublished data), we set the habitat quality value so that it declined to 0.05 over the following 100 years. After this period, the trend was reversed as a result of the recruitment of such trees, and it was specified to return gradually to 0.15. These values for the habitat suitability index mean that, whilst these areas would facilitate the movement of animals between patches of old growth forest, they would support relatively low densities of residents.



**Fig. 4.** The response curve for temporal variations in habitat suitability for *G. leadbeateri* in a patch of old growth forest burnt after five and 105 years, and five and 205 years. The line in each of the diagrams 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.



*Patch Type 3 -- The remainder of the forest landscape.*

Any part of the Murrindindi and Steavenson Forest Blocks that was not assigned to either of the two types of patches described above was assumed to be available for logging. The temporal change in the habitat suitability index for these areas was dependent upon the rotation time. If the interval between clearfelling operations was < 150 years, the value for habitat remained at zero. This was because such a frequency of timber harvesting events would impede the development of sufficient trees with hollows and prevent logged areas from supporting suitable habitat for *G. leadbeateri* (Lindenmayer, 1992a,b). For simulations where the rotation time exceeded 150 years, we set the habitat quality index so that it gradually approached that of old growth forest (i.e. = 0-3; see above). If these areas were then clearfelled, the value for habitat suitability reverted to zero and did not begin to increase until the stand exceeded 150 years of age. These values have been derived using information on the age of trees that are likely to develop cavities suitable for occupation by *G. leadbeateri* (Smith & Lindenmayer, 1988; Lindenmayer *et al.*, 1991c, 1993b).

*Patch Type 4 -- Logging coupes where modified silvicultural practices were employed*

We simulated an array of management options where existing clearfelling practices were modified. In these cases, parts of specified logging coupes were left unlogged and allowed to reach ecological maturity. The variations in habitat suitability indices associated with the range of different scenarios were complex and they are outlined in more detail below (see also Appendix 2). *Simulating the impacts of wildfires on habitat suitability* Logging and wildfires are the two major forms of disturbance within the montane ash forests of the central highlands of Victoria. There have been more than ten wildfires in the region since European settlement (Lindenmayer *et al.*, 1991d). Those in 1939 burnt 70% of the region (Noble, 1977), and they had a major impact on (1) vegetation structure within stands of montane ash forest (Lindenmayer *et al.*, 1991d); (2) the suitability of the forest for *G. leadbeateri* (Lindenmayer *et al.*, 1991a); and (3) the spatial arrangement of habitat patches (Lindenmayer *et al.*, 1993c; Possingham *et al.*, 1994). Because wildfires have significantly influenced a range of key characteristics of the vegetation in ash-type eucalypt forests, we incorporated the impacts of *both* logging and fires in our analyses. Based on information on the incidence of wildfires in the central highlands of Victoria since European settlement, we modelled fire regimes in which the annual probability of fire was set to 1% with values of 50% and 75% for the average proportion of patches burnt in any given conflagration.

Clearly, many other possible fire regimes could have been examined, and a more detailed study of the impacts of wildfire *per se* on populations of *G. leadbeateri* is presented elsewhere (Lindenmayer & Possingham, in press).

Because the suitability of nest sites and foraging substrates for *G. leadbeateri* are significantly influenced by wildfires (Smith & Lindenmayer, 1992; Lindenmayer *et al.*, 1991b, 1993b), we developed a number of submodels to track the interrelationships between these habitat components and fire events (Fig. 4). These submodels were incorporated within ALEX to allow temporal variations in habitat patch suitability to be modelled. The submodels were based on information from studies of (1) the response of ash-type eucalypt trees and stands of *Acacia* spp. to fire (Mount, 1979; Noble & Slatyer, 1980; Ashton, 1981a,b; Adams & Attiwill, 1984; Lindenmayer *et al.*, 1991d, 1993d; Ough & Ross, 1992; Smith & Lindenmayer, 1992); (2) the ontogeny of cavities in montane ash trees (Ambrose, 1982; Smith & Lindenmayer, 1988; Lindenmayer *et al.*, 1993b); and (3) the decay and collapse of trees with hollows (Lindenmayer *et al.*, 1990c).

Post-fire salvage clearfelling operations are typically employed to cut stands of montane ash forest that are damaged in a wildfire (Noble, 1977; McHugh, 1991; Smith & Lindenmayer, 1992). Such activities have a major impact on habitat development for *G. leadbeateri*, particularly if large burnt trees with hollows are felled (Smith & Lindenmayer, 1992). In the absence of such activities, large burnt trees in these areas retain the potential to provide nest sites for *G. leadbeateri*. *Output data derived from computer simulation modelling* Possingham *et al.* (1992, 1994) and Possingham and Davies (in press) describe the outputs produced from the application of ALEX. The main outputs in this study were the probability of extinction and the incremental probability of extinction. The 'steady state' or incremental probability of extinction was the extinction probability averaged over a series of time steps, each of the same duration (150 years in this study). It was derived by the following method. A value for the predicted probability of extinction was generated for each 150 year time interval of a simulation. This value was a function of the 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.

Estimates of the probability of extinction and the incremental probability of extinction were based on a minimum of 300, and up to 1000, simulations that were completed for each scenario. The standard deviations associated with these measures were generated from the formula  $SD = \sqrt{\ln p(1-p)}$ , where  $n$  is the number of simulations, and  $p$  is the probability of extinction during a given time frame. Thus, for example, a maximum standard deviation of about +1% in the extinction probability would be associated with scenarios where 1000 runs were completed.

### **The range of management options examined in the study**

We examined several possible modifications to forest management that could be applied in the Murrindindi and Steavenson Forest Blocks. These included the maintenance of existing forest management practices, variations in the rotation time, and changes to current clearfelling operations. Clearly many others could have been investigated such as high-lead and cable logging. However, we limited our analyses to those approaches which are most likely to be considered as potentially suitable strategies for timber harvesting in the montane ash forests of the central highlands of Victoria. A patch structure comprised of stands of old growth forest and stands occurring on steep and streamside areas was used in all of the management options that were examined. Hence, the principal modifications in the patch structure between the various scenarios involved changes in the way we simulated logging operations within the remaining part of the forest landscape that was available for timber harvesting.

#### *Case 1 -- No change to present forest management strategies*

Here, the probability of extinction of *G. leadbeateri* was estimated for patch structures comprised of existing areas of suitable habitat and forest excluded from timber harvesting in both the Murrindindi and the Steavenson Forest Blocks. These simulations were designed to test the response of the species to the 'status quo' where there were no changes to existing forest management strategies. For these analyses we assumed that the part of forest landscape that was available for timber harvesting was clearfelled on average every 100 years and never supported suitable habitat for populations of *G. leadbeateri*. The simulations for the Murrindindi Forest Block were completed in the absence of wildfires. For the Steavenson Forest Block, we set the incidence of wildfires to an annual probability of 1% with 50% or 75% of patches burnt in any given fire event. Notably, the impacts of post-fire salvage logging were not modelled in either of the two forest blocks that were examined.

#### *Case 2 -- Variation & logging rotation times in the Murrindindi Forest Block & the absence of wildfires*

The results of our analyses indicated that populations of *G. leadbeateri* may persist for only a limited period within the Murrindindi Forest Block (median time to extinction = 10 years). To overcome the problems associated with such a small area of old growth in the Murrindindi Forest Block, we employed a forward time projection of 150 years and completed simulations of metapopulation dynamics starting from this time. We recorded results only after a further 150 years when the dynamics of forest age class distribution had attained an equilibrium distribution. We assumed that populations of animals would persist or be restored in this area 150 years from now. These procedures were necessary to explore the potential long-term benefits for the conservation of *G. leadbeateri* that may flow from efforts to modify the forest age class distribution that presently characterises the Murrindindi Forest Block. The patch structure that resulted from the time jump that was applied in the Murrindindi Forest Block was as follows: (1) existing areas of old growth forest continued to persist as ecologically mature forest; (2) forests in streamside reserves and on steep terrain matured and developed a habitat quality value of 0.15 (see above); (3) the remaining area within the Murrindindi Forest Block was partitioned to give an evenly distributed sequence of forest age classes. Each forest age cohort was set five years apart giving stands that ranged from 0 to 200 years old. Clearfelling on a rotation of 50, 100, 150, 200, 250, 300, 350 and 400 years was then simulated to occur within the part of the forest landscape that was available for timber harvesting.

#### *Case 3 -- Variation in logging rotation times in the Steavenson Forest Block*

Here, the simulations were similar to those described in Case 2, but with the following modifications. No time projection was applied because the initial analyses for the Steavenson Forest Block indicated that populations of *G. leadbeateri* had a reasonable probability of persistence during the next 150 years (Table 2). In

addition, a limited range of fire regimes was incorporated in the analyses; viz., a fixed annual probability of fire of 1% with 50% and 75% of patches burnt in any given conflagration. Post-fire salvage logging operations were simulated to occur in those areas of burnt forest that were available for timber harvesting. We assumed that old growth forest and other excluded areas (e.g. forest on steep slopes and patches retained within coupes) were not salvage logged if they were burnt.

**Table 2. The estimated probability of extinction (%) of populations of *G. leadbeateri* in the Murrindindi and Steavenson Forest Blocks in response to current forest management strategies for the species (Macfarlane & Seebeck, 1991)**

Simulations of the Murrindindi Forest Block were completed in the absence of wildfires. For the analyses of the Steavenson Forest Block we set the annual probability of a fire to 1% and the average number of patches that were burnt in a conflagration was either 50% or 75% (see text for further explanation). Post-fire salvage logging operations were not incorporated in the analysis of the Steavenson Forest Block.

Proportion of patches burnt in a wildfire	Extinction probability at various times					P[I] <sup>a</sup>
	P <sub>150</sub>	P <sub>300</sub>	P <sub>450</sub>	P <sub>600</sub>	P <sub>750</sub>	
<b>Steavenson Forest Block</b>						
50%	17	49	72	82	91	42
75%	42	79	91	97	99	60
<b>Murrindindi Forest Block</b>						
No fires	100	100	100	100	100	100

<sup>a</sup>Column 7 contains the values for the incremental probability of extinction (P[I]). This was calculated as follows: the probability of extinction for each of the 150-300, 300-450, 450-600 and 600-750 year time steps was derived; these values were then averaged to give the incremental probability of extinction (see text for further details).

#### *Case 4 -- Changed logging practices in harvested areas within the Murrindindi Forest Block*

The patch and landscape configuration, as well as the 150 year time projection used in the simulations in Case 4, were the same as those described for Case 2. However, we substantially modified the way we modelled logging operations. A number of factors were varied to accommodate simulated modifications to timber harvesting operations in the Murrindindi Forest Block. These included (1) the amount of forest that retained within each logging coupe; and (2) temporal changes in the habitat quality value of the unlogged area within each coupe.

We set the size of logging coupes to 50 ha. Each area was then partitioned into two parts -- a logged and a retained component. A clearfelling operation was simulated every 50 years within the part of each coupe that was available for timber harvesting and we assumed that populations of *G. leadbeateri* did not persist in these areas. Because retained patches would be surrounded by a larger logged area that is then burnt by a very high-intensity regeneration fire, we assumed that animals would have to recolonise the retained patches to re-establish populations in the harvested coupe. Temporal variations in the habitat suitability values within retained areas were then modelled as follows. In the absence of wildfire, patches of unlogged forest would develop into old growth stands and contain large trees with hollows that could provide suitable nest sites for *G. leadbeateri*. Given this, we set the habitat suitability index of these areas to be the same as if they were old growth. The development of dense regrowth forest in the logged and regenerated coupe adjacent to the retained area would lead to the creation of a type of 'edge habitat' comprised of potential nest trees and a dense forest understorey. We set the habitat suitability index to increase gradually to 1 after 30 years to reflect these changes in vegetation structure. This was because high densities of *G. leadbeateri* have been recorded in forests that are characterised by such a combination of habitat attributes (Lindenmayer *et al.*, 1991a). The value of the habitat quality index reverted to 0.3 each time the adjacent stand was logged (i.e. every 50 years) (see Appendix 2).

A range of simulations was completed where the amount of forest that was retained within a coupe was varied from 10, 20, 40 and 100% of a logged area. In each case we set the total amount of forest that was set aside under these various management regimes to approximately 150 ha. Notably, we could have modelled a total area of retained habitat that was smaller or larger than 150 ha, but it was the *relative* outcomes of the various options for forest management that were of greatest interest. We compared the results of simulations in the Murrindindi Forest Block where (1) 10% of 24 logging coupes each of 50 ha was excluded from timber harvesting; (2) 20% of the forest was retained within each of 12 logging coupes; (3) logging was excluded from 40% of each of six coupes; and (4) three 50 ha areas were permanently excluded from wood production. This approach was used to facilitate the comparison of the effectiveness of the different approaches.

*Case 5 -- Changed logging practices in harvested areas within the Steavenson Forest Block*

Here, Case 4 was run in the Steavenson Forest Block but without a 150 year time projection and with the addition of the fire and salvage logging regimes outlined in Case 3. Thus, the development of suitable habitat within the retained patches was delayed for 150 years until such stands attained ecological maturity and supported large trees with hollows. For this phase of our analyses we used rotation times of 50 and 100 years for the part of each coupe that was not excluded from logging. Where the 100 year interval between logging operations was applied, the response of habitat quality index was the same as described in Case 4, except that it began to decline once the forest surpassed an age of 60 years and it gradually approached that of old growth forest (= 0.3) over the subsequent decades. These variations were imposed to mimic the mortality of *Acacia* spp. trees that is associated with the processes of stand maturation in ash-type eucalypt forests (Adams & Attiwill, 1984; Smith & Lindenmayer, 1992).

**Table 3. The predicted probability of populations of *G. leadbeateri* in response to varying logging rotation times in the Murrindindi Forest Block**

The impacts of wildfires were not incorporated in the analyses. For explanation of the incremental probability of extinction (P[I]) in column 7, see Table 2.

Rotation time	Extinction probability at various times					
	P <sub>150</sub>	P <sub>300</sub>	P <sub>450</sub>	P <sub>600</sub>	P <sub>750</sub>	P[I] <sub>150</sub>
50 years	100	100	100	100	100	100
100 years	100	100	100	100	100	100
150 years	1	100	100	100	100	100
200 years	0	35	61	77	87	40
300 years	0	1	2	3	4	1
400 years	0	0	1	1	1	1

## RESULTS

### Case 1 - Maintenance of present forest management strategies

The continuation of current forest management practices was predicted to produce a pessimistic outcome for the Murrindindi Forest Block even though we excluded the influence of wildfires and salvage harvesting (Table 2). The values for the predicted probability of extinction of *G. leadbeateri* in this case were identical for all of the time steps that were examined. This was because no populations were predicted to persist beyond the first 150 year time interval. Indeed, the median time to extinction of *G. leadbeateri* in this forest block was only 10 years (Table 2). The results of our analyses indicated that *G. leadbeateri* was more likely to persist in the Steavenson Forest Block under the present forest management regimes, although the corresponding values for the probability of extinction were relatively high in both fire regimes that were modelled (Table 2).

### Case 2 - Variation in logging rotation times in the Murrindindi Forest Block without wildfire

The relationships between logging rotation times and the persistence of populations of *G. leadbeateri* in the Murrindindi Forest Block are presented in Table 3. The results demonstrated that there was no positive effect on population persistence until the rotation time exceeded 150 years. Increasing the rotation time beyond 200 years resulted in a significant reduction in the predicted probability of extinction. For example, the incremental probability of extinction (P[I]) for any 150 year period approached 1% when the interval between logging operations was longer than 300 years (Table 3).

### Case 3 - Variation in logging rotation times in the Steavenson Forest Block

As in Case 2, our analyses indicated that there was a general decline in extinction probability with an increase in the rotation time in the Steavenson Forest Block. However, these changes were minimal when the rotation time was < 150 years and a significant enhancement of viability was predicted to occur only when there was a longer period between timber harvesting operations (Table 4). These general trends in the data were similar in both of the fire regimes that were modelled, although the range of values for both the predicted probability of extinction and the incremental probability of extinction (P[I]<sub>150</sub>) were higher when fires burnt 50% of patches than where 75% of patches were burnt in a conflagration (Table 4). Moreover,

reductions in the extinction probability using rotation times of 300 and 400 years were more pronounced when a more moderate fire regime was employed (Table 4).

**Cases 4 & 5 -- The impacts of changed silvicultural practices within logged areas in the Murrindindi and Steavenson Forest Blocks**

The results of analyses where different amounts of forest were retained within logged coupes in the Murrindindi Forest Block are presented in Table 5. Here, the value for the incremental probability of extinction was markedly lower in simulations with three unlogged 50 ha areas, than where the other approaches for setting aside forest were modelled (Table 5). Table 6 contains the results of analyses where different strategies for conserving unlogged areas in the Steavenson Forest Block were simulated. All of the approaches for retaining areas of forest reduced the values for the incremental probability of extinction below those observed in simulations where no conservation strategies were employed. However, the lowest values for this measure were recorded when three 50 ha areas were withdrawn from timber harvesting. Notably, these trends were consistent irrespective of the rotation times for logging within those parts of coupes that were not retained (50 and 100 years) (Table 6).

**Table 4. The predicted probability of populations of *G. leadbeateri* in response to varying logging rotation times in the Steavenson Forest Block**

A value for the incremental probability of extinction P[I] is given in column 7. An annual probability of fire of 1% was employed for these scenarios and the values in Section A are derived from simulations where an average of 75% of patches were burnt. Section B contains the results of runs in which an average of 50% of patches were destroyed in a fire.

Rotation time	Extinction probability at various times				
	P <sub>150</sub>	P <sub>300</sub>	P <sub>450</sub>	P <sub>600</sub>	P <sub>700</sub>
<b>Section A — 75% of patches burnt in a fire</b>					
50 years	37	76	92	95	98
100 years	42	78	93	97	98
150 years	41	76	93	97	98
200 years	37	69	87	95	98
300 years	41	64	83	88	94
400 years	40	61	81	90	95
<b>Section B – 50% of patches burnt in a fire</b>					
50 years	13	43	66	81	88
100 years	12	40	65	80	88
150 years	16	45	64	77	86
200 years	14	38	61	73	83
300 years	14	35	52	66	72
400 years	10	25	40	49	58

**Table 5. Values for the predicted incremental probability of extinction  $P[I]$  of simulated populations of *G. leadbeateri* during a 150 year period in the Murrindindi Forest Block**

The area of retained habitat is approximately 150 ha in each case. The asterisk highlights simulations where three areas, each of 50 ha, were totally withdrawn from harvesting. A rotation time of 50 years was used for these analyses. The annual probability of wildfire was 1% and an average of 50% of patches were burnt in a fire.

No. coupes treated	Proportion of coupe retained	$P[I]_{150}$
24	10%	77
12	20%	80
6	40%	79
3*	100%	50

**Table 6. Values for the predicted incremental probability of extinction  $P[I]$  of simulated populations of *G. leadbeateri* during a 150 year period in the Steavenson Forest Block**

For these simulations the annual probability of wildfire was set to 1% and 50% of patches were burnt in a fire. The area of retained habitat is approximately 150 ha in each case, except where no reserved habitat was modelled. The asterisks highlight simulations where three areas, each of 50 ha, were totally withdrawn from harvesting.

Rotation time	No. coupes treated	Proportion of coupe retained	$P[I]_{150}$
No retained forest	NA	NA	39
50 years	24	10%	23
50 years	12	20%	25
50 years	6	40%	22
50 years	3*	100%	18
No retained forest	NA	NA	39
100 years	24	10%	24
100 years	12	20%	22
100 years	6	40%	24
100 years	3*	100%	18

## DISCUSSION

### General findings and the maintenance of present forest management strategies

Our findings indicated that there are substantial differences between the Murrindindi and Steavenson Forest Blocks in the likelihood of persistence of *G. leadbeateri* (Table 2). These results are related to differences between the Murrindindi and Steavenson Forest Blocks in the amount and spatial distribution of suitable habitat for the species (compare Figs 2 and 3). Our findings from simulations of the Murrindindi and Steavenson Forest Blocks are likely to provide the range of typical values for the probability of extinction of populations of *G. leadbeateri* that could be expected from other timber production forest blocks in the central highlands of Victoria. This is because the area of suitable habitat in the Murrindindi and Steavenson Forest Blocks is near the lower and upper limits for these types of forest in other blocks in the region (J. Smith, pers. comm., Department of Conservation & Natural Resources, unpublished data). Hence, there is insufficient suitable habitat in either block to support populations that are secure in the long term.

Given that there appears to be a need for upgraded management strategies to enhance the conservation of *G. leadbeateri*, it is important to identify which ones are likely to be the most effective and, in this case, also impinge least on other forest uses such as the production of timber and pulpwood. However, the development of enhanced strategies must be considered in terms of the protracted period (>100-150 years) that must elapse before conservation efforts within the extensive areas of existing regrowth montane ash forest may make a positive contribution to the persistence of *G. leadbeateri*. This is a consequence of the very old trees used as nest sites by the species (Smith & Lindenmayer, 1988;

Lindenmayer *et al.*, 1991c). Despite this, there is nevertheless considerable merit in taking action now in an attempt to redress the problems associated with the shortage of suitable habitat. This is because long-term strategies could eventually allow (1) the maintenance or establishment of self-sustaining populations and thus reduce and/or obviate the need for intensive management efforts; and (2) the creation of suitable areas that may be useful for future translocation and/or reintroduction programmes.

### **The impacts of variations in rotation times**

The results of simulations indicated that increasing the rotation time could have a positive effect on the persistence of populations of *G. leadbeateri*. However, even if the rotation time were more than tripled from the present interval of 50-80 years, this would still only provide suitable habitat for a relatively short period (e.g. 50 years) before such areas would eventually be logged again and become unsuitable for *G. leadbeateri*. Hence, a given area of timber production forest will remain unsuitable for a significant proportion of any given rotation period because it will be a long time before suitable hollows begin to develop. Although we recorded some encouraging results from our simulations of the Murrindindi Forest Block, these findings require considerable qualification because of the number of simplifying assumptions that were employed. First, we excluded the impacts of wildfires. Second, we have applied a 150 year time projection to overcome the problems resulting from our initial forecasts from Case I which indicated that populations of *G. leadbeateri* would disappear quickly from this forest block. These factors made our findings highly optimistic. Our results from the Steavenson Forest Block are likely to have been more realistic and they suggest that even under the best circumstances (i.e. a low-intensity fire regime and a 400 year rotation time), the extinction rate would only be halved (see Table 4). In summary, the results of this study indicate that the effectiveness of extending the interval between logging operations may be limited by key ecological processes such as the time required to recruit suitable nest sites for *G. leadbeateri*.

A number of other important factors need to be considered in assessing the merits of significantly increasing the rotation time. For example, trees in stands that are > 250 years old are likely to have a decayed and hollow centre (Ambrose, 1982) and contain numerous cavities (Lindenmayer *et al.*, 1993b) which would considerably reduce their value as sawlogs. Finally, a shift to a much longer rotation would necessarily be associated with an immediate and dramatic reduction in yields of timber and pulpwood from the montane ash forests. This would be problematic, particularly given legislated commitments by the Victorian State Government to provide large quantities of wood to the Forest Industry (Government of Victoria, 1986).

### **Changed silvicultural practices and a comparison between management options**

The impacts of clearfelling on forest wildlife are controversial and many authors have called for such practices to be modified (e.g. Rawlinson & Brown, 1980; Smith & Lindenmayer, 1988, 1992; Gruen *et al.*, 1989). Indeed, a major focus of Victorian Government research has been an examination of the environmental impacts of clearfelling and an assessment of alternative forestry practices (Squire, 1987; Squire *et al.*, 1991b). Our analyses focused on simulating the retention of 10, 20, 40 and 100% of the forest within a logging coupe and predicting the impacts of such actions on the persistence of populations of *G. leadbeateri* in the Murrindindi and Steavenson Forest Blocks. All of these management approaches were predicted to make a significant positive contribution to the persistence of *G. leadbeateri*. However, the trends from our analyses indicated that, in general, the most effective conservation strategy was to withdraw three proposed 50 ha logging coupes from timber harvesting and set them aside as permanent reserves (Tables 5 and 6). Thus, based on the results of this study, it appears that the long-term conservation of *G. leadbeateri* in wood production areas may be better served by complete reservation of a number of areas from timber harvesting, rather than a major modification of existing clearfelling practices. Importantly, the permanent reservation of areas of forest may be a more practical management option than the modification of silvicultural practices within logging coupes. Attempts to modify present clearfelling operations have been beset by a number of problems. For example, trees that are retained within harvested areas are frequently badly damaged and/or killed by high-intensity stand regeneration fires (Lindenmayer *et al.*, 1990b; Milledge *et al.*, 1991), and they are highly susceptible to being windthrown (Lindenmayer *et al.*, unpublished data). In addition, the retention of patches of forest within logged areas may create a major occupational safety hazard for timber workers, particularly when the branches of cut trees become caught in the crowns of unharvested stems (Squire, 1987). This study was confined to a limited comparison of some management options for the conservation of *G. leadbeateri*. Although the most appropriate approach that we identified was to exclude areas of forest from logging, we did not attempt to determine either (1)

how much reserved forest should be set aside in any given wood production block, or (2) the most effective design/s for the implementation of a network of reserves for *G. leadbeateri*. These are complex issues that will be tackled in another study.

### **Some further implications for integrated forest and wildlife management**

In this investigation we have examined the efficacy of three possible strategies for enhancing the conservation of *G. leadbeateri*: (1) changing the rotation time; (2) modifying silvicultural practices; and (3) reserving areas from timber harvesting. Of the three approaches, the most effective appeared to be the complete withdrawal of areas from wood production. Our findings from simulations of different levels of habitat retention within logged areas have already been discussed. However, our conclusions are further supported by the outcomes of two scenarios (Cases 3 and 5) for the Steavenson Forest Block where the simulated timber harvesting practices were different but the fire regimes and patch structures were identical. The value for the incremental probability of extinction in the Steavenson Forest Block when just three 50 ha were set aside ( $P_{ext}$  = 18%; Table 6) was lower than all of the rotation times that were examined (Table 4). The only exception was for a rotation time of 400 years, when the values for  $P_{ext}$  were almost identical (18 and 17% respectively). Thus, we predict that the reservation of 150 ha would have a similar positive impact on metapopulation viability as clearfelling the Steavenson Forest Block on a 400 year rotation. Although we have not presented the results, when we simulated the reservation of more areas, it depressed the associated value for the extinction probability well below that generated from modelling very long rotation times. The long-term value of reserving areas of forest is that it will add to the existing mosaic of old growth patches in a given forest block. Furthermore, the addition of only 150 ha of reserves in any forest block would substantially increase the overall area of old growth that it contained. A key part of the present management strategies for conservation of *G. leadbeateri* is the use of a set of 'movable reserves' where areas of presently suitable habitat are set aside as temporary refuges until changes in vegetation structure mean they become available for clearfelling (see Macfarlane & Seebeck, 1991). The results of our analyses indicate that the permanent reservation of areas of forest appears to be a more effective long-term strategy. This is because it overcomes difficulties with the recruitment of new areas of suitable habitat which is a major problem associated with the application of a movable and temporary reserve system (Lindenmayer & Norton, 1993).

Whilst the reservation of patches was found to be the best conservation strategy for *G. leadbeateri*, we do not dismiss the potential value of attempts to identify forestry practices that are more environmentally sensitive than clearfelling. There will be many taxa, particularly those that are dependent on elements of old growth forest such as trees with hollows, that would benefit from modified methods of timber harvesting (Scotts, 1991; Lindenmayer, 1992a, b). Given this, there is considerable merit in continuing to trial a range of different silvicultural systems in Victorian forests. Furthermore, it may be appropriate to begin to move away from the concept that the same silvicultural methods need to be applied in all areas which are designated for logging. This would result in different prescriptions being used in different sites and allow some coupes to be managed on a longer rotation, others to support a number of retained stems, and clearfelling to continue in a proportion of the remaining areas (Loyn, 1985; Lindenmayer, 1994). Notably, we did not examine the economic costs and trade-offs associated with the various forest management strategies that were explored in this study. These factors are clearly very important in any assessment of the efficacy of alternative silvicultural practices (for example see Hyde, 1989), although this was well beyond the scope of this examination. However, approaches such as those applied in other investigations of montane ash forests (e.g. McKenney & Common, 1990) could be useful as a topic for a subsequent study.

The extensive stands of old growth forest within water catchment forests in the central highlands of Victoria where logging is presently excluded will be fundamentally important for the long-term preservation of *G. leadbeateri* (Lindenmayer & Norton, 1993). Despite this, we also consider that strategies to enhance the conservation of the species in wood production areas will also be important. This is because (1) there is a reasonable probability that catastrophic wildfires could eliminate the species from the water catchments ( $P_{ext} = 15\%$ ) (Lindenmayer & Possingham, in press); (2) present forest use and conservation legislation require native wildlife to be conserved *throughout* their known distributions (Government of Victoria, 1988, 1992); and (3) maintaining populations of *G. leadbeateri* in many forest blocks reduces the chance that all of them would be destroyed in a major conflagration, giving a 'risk-spreading' type of conservation strategy. Indeed, the continued suppression of wildfires will be important



not only for the management of *G. leadbeateri* but also for other species of arboreal marsupials that exhibit a similar pattern of dependence on the abundance of trees with hollows and will be vulnerable to the changes in vegetation structure associated with major conflagrations (e.g. greater glider *Petauroides volans*; Possingham *et al.*, 1994).

### LIMITATIONS OF THE STUDY

There were a number of assumptions and limitations that underpinned our study and the most important ones are briefly outlined below.

Several simplifying assumptions were applied in most of the scenarios that were completed for the Murrindindi Forest Block. In particular, we employed a 150 year time projection to overcome the problems of the very limited areas of suitable habitat and the associated high values for the predicted probability of extinction (Table 2). This assumed that there would be no fires within the block over the next 200 years. Although such a time projection was unrealistic, it provided an indication of the potential long-term benefits for *G. leadbeateri* of adopting upgraded conservation strategies.

For the purposes of our analyses, we modelled each forest block in isolation and assumed it behaved as a 'closed system'. This assumption is unlikely to have influenced our results for the Murrindindi Forest Block which is surrounded by other forest blocks that are also characterised by few and very small areas of old growth montane ash forest (J. Smith, pers. comm.; Department of Conservation & Natural Resources, unpublished data). However, for the Steavenson Forest Block, there could be a trickle of immigrants from the O'Shannassy Water Catchment if suitable habitat continued to remain in that area. Hence, we may have underestimated the probability of extinction of populations of *G. leadbeateri* in the Steavenson Forest Block. This problem could have, in part, been overcome by modelling the dynamics of populations of *G. leadbeateri* in larger areas (e.g. combinations of many forest blocks). However, modelling larger areas, and thus the use of even more complex arrays of habitat patches, would not have led to a change in the *relative* results of our analyses which served to highlight the most effective forest management strategy for maintaining self-sustaining populations of *G. leadbeateri* in wood production areas.

For the purposes of our analyses we employed generous values for migration and diffusion which resulted in only relatively limited constraints on the movement patterns of *G. leadbeateri*. Thus, we assumed that the species was capable of moving readily through the forest environment and able to recolonise logged and regenerated areas. This would be important for strategies such as extended logging rotation times and modified clearfelling practices as the success of these management options is dependent on recurrent recolonisation events. This is because these types of forest disturbance result both in (1) animals being eliminated from an area; and (2) patches supporting suitable habitat for only a relatively short period before logging operations are repeated. Alternatively, permanently reserved areas may remain suitable for longer and periodic localised extinction would be less frequent (until a fire occurs), making the recolonisation and dispersal capability of *G. leadbeateri* less important than in the other strategies that were examined. Notably, if the movement abilities of wild *G. leadbeateri* are more constrained than modelled in this study, the strategy of reserving areas of forest would have been even more effective relative to the other management approaches which were examined.

Although we employed a complex patch structure for the two forest blocks that were modelled, it did not include stands of regrowth forest that presently support numerous dead trees with hollows. Logging is presently excluded from these areas, although they will become available for timber harvesting when the process of stagfall results in them supporting less than four trees with hollows per ha (Macfarlane & Seebeck, 1991). This type of forest may provide suitable habitat for *G. leadbeateri* (Lindenmayer *et al.*, 1991a), but their value will be short-lived because of the high rates of decay and collapse of trees with hollows in these areas (Lindenmayer *et al.*, 1990c). Therefore, such areas will remain suitable for the species for only a relatively short part of the time horizon simulated in our study. Thus, the omission of these areas would have made only a minimal difference, if any, to the outcomes of our analyses.

For the purposes of our analyses, we assumed that post-fire salvage logging operations would be limited to those parts of the forest that would normally be available for timber harvesting. Therefore, we assumed that old growth forest and other excluded areas (e.g. forest on steep slopes and patches retained within coupes) were not salvage harvested. We are not able to predict if such areas would be exempt from salvage logging in the event of a major wildfire. Notably, our estimates of the probability of extinction would have been much higher if we had incorporated the impacts of salvage logging within patches of old growth forest. Furthermore, if burnt patches were then added to the rest of a given forest block that was

available for clearfelling on less than a 100 year rotation, the chances of *G. leadbeateri* being totally eliminated from that block would be greatly increased.

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## APPENDIX 1. THE SUBMODELS USED IN ALEX TO TRACK HABITAT QUALITY DYNAMICS IN DIFFERENT TYPES OF HABITAT PATCHES

This appendix contains an outline of the submodels added to ALEX and used to track habitat quality dynamics within each of the patches which together comprised the patch structures used to simulate metapopulations of *G. leadbeateri* in the Murrindindi and Steavenson Forest Blocks. For the purposes of our analyses, we assumed that areas of forest on steep and rocky terrain and in streamside reserves which are presently excluded from timber harvesting only very rarely support resident and/or breeding animals (Lindenmayer *et al.*, 1991a, 1994a). However, we allowed such areas to facilitate the movement of animals between habitat patches. Information on the temporal dynamics of areas where modified silvicultural practices were simulated are presented in Appendix 2. Appendix 1 focuses on the dynamics of the key habitat components within patches of old growth forest. Note that these areas are not available for timber harvesting (Macfarlane & Seebeck, 1991) and, in this study, we assumed that they were also exempt from post-fire salvage logging operations.

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

The availability of food resources and the abundance of nest sites within large trees with hollows affect the quality of habitat for *G. leadbeateri* (Lindenmayer *et al.*, 1991a, 1994a). We use three habitat variables within ALEX to model the dynamics of these two factors: (1) the first reflects availability of food for *G. leadbeateri*; (2) the second tracks the abundance of cavities in mature living trees; (3) the third corresponds to the abundance of hollows in dead and/or highly senescent trees. ALEX tracks the dynamics of these three habitat variables for each patch and integrates them to give an overall measure of habitat quality (see below). The reciprocal of habitat quality value is the minimum area required for a female to breed. For example, a maximum of 12 females can breed in a 60 ha patch that has a habitat quality value of 0.2.

#### 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. There is typically a pulse of young *Acacia* spp. trees after a fire (Adams & Attiwill, 1984). There is a pronounced decline in the number of *Acacia* spp. trees as the forest ages (Smith & Lindenmayer, 1988, 1992) and such stems occur in lower numbers within old growth montane ash forests than in regrowth forest (Adams & Attiwill, 1984). After each wildfire, the trajectory of  $H_1(t)$  is described by the equation:

$$\begin{aligned} H_1(t) &= 0 & 0 \leq t < 15 \\ &= (t-15)/20 & 15 < t < 35 \\ &= 1 & 35 < t < 60 \\ &= 1-0.7(t-60)/40 & 60 < t < 100 \\ &= 0.3 & t > 100. \end{aligned} \quad (A1)$$

#### 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. The equation describing the dynamics of  $H_2(t)$  has been derived from an understanding of the abundance and ontogeny of cavities in ash-type eucalypt trees (Ambrose, 1982; Lindenmayer *et al.*, 1993b) and the longevity of this tree species (Ambrose, 1982; Banks, 1993). The dynamics of  $H_2(t)$   $t$  year after a fire (where  $H_2(0)$  is the value before the fire) are:-

$$\begin{aligned} H_2(1) &= 0.15 \cdot H_2(0) \\ H_2(t + 1) &= 0.995 \cdot H_2(t) & 0 < t < 150 \\ &= 0.995 H_2(t) + 1.6(t-150)/150 & 150 < t < 300 \\ &= 0.995 H_2(t) + 1.6 & t > 300. \end{aligned} \quad (A2)$$

*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 (Lindenmayer *et al.*, 1990c, unpublished data). However, the number of hollows in this category of trees may increase substantially after a fire because, unlike many species of eucalypts, mature living trees may be badly damaged or killed by such events (Lindenmayer *et al.*, 1991b, 1991d, 1993b). The dynamics of this variable were as follows:-

$$\begin{aligned} H_3(1) &= 5 \cdot H_2(0) \\ H_3(t + 1) &= 0.96H_3(t) + 0.02H_2(t) \quad t > 0. \quad (A3) \end{aligned}$$

A long time after the fire,  $H_2(t) = 100$  (i. e. the abundance of hollows is capped at this value), and from eqn (A3),  $H_3(t)$  tends toward 50.

*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 breeding size of a 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 the availability of food resources limits the value of the habitat quality to 0.3 (eqn (A1)).

The temporal dynamics of the various habitat attributes and thus, in turn, the habitat suitability index are considerably more complex when fire regimes are incorporated in the analysis. The response curves that result from such forms of disturbance are strongly influenced by the age of a stand when it is burnt (Lindenmayer *et al.*, 1991b, 1993b). This is highlighted by Fig. 4, which shows some of the variations in the habitat suitability index which result from fires in stands of different ages. For example, if a fire burns a given area of montane ash forest that is < 120 years old, then although the trees in such stands may be killed they are likely to be too small to form suitable nest sites for *G. leadbeateri* (Lindenmayer *et al.*, 1993b). Note that we assumed that there would not be post-fire salvage logging operations in stands of old growth forest that were burnt.

## **APPENDIX 2. A DESCRIPTION OF THE SUBMODEL USED IN ALEX TO TRACK HABITAT QUALITY DYNAMICS IN LOGGING COUPES WHERE MODIFIED SILVICULTURAL PRACTICES WERE SIMULATED**

In Cases 4 and 5 of this study we examined the relationship between the persistence of populations of *G. leadbeateri* and modified silvicultural practices where parts of logging coupes were retained during timber harvesting operations. We completed simulations where 10, 20 and 40% of logging coupes were retained (see text). Here we refer to these unlogged areas as 'retained patches'.

Clearfelling operations were simulated to recur at intervals of either 50 or 100 years in the part of each coupe that was not retained. Thus, there were no potential nest sites in these areas and large trees with hollows were confined to the retained patches in each logging coupe. The dynamics of cavity recruitment with the retained areas was the same as in stands of old growth forest. We assumed that stands of *Acacia* spp. trees remain with retained patches and provide food for *G. leadbeateri*. The levels of food availability were set so they were the same as old growth forest (= 0.3; see above). However, as stands of *Acacia* spp. mature within the adjacent logged and regenerated stands of forest, there would be a significant increase in the availability of food resources (Smith & Lindenmayer, 1992). This would, in turn, create a type of ecotone between the retained and surrounding logged areas comprised of large trees with hollows adjacent to a dense understorey of *Acacia* spp., which would provide suitable habitat for *G. leadbeateri* (Lindenmayer *et al.*, 1991a). To reflect such changes in habitat structure, we allow habitat quality in the retained patches to increase after logging. However, this value reverted to that characteristic of old growth forest (= 0.3) each time the remainder of the coupe was clearfelled. For those simulations where modified logging practices were simulated and the rotation time was 50 years, the trajectory of the habitat quality variable was:

$$\begin{aligned}
Q(t) &= 0.3 & 0 \leq t \leq 21 \\
&= (t-15)/20 & 21 \leq t \leq 35 \\
&= 1 & 35 \leq t \leq 50.
\end{aligned}$$

We included a modified submodel to track changes in stand structure associated with the mortality and decline of *Acacia* spp. trees in maturing stands of ashtype eucalypt forests (see Adams & Attiwill, 1984) for those simulations of the Steavenson Forest Block where an interval of 100 years was set between harvesting operations in the part of a coupe that was not retained (see Case 5). In this case, there was a decline in the habitat suitability index after stands of forest exceeded 60 years of age and it approached that of old growth forest. As in simulations with a 50 year rotation, the value of the habitat suitability index of the retained patch reverted to that of old growth forest each time the surrounding coupe was cut. For those simulations where modified logging practices were simulated and the rotation time was 100 years, the trajectory of the habitat quality variable was:

$$\begin{aligned}
Q(t) &= 0.3 & 0 \leq t \leq 21 \\
&= (t-15)/20 & 21 \leq t \leq 35 \\
&= 1 & 35 \leq t \leq 60 \\
&= 1 - 0.7(t-60)/40 & 60 \leq t \leq 100.
\end{aligned}$$

For all simulations where modified logging practices were modelled, more complex habitat response curves than described above may arise when the impacts of both timber harvesting and wildfires are incorporated in the analyses. Thus, when the effects of fires are included, patches of forest which are retained within logging coupes may not always support stands of old growth forest. Notably, for the purposes of this study, we assumed that areas of retained forest were not salvage logged if they were burnt.