

# Economics of a nest-box program for the conservation of an endangered species: a reappraisal

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**Abstract:** An optimization model is developed to identify timing and placement strategies for the installation of nest boxes and the harvesting of timber to meet joint timber-wildlife objectives. Optimal management regimes are determined on the basis of their impacts on the local abundance of a threatened species and net present value (NPV) and are identified for a range of NPV levels to identify production possibility frontiers for abundance and NPV. We apply the model to a case study focusing on an area of commercially productive mountain ash (*Eucalyptus regnans* F. Muell.) forest in the Central Highlands region of Victoria, Australia. The species to be conserved is Leadbeater's possum (*Gymnobelideus leadbeateri* McCoy), which is locally limited by a scarcity of nesting hollows. The modeling is exploratory but indicates that nest boxes may offer a promising population recovery tool if consideration is taken of their placement and areal extent through time.

**Résumé :** Les auteurs ont développé un modèle d'optimisation pour identifier les stratégies concernant le moment et l'emplacement pour l'installation de nichoirs et la récolte de bois afin de rencontrer les objectifs conjoints pour la matière ligneuse et la faune. Les régimes optimaux d'aménagement sont déterminés sur la base de leurs impacts sur l'abondance locale d'une espèce menacée et la valeur nette actualisée. Ils sont identifiés pour une gamme de niveaux de valeur nette actualisée afin d'identifier les limites possibles de production en fonction de l'abondance et de la valeur nette actualisée. Nous appliquons le modèle à une étude de cas concentrée dans une zone de forêt commerciale productive d'eucalyptus géant (*Eucalyptus regnans* F. Muell.) sur le plateau central dans la région de Victoria en Australie. L'espèce à conserver est le bucurve du Sud (*Gymnobelideus leadbeateri* McCoy) qui est localement en nombre limité à cause de la rareté des cavités pouvant servir de nichoir. La modélisation est exploratoire mais indique que les nichoirs peuvent constituer un outil intéressant pour rétablir la population si leur emplacement et leur répartition dans le temps sont pris en considération.

[Traduit par la Rédaction]

## Introduction

A large number of studies have addressed the conflict faced by public forest agencies in promoting timber production and wildlife conservation objectives in commercially productive native forest (Loyn 1985; Norton and Dovers 1994; Rochelle et al. 1999). These studies typically focus on problems where the adverse impacts on wildlife caused by timber production can be mitigated by modifying silvicultural practices (e.g., changing harvest rotations to improve habitat) and (or) reserving land for habitat. Less attention has been given to forest management problems that cannot be resolved solely by habitat retention and (or) modified silviculture. Such problems include those where past forest disturbance has reduced the availability of old trees

with hollows suitable for nesting, and involve high-profile species such as Leadbeater's possum (*Gymnobelideus leadbeateri* McCoy; LBP hereafter) (Smith and Lindenmayer 1992; MacFarlane and Loyn 1994) and the red-cockaded woodpecker (Hyde 1989). Both of these species are threatened by a decline in hollows that would occur even if timber harvesting were to cease. If we are to prevent these species' populations declining, perhaps to extinction, nest site availability must be increased through measures such as the installation of nest boxes (Franzreb 1997) or other measures that artificially enhance nesting capacity, such as deliberately damaging trees to stimulate hollows formation (Bull and Partridge 1986).

An important criterion in assessing wildlife conservation opportunities is their cost effectiveness, given that resources available for multiple-use forest management are limited. In this paper, we investigate the cost effectiveness of a nest-box program for conserving the arboreal marsupial LBP, which is threatened by a decline in hollow-bearing trees in the commercially productive ash forests of the Central Highlands region of Victoria, Australia (Lindenmayer et al. 1997; Smith and Lindenmayer 1992).

Nest-box programs have successfully been used as recovery tools for critically endangered populations of a number of species, including the red-cockaded woodpecker (Franzreb 1997) and great-crested flycatcher (White and

Received June 16, 2000. Accepted July 27, 2001. Published on the NRC Research Press Web site at <http://cjfr.nrc.ca> on October 26, 2001.

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Seginak 2000). However, a survey of articles listed in *ECONLIT*, *CAB Abstracts*, and *Biological Abstracts* from 1990 to 2000 reveals only one study that primarily focuses on the cost effectiveness of nest boxes as a population recovery tool, that of McKenney and Lindenmayer (1994) (ML hereafter). Of the other studies that consider nest boxes, most focus on their use as a research instrument, for example, to assist in monitoring populations (as in Hayward et al. 1992), rather than as a conservation instrument per se (as in Lindenmayer et al. 1991).

The study of ML is the first to estimate the economic cost of a nest-box program for wildlife conservation in commercially productive forest. Discounted nest-box costs over a 200-year time horizon were compared with those of land reservation as alternative conservation strategies. One of their findings was that the cost of a nest-box program to conserve LBP can be significant. However, ML did not investigate how this cost might be reduced, for example, by modifying the areal extent and spatial arrangement of nest boxes through time. Perhaps more importantly, ML's formulation of the management problem as an "either (or)" choice between logging bans and a nest-box program is inappropriate if land reservation alone is unable to prevent the likely extinction of LBP in commercially productive ash forests. Simulation studies of the species (Lindenmayer and Possingham 1995, 1996) and field studies on the species' habitat dynamics (Lindenmayer et al. 1997) indicate that LBP faces a high risk of extinction in commercial ash forests even if these forests were made unavailable for timber harvesting.

ML estimated nest-box costs on a per-hectare basis under alternative discount rates and alternative nest-box replacement rates, densities, and installation-maintenance costs. The ecological effectiveness of nest boxes, and their optimal placement and areal extent through time, were not considered. However, research indicates that LBP populations can be sensitive to the areal extent and spatial arrangement of habitat (Lindenmayer and Possingham 1996). The area, placement, and timing of nest-box installations also are likely to have important cost implications. For example, it may be cost effective to restrict nest boxes to those areas and time periods in which natural hollows are expected to limit abundance. Accounting for these spatial-temporal aspects of a nest-box program is complex because of the large number of possible nest-box, habitat reservation, and timber harvest choices, and selection is best conducted using optimization or heuristic techniques. We demonstrate with an optimization model that consideration of the spatial and timing aspects of a nest-box program can provide important information for assessing its cost effectiveness.

## The optimization model

### Model overview

The aim is to determine the areal extent and placement of nest boxes, habitat reservation, and timber harvests through time that result in maximum final-period abundance of LBP, subject to achieving a minimum net present value (NPV) from timber returns. A range of minimum NPV levels is considered to indicate the trade-off between abundance and NPV. Linear programming was selected as the appropriate

technique for solving this problem, particularly given the size of the problem. Although this means that the problem is restricted to being deterministic and relying on linear relationships, other techniques capable of overcoming these limitations, such as dynamic programming, would be very difficult to use to solve a problem of this size.

The forest is partitioned into square cells in a grid approximation of the habitat patches and timber stands within a particular forest management area (Fig. 3). Each cell contains one or more stands, with trees in any given stand having the same initial age. Initial ages of montane ash stands at a 40-ha grid resolution were estimated using 1994 forest inventory data on stand ages and dominant tree species that were digitized by the Victorian Department of Natural Resources and Environment (DNRE) and stored in a geographic information system (GIS). The mix of initial stand ages in a given cell (Fig. 3) determines the cell's initial endowments of timber (according to Table 3) and nesting capacity (according to eq. A2). Initial food capacity in a particular cell depends not only on the mix of stand ages within that cell (according to eq. A1) but also the ages of stands within feeding distance of animals nesting in that cell. Because of the absence of data on initial populations of LBP, initial abundance in each cell was set at 50% of the cell's initial nesting capacity, on the grounds that, in most or all cells initially colonized by LBP, nesting capacity is likely to be limiting.

Decision variables comprise alternative management schedules, each representing a sequence of combined nest-box and harvest actions over the modelled time horizon. One or more schedules can be selected for each cell. Some schedules involve harvesting in one or more periods without installing nest boxes in any period, other schedules involve installing nest boxes in one or more periods without harvesting, while most schedules involve some combination of timber harvesting and nest-box installation in various periods. This allows us to identify circumstances where it is optimal to implement a nest-box program jointly with reservation of habitat (a possibility not considered by ML), as well as circumstances where it is optimal to use only one of these population recovery instruments.

Associated with each management schedule is a sequence of carrying capacities (both nesting and food capacities), a sequence of harvested timber volumes, and a particular NPV (calculated as discounted timber revenues net of timber-management costs and nest-box costs). Nest boxes supplement the nesting capacity provided by hollow-bearing trees. Harvesting eliminates nesting capacity by removing all hollow-bearing trees but stimulates increased food production after temporarily eliminating the food resource.

We use a relatively simple model of LBP population growth and dispersal, based on published and unpublished studies of the species, to estimate the local response of the species to alternative management choices. Specifically, we assume that at any point in time, abundance in a particular cell is determined by either or both of the following factors: (i) its carrying capacity and (ii) net additions to its population from the previous period caused by reproduction net of deaths within the cell and immigration from other cells net of emigration to those cells. Carrying capacity depends on the availability of hollows (both natural and artificial) and

food. Food capacity depends on both the physical availability of food resources and the ability of animals to exploit this food resource, which we assume declines with distance from the nesting cell due to energetic costs. Dispersal is modeled as a set of proportions, each representing the proportion of animals residing in a particular cell that disperse to another cell. It is assumed that this proportion declines exponentially with distance and that the total proportion that disperse a given distance from a particular nesting cell is uniformly distributed over all possible directions from that cell. This assumption of passive dispersal behavior makes populations vulnerable to removal of habitat caused by timber harvesting, which can lead to increased dispersal mortality as a result of animals dispersing into nonhabitat or fully occupied habitat.

### Model formulation

The linear programming model is

$$[1] \quad \text{Maximize } L_T = \sum_i P_{iT}$$

where  $L_T$  is the total adult female population of LBP over the entire management area at the beginning of the final time period,  $T$ , and  $P_{iT}$  is the adult female population of LBP nesting in cell  $i$  at time  $T$ , subject to

$$[2] \quad P_{i0} = N_i; \quad \forall i$$

$$[3] \quad P_{it} \leq \sum_j g_{ji}(1+r_j)P_{j(t-1)}; \quad \forall i; \quad t = 1, 2, \dots, T$$

$$[4] \quad P_{it} \leq \sum_k \sum_{m=1}^{M_{ik}} a_{ikmt} S_{ikm}; \quad \forall i; \quad t = 1, 2, \dots, T$$

$$[5] \quad P_{it} \leq \sum_j d_{ji} Z_{jit}; \quad \forall i; \quad t = 1, 2, \dots, T$$

$$[6] \quad \sum_i Z_{jit} \leq \sum_k \sum_{m=1}^{M_{jk}} f_{jkmt} S_{jkm}; \quad \forall j; \quad t = 1, 2, \dots, T$$

$$[7] \quad \sum_i \sum_{k=1}^{K_i} \sum_{m=1}^{M_{ik}} (x_{ikm} - c_{ikm}) S_{ikm} \geq V$$

$$[8] \quad \sum_{m=1}^{M_{ik}} S_{ikm} = A_{ik}; \quad \forall i, k$$

$$[9] \quad \frac{1}{T} \sum_i \sum_{k=1}^{K_i} \sum_{m=1}^{M_{ik}} \sum_{t=1}^T w_{ikmt} S_{ikm} = B$$

$$[10] \quad B - (1 + \psi) \sum_i \sum_{k=1}^{K_i} \sum_{m=1}^{M_{ik}} w_{ikmt} S_{ikm} \leq 0; \quad t = 1, 2, \dots, T$$

$$B - (1 - \psi) \sum_i \sum_{k=1}^{K_i} \sum_{m=1}^{M_{ik}} w_{ikmt} S_{ikm} \geq 0; \quad t = 1, 2, \dots, T$$

$$[11] \quad \sum_i \sum_{k=1}^{K_i} \sum_{m=1}^{M_{ik}} [w_{ikmt} S_{ikm} - (1 + \psi) w_{ikm,t-1} S_{ikm}] \leq 0; \quad t = 2, 3, \dots, T$$

$$\sum_i \sum_{k=1}^{K_i} \sum_{m=1}^{M_{ik}} [w_{ikmt} S_{ikm} - (1 - \psi) w_{ikm,t-1} S_{ikm}] \geq 0; \quad t = 2, 3, \dots, T$$

where  $P_{i0}$  is the adult female population of LBP nesting in cell  $i$  at time 0;  $P_{it}$  is the adult female population of LBP nesting in cell  $i$  at the beginning of period  $t$  ( $t = 1, 2, \dots, T$ );  $N_i$  is the initial population in cell  $i$  at the start of the planning horizon;  $g_{ji}$  is the proportion of the adult female population in cell  $j$  in one period that disperse to cell  $i$  at the beginning of the next period;  $r_j$  is the net per-capita periodic reproduction rate (not accounting for dispersal mortality) in cell  $j$ , when habitat is not limiting;  $M_{ik}$  is the number of management schedules being considered for initial age-class  $k$  in cell  $i$ ;  $K_i$  is the number of initial age-classes in cell  $i$ ;  $a_{ikmt}$  is the nest site capacity (measured in terms of adult females) produced in period  $t$  per hectare in initial age-class  $k$  in cell  $i$  that is managed according to management schedule  $m$ ;  $S_{ikm}$  is the area (in hectares) in cell  $i$  and initial age-class  $k$  allocated to the  $m$ th multiperiod management schedule;  $d_{ji}$  is the utilization efficiency of food produced in land unit  $j$  and consumed by animals nesting in land unit  $i$ ;  $Z_{jit}$  is the amount of food produced in cell  $j$  that is made available for consumption by animals nesting in cell  $i$  during period  $t$ ;  $f_{ikmt}$  is the amount of food produced in period  $t$  per hectare in initial age-class  $k$  in cell  $i$  that is managed according to management schedule  $m$ ;  $x_{ikm}$  is the present value of timber revenues (from sale of periodic harvests of various log grades)

per hectare in initial age-class  $k$  in cell  $i$  that is managed according to management schedule  $m$ ;  $c_{ikm}$  is the present value of timber management costs and nest-box costs per hectare in initial age-class  $k$  in cell  $i$  that is managed according to management schedule  $m$ ;  $A_{ik}$  is the area of initial age-class  $k$  in cell  $i$ ;  $V$  is the minimum NPV to be obtained from management of the planning area over the planning time horizon;  $B$  is the mean harvested timber volume over all periods;  $w_{ikmt}$  is the volume of sawlogs expected in time period  $t$  per hectare in initial age-class  $k$  in cell  $i$  that is managed according to management schedule  $m$ ; and  $\psi$  is an upper and lower proportional limit on allowable deviation of the current harvest volume from the previous period's harvest volume and from the average harvest volume over all periods.

We model only female possums as this is likely to be the limiting sex in most populations (Lindenmayer and Possingham 1995). Equations 1–6 make up a population model that produces deterministic estimates of adult female LBP abundance at the beginning of each period,  $t$ , under alternative spatially and temporally explicit management choices. Equations 1–3 define a discrete-time reaction-diffusion system based on the approach introduced by Hof et al. (1994) and extended by Bevers et al. (1997) and Bevers and Hof (1999). Equation 1 maximizes a deterministic estimate of total adult

female abundance at the beginning of period  $T$ , summed over all cells within a particular management area.

Equation 2 sets initial abundance levels. Equation 3 limits abundance in cell  $i$  to that cell's previous abundance expanded by the net population growth rate minus the proportion that leave cell  $i$  in each period ( $1 - g_{ii}$ ), plus the number of immigrants from other cells. The coefficient  $g_{ji}$  is the proportion of potential dispersers in cell  $j$  that disperse to cell  $i$  at the beginning of each period ( $g_{ji}$  is the proportion of potential dispersers that remain in the  $i$ th natal cell). Because dispersal from any given cell is assumed to be random in direction, regardless of whether that cell lies near suitable habitat or not, dispersal mortality can occur through animals dispersing into fully occupied habitat or nonhabitat (note that dispersal mortality is not accounted for in the net population growth rate,  $r$ ). We conservatively assume that no animals can enter the planning area from outside its boundaries and that animals that leave the planning area perish (as in Lindenmayer and Possingham 1996).

Equation 4 limits abundance in cell  $i$  to the amount of nesting capacity produced by the combination of management schedules ( $S_{ikm}$ ) selected for that cell. Harvests and nest-box installations are modeled at the beginning of each period, thus nesting capacity falls to zero in the harvest period unless nest boxes are installed. Total nesting capacity is calculated as the sum of the capacities from hollow-bearing trees and nest boxes, up to a maximum capacity. For example, in our case study, installing nest boxes in an old-growth stand would not add to the stand's nesting capacity as this is already at its maximum level of one animal per hectare (see Appendix).

Equation 5 limits abundance in cell  $i$  to the amount of food available in that cell and cells within foraging distance of it, as determined by (i) the mix of management schedules selected for those cells (which determine future stand ages) and (ii) the allocation of the food resource among those cells according to eq. 6. These two equations are based on eqs. 6 and 7 in Bevers and Hof (1999). The food utilization efficiency parameter values ( $d_{ji}$ ) decline with distance between the food source ( $j$ ) and the nest site ( $i$ ). In our case study, total food capacity is calculated according to eq. 13 in the Appendix, and hypothetical food utilization efficiencies ( $d_{ji}$ ) are used because of data limitations.

Carrying capacity in any particular cell is determined by the constraints in eq. 4 and (or) 5, whichever is limiting. Abundance ( $P_{it}$ ) in that cell in any period,  $t$ , is determined by the cell's carrying capacity and (or) by the growth-dispersal conditions in eq. 3, whichever is limiting.

Forest management is further constrained by the requirement that a minimum NPV be produced, calculated as the discounted returns from harvested timber ( $x_{ikm}$ ) net of discounted timber management costs and nest-box costs ( $c_{ikm}$ ), as specified in eq. 7. It is assumed that all costs are incurred at harvest time. Timber management costs include road maintenance and stand regeneration costs but not harvesting costs as the focus of our case study is on the particular planning problem facing DNRE, which manages public forests in the Central Highlands. There, harvesting costs are borne

by private contractors. We assume that the road network is already in place and requires only maintenance. For any cell,  $i$ , road maintenance cost depends on the distance of that cell from the established road network and is assumed to be a linear and divisible function of the proportion of that cell which is harvested. By varying  $V$  in eq. 7 and repeatedly solving the model, a production possibility frontier (PPF) is generated showing the trade-off between final period abundance and discounted net timber value.

Equation 8 ensures that the total hectares assigned to management schedules within land units of initial age-class  $k$  in cell  $i$  must equal the area of that age-class in this cell,  $A_{ik}$ .

Equations 10 and 11 ensure that an approximately even sawlog flow is maintained. Equation 10 ensures that the current-period harvest volume cannot deviate by a proportion greater than  $\psi$  from the average harvest volume over all periods,  $B$  (computed in eq. 9), while eq. 11 ensures that the current-period harvest volume cannot deviate by a proportion greater than  $\psi$  from the previous-period harvest volume.

## Case study

Our case study focuses on a timber management block within the Central Highlands region. Habitat and population parameter values are briefly discussed and the study region described, followed by a presentation of results. A 150-year time horizon is used to capture natural tree hollow dynamics, with 10-year time periods to limit model size.

### Habitat capacities

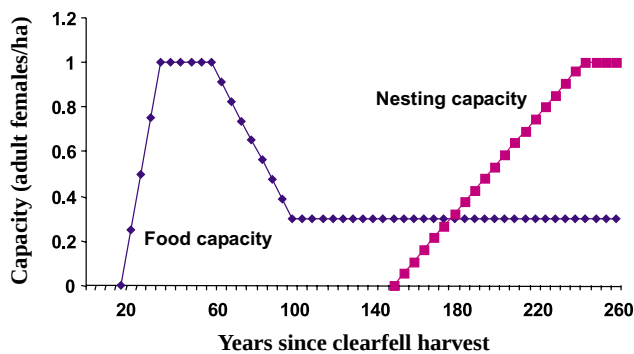
Equations to predict  $f_{kmt}$  and  $a_{kmt}$  under alternative management choices are adapted from Lindenmayer and Possingham (1996) and are set out in the Appendix. These are illustrated together in Fig. 1 to indicate the limiting habitat factor(s) at different stand ages.

Our 150-year time horizon is long enough to allow all ash stands to potentially develop nest trees, provided they are not harvested. Harvesting eliminates the food resource for two periods and eliminates nesting capacity for the remainder of the study time horizon. Nesting capacity in existing old-growth stands is set at 1.0 and remains at this value as long as the stands remain unharvested.

Unpublished research conducted over the past 20 years indicates that LBP will readily use nest boxes if the boxes are appropriately designed and located, as explained below. Indeed, LBP is ideally suited to the use of nest boxes. The species' colonial behavior and the fact that it occurs in high densities allows for high nest-box occupancy rates in the vicinity of existing colonies, while the animals' small size means that small boxes having low construction costs can be used (D. Harley, in preparation<sup>2</sup>). Four separate field studies have detected the species in nest boxes (D. Harley, in preparation;<sup>2</sup> D.B. Lindenmayer, personal communication; C. MacGregor, personal communication; M. MacFarlane, unpublished data; S. Ward, personal communication), three of which were conducted in montane ash forest. MacFarlane found a 30% occupancy rate in montane ash forest (M. MacFarlane, unpublished data). A higher occupancy rate was found in lowland swamp forest (*Eucalyptus camphora*

<sup>2</sup>Harley, D. The conservation biology of Leadbeater's possum in lowland swamp forest. Ph.D. dissertation, Department of Biological Sciences, Monash University, Clayton, Victoria, Australia. In preparation.

**Fig. 1.** Food and nesting capacities through time in stands regenerating from clearfell harvesting  $y$  years after harvesting.



R. Baker.) at Yellingbo Nature Conservation Reserve, with 80% of the boxes utilized there (D. Harley, in preparation<sup>2</sup>). In contrast, D.B. Lindenmayer (personal communication) and C. MacGregor (personal communication) (LM hereafter) found a significantly lower occupancy rate in their montane ash study, with only 5 of 96 boxes used by LBP to date,<sup>3</sup> although it is important to note that the LM study did not solely target LBP populations.

It is important to identify the reasons for these different nest-box usage rates as these are likely to bear on the ecological efficacy of nest boxes as a population recovery tool for LBP. There are inadequate data at this stage to determine the effect of climatic differences between the sites used in the above nest-box studies (e.g., there are lower temperatures in montane ash forest than lowland swamp forest). However, we note that all the boxes colonized in the study of M. MacFarlane (unpublished data)<sup>4</sup> continued to be occupied in winter. A more likely explanation for the lower occupancy rate found in the LM study relates to differences between its methods and those of the Harley and MacFarlane studies. Of particular importance is the method used to select nest-box sites. Most boxes in the Harley and MacFarlane studies were deliberately located near sites where LBP was known to occur immediately prior to nest-box installation, and therefore, boxes were colonized by possums already resident in the area. In contrast, the proximity of nest boxes to existing LBP colonies was not considered in the selection of sites in the LM study (D.B. Lindenmayer, personal communication; C. MacGregor, personal communication). In a survey of nest-box utilization patterns of possums and gliders, Menkhorst (1984) notes that nest-box usage by these species requires that there be resident populations in close proximity to the boxes. The importance of nest-box proximity to resident colonies is particularly evident in the Harley study. Harley installed boxes in two stages, with many boxes randomly located in the first stage. In the second stage, additional boxes were installed at sites where LBP colonies were known to occur, as revealed by the colonization events of the first stage. The occupancy rate rose almost threefold between the first and second stage

(D. Harley, in preparation<sup>2</sup>). A second methodological difference between the LM study and those of Harley and MacFarlane is the entrance hole diameters of the nest boxes used. The review of Menkhorst (1984) indicates that many species of possums and gliders exhibit a strong preference for holes similar to their body size. All boxes in the Harley and MacFarlane studies had openings approximating the body size of LBP (D. Harley, in preparation;<sup>2</sup> M. MacFarlane, personal communication). In contrast, half of the boxes used in the LM study had much larger entrance diameters, more than twice that of the boxes used in the Harley and MacFarlane studies (D.B. Lindenmayer, personal communication; C. MacGregor, personal communication).

The contribution of nest boxes to the nesting capacity of a particular land unit for LBP will depend on a range of factors. Those factors that have been found to strongly influence nest-box occupancy rates in previous studies of the species are the availability of food in the area, the number of hollow-bearing trees, and the proximity of the boxes to existing colonies (D. Harley, in preparation;<sup>2</sup> M. MacFarlane, unpublished data). Each of these factors are accounted for in our spatial-dynamic model. In our model, nest boxes enhance nesting capacity only at sites where hollows limit abundance, provided that there are LBP colonies nesting at these sites or within dispersal distance of them. We conservatively assume that nest boxes installed at 10/ha have a much lower nesting capacity (at 0.1 adult females/ha) than that provided by 1 ha of old-growth forest (1 adult female/ha). An alternative way of expressing this is that we assume the territory size of a LBP colony supported by nest boxes would be 10 times as large as that of a colony residing in an area with abundant natural hollows and an abundant food resource. The high nest-box occupancy rates found in the Harley and MacFarlane studies indicate that, if nest boxes are placed in stands with abundant food and a shortage of natural hollows, territory size is likely to be much smaller than that which we have assumed. Despite our use of a highly conservative estimate of nest-box capacity in our baseline model, we also consider the effects of using a lower nest-box capacity.

### Reproduction and dispersal

Young possums disperse from the natal territory before they are fully grown, at about 10 months for females and 15 months for males (Smith 1984). Their dispersal behavior is poorly understood but has been modeled as random in direction from the natal (or source) patch and independent of the density of animals in the source and destination patches (as in Lindenmayer and Lacy 1995). Dispersing animals, particularly females, suffer high mortality because of their exclusion from established colonies (Smith 1984). Parameter values used in our case study to estimate population growth and dispersal rates are documented in Table 1.

To limit model size, our population model (eqs. 1–6) is not age structured, even though we assume that only sub-adults disperse. By ignoring age structure, it is assumed that

<sup>3</sup>Three of these boxes contained animals at the time of inspection, with two other boxes containing LBP nest material at the time of inspection (C. MacGregor, personal communication).

<sup>4</sup>If it were found that the lower temperatures in montane ash forest depress occupancy rates, this could be addressed by using thicker nest-box walls (see Menkhorst 1984, and references therein).

**Table 1.** Life history parameter values for Leadbeater's possum.

| Parameter                                                                            | Base value        |
|--------------------------------------------------------------------------------------|-------------------|
| Subadults that potentially disperse (%)                                              | 70 <sup>a</sup>   |
| Mean dispersal distance ( $\sigma$ ; km)                                             | 2 <sup>a</sup>    |
| Maximum population growth rate ( $r$ ; assuming habitat is not limiting)             | 1.15 <sup>b</sup> |
| Adult survivorship                                                                   | 0.75 <sup>a</sup> |
| Fecundity                                                                            | 0.40 <sup>a</sup> |
| Initial abundance in cell $i$ ( $N_i$ ; % of initial carrying capacity) <sup>c</sup> | 50                |

<sup>a</sup>Taken from Lindenmayer and Possingham (1995, 1996), Lindenmayer and Lacy (1995), and Lindenmayer et al. (1993a).

<sup>b</sup>Calculated as  $r$  minus adult survivorship.

<sup>c</sup>As in Lindenmayer and Lacy (1995).

the ratio of subadults to adults in each cell remains constant. A more realistic assumption is that this ratio is not constant (particularly in the presence of dispersal), but identifying different age groups to capture changes in age-class ratios over time requires a substantial increase in data, some of which are not available for the species (e.g., age-dependent dispersal rates). Wennergren et al. (1995) find that the benefits of adding age structure to spatial population models is questionable. These benefits, if they exist, would be particularly small if the ratio of subadults to adults in each land unit does not change dramatically over time and if animals mature at a young age (as in the case of LBP). It is important to balance the advantages of adding age structure to our model, which are uncertain and likely to be small, with the additional computational costs involved, which are substantial.

In our unstructured model, cell-to-cell dispersal proportions (the  $g_{ji}$  coefficients in eq. 3) are calculated over a number of steps. We begin by assuming that these proportions decline exponentially with distance (as in Lindenmayer and Possingham 1996), according to the following equation (Bever and Flather 1999, p. 63):

$$[12] \quad p_d(d) = \sigma^{-1} e^{-(d-\theta)/\sigma}; \quad d > \theta, \sigma > \theta, \sigma > 0$$

where  $d$  is dispersal distance,  $\sigma$  represents mean dispersal distance (2 km in our case study), and  $\theta$  is the minimum dispersal distance (zero in this case). Combining eq. 12 with our assumption of random dispersal direction produces a bivariate probability distribution, which we numerically integrate over distances and angles defined by the boundaries of each destination cell ( $i$ ) relative to the center of each source cell ( $j$ ) to produce a set of dispersal proportions for subadults. These are too high given our assumption that only subadults disperse and, therefore, are multiplied by adult survivorship (0.75), fecundity (0.4), and the proportion of subadults that potentially disperse (0.70), to produce the  $g_{ji}$  values in eq. 3. The resulting  $g_{ji}$  express the number of subadult dispersers from any given cell as a constant propor-

**Fig. 2.** Forage utilization efficiency parameter values defined over a maximum foraging distance of one cell, with the center cell designated as the nest site cell, and each of the nine cells as a potential forage source.

|             |             |             |
|-------------|-------------|-------------|
| <b>0.20</b> | <b>0.30</b> | <b>0.20</b> |
| <b>0.30</b> | <b>0.80</b> | <b>0.30</b> |
| <b>0.20</b> | <b>0.30</b> | <b>0.20</b> |

tion of the number of adult females in that cell surviving from the previous period.<sup>5</sup>

### Foraging behavior

Foraging efficiency (represented by the  $d_{ji}$  in eq. 5) is assumed to decline with distance from the nest cell, reflecting energetic costs and the risk of predation during foraging. There are inadequate data to estimate  $d_{ji}$  for the study region, although Smith (1984) finds that resident possums in montane ash forest rarely feed beyond a 100-m radius from their nests. This implies that using a grid of 40-ha square cells, a high proportion of animals residing in a particular cell would feed solely in that cell, with only a small proportion likely to feed in adjacent cells. This is approximated in our case study by using the hypothetical  $d_{ji}$  illustrated in Fig. 2.

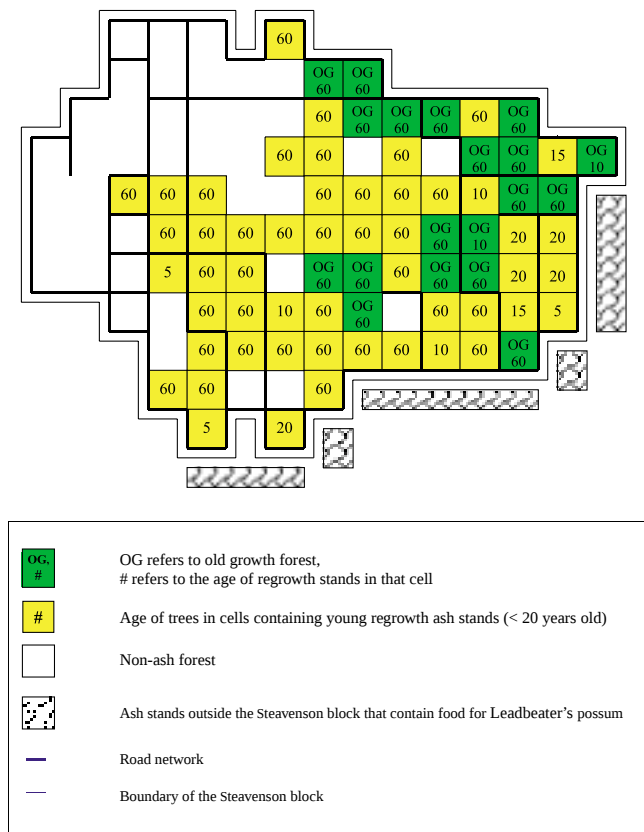
### The study region

The Steavenson block is an administrative land unit of 4470 ha in the Central Highlands region managed by DNRE for its timber and conservation values. It supplies approximately 80 000 m<sup>3</sup> of ash-species sawlogs and 160 000 m<sup>3</sup> of ash pulplogs per decade to local sawmills and pulpmills (M. Woodman, Senior Forester, DNRE, personal communication). A grid comprising seventy 40-ha cells approximates the habitat and timber resources within ash stands in the study region, as illustrated in Fig. 3. Data on harvests subsequent to 1994 currently are not available, and we have assumed that no harvests occurred since 1994. Our choice of 2000 as the base year of our modelling, therefore, entails some overestimation of the area of 1939-regrowth stands and underestimation of the area of recently harvested stands.

Approximately 60% of the block contains ash forest (shaded cells in Fig. 3), with the remainder made up of mixed-species eucalypt forest unsuitable for colonization by LBP (unshaded cells). Suitable foraging habitat occurs not only within the Steavenson block, but also in some adjacent

<sup>5</sup> See Bevers and Flather (1999, Appendix) for a more general method of capturing different dispersal rates between adults and maturing juveniles.

**Fig. 3.** Grid approximation of current habitat patch arrangements in the Steavenson block. The DNRE forest inventory data used (provided by F. Hamilton, Forest Resource Inventory, DNRE) do not indicate precise ages of the old-growth stands. These stands are assumed to be 250 years old.



blocks (from hatched areas in Fig. 3).<sup>6</sup> The area of habitat currently suitable for LBP is small, comprising 280 ha of old-growth stands (within cells labeled OG).<sup>7</sup> This is less than the 600 ha of suitable habitat that Lindenmayer et al. (1993b) found to be the minimum that may be required to support populations of LBP with a reasonable probability of persistence for at least 100 years. Suitable habitat in the Steavenson block also appears to be fragmented. Populations of LBP inhabiting small areas of fragmented habitat may decline for reasons including inbreeding depression (Lindenmayer and Lacy 1995), environmental and demographic stochasticity (Lindenmayer and Lacy 1995), and dispersal mortality (Lindenmayer and Possingham 1996). The optimization model presented above does not capture stochastic or genetic influences on abundance but does account for population decline resulting from high dispersal mortality because of insufficient habitat. If currently suitable habitat in the Steavenson Block is indeed inadequate because of a shortage of nesting hollows, a nest-box program might have a relatively large impact on abundance compared with reservation of young stands to provide future habitat.

<sup>6</sup>These are illustrative only because of limited data on habitat in adjacent blocks.

<sup>7</sup>Habitat also exists in younger forest containing hollow-bearing trees that are remnants of previous wildfires, but these remnant nest trees are expected to collapse soon (Lindenmayer et al. 1997) and, therefore, are not accounted for in our model.

**Table 2.** Parameter values used in case study to estimate net present value.

| Parameter                                                | Base value          |
|----------------------------------------------------------|---------------------|
| Sawlog price (A\$/m <sup>3</sup> )                       | 35.64 <sup>a</sup>  |
| Pulplog price (A\$/m <sup>3</sup> )                      | 6.09 <sup>a</sup>   |
| Road cost (A\$/km)                                       | 15 000 <sup>b</sup> |
| Road cost (A\$/ha)                                       | 250                 |
| Regeneration cost (A\$/ha)                               | 350 <sup>c</sup>    |
| Nest-box cost (A\$/ha at 10 boxes/ha per 10-year period) |                     |
| Materials and construction labor                         | 600 <sup>d</sup>    |
| Installation                                             | 400 <sup>e</sup>    |
| Total cost                                               | 1000                |
| Discount rate (%)                                        | 4 <sup>f</sup>      |

<sup>a</sup>Mean royalty for logs sourced from the Central Highlands in the first 4 months of 2000 (C. Harvey, DNRE, personal communication).

<sup>b</sup>Source: K. Maplestone, DNRE (personal communication).

<sup>c</sup>Source: M. Woodman, DNRE (personal communication).

<sup>d</sup>Estimate is for a durable box design, likely to last for at least 10 years (M. MacFarlane, formerly DNRE, personal communication). We conservatively assume replacement occurs after 10 years.

<sup>e</sup>The cost will vary according to factors such as site accessibility, terrain, and stand density. The estimate is based on labor requirements of approximately 1 h/box (P. Menkhorst, DNRE, personal communication), and A\$400 can be viewed as an upper-bound cost estimate.

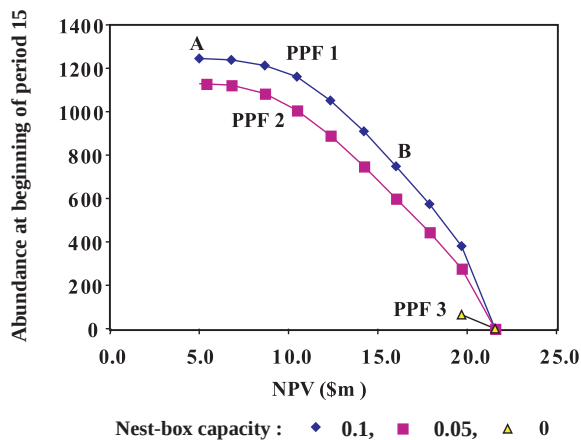
<sup>f</sup>The rate used by DNRE in evaluating its programs (Victorian Government 1986).

## Results

The model was solved on a personal computer using the spreadsheet-based linear programming solver, What'sBest! Extended version 5.0 (Lindo Systems). Merchantable sawlog and pulpwood volume yields at different stand ages (Appendix) were predicted using the ash stand simulation model STANDSIM (Coleman 1989). Present values of regeneration, road, and nest-box costs were estimated using information obtained from DNRE staff and are documented in Table 2. Nest-box costs are likely to be sensitive to the method used to initially identify LBP colonies. As noted above, Harley used a method in which a random initial placement of boxes helped identify colony sites, followed by more concentrated nest-box installations in close proximity to boxes that were colonized after the first placement. MacFarlane identified initial colony locations by means of stag watching.

To limit model size, we have restricted management scheduling flexibility. Schedules allow for initially harvesting at the beginning of any of the 15 time periods (or not at all) and reharvesting at the start of any period in which regrowth is four periods old or eight periods old. Nest boxes can be installed in groups of three successive periods, beginning with periods 1, 4, 7, 10, and 13, or in all periods or not at all. NPV per hectare ( $x_{ikm} - c_{ikm}$  in eq. 7) varies significantly between different management schedules and initial stand age-classes, being highest in old-growth stands for schedules with no nest-box installations in any period and successive harvests in periods 1, 5, 9, and 13 (A\$16 824).

**Fig. 4.** NPV – final abundance trade-offs at different nest-box capacities.



Installing nest boxes reduces NPV by A\$13 if boxes are installed only in the final three periods and ranging up to A\$2076/ha if boxes are installed in all periods.

Timber-flow constraints (eqs. 10 and 11) are not included in our base analysis but are briefly discussed in a later section. Trade-offs were identified with and without nest boxes under alternative assumptions about their carrying capacities and are illustrated in Fig. 4.

Two striking features of these trade-off relationships are that when nest boxes are installed, there is (i) a large increase in abundance at most levels of NPV even at a low nest-box capacity and (ii) a significantly expanded range over which there is a positive trade-off between NPV and final abundance. The following discussion focuses on these two features.

The large increase in final abundance facilitated by nest boxes appears to reflect inadequate habitat over the first seven periods, as illustrated in Fig. 5.

Because the spatial arrangement of existing old growth is inefficient, total abundance is limited by reproduction–dispersal rates (constraint in eq. 3) rather than carrying capacity when nest boxes are not installed (Fig. 5a). Reproduction–dispersal conditions are such that abundance declines over the first seven periods despite the existence of unexploited but poorly arranged carrying capacity, indicating a high rate of dispersal mortality. When dispersal mortality is sufficiently large it can outweigh additions to populations caused by reproduction, with the effect that total abundance declines. In such circumstances, the habitat and population parameters governing population outcomes are said to lie below an extinction threshold (Bever and Flather 1999; Lande 1987). It appears that modeled habitat and population parameters in our case study are below threshold. If nest boxes are not installed, abundance begins to increase only when recruitment of new nest trees in unharvested 1939-regrowth stands enlarges the size of the habitat complex, beginning in period 9.

Inadequate habitat when nest boxes are not installed also helps explain the more restricted range over which there is a positive trade-off between NPV and final abundance. With-

out nest boxes, NPV can be increased from A\$0 to A\$20.5 million without final abundance falling from its maximum achievable level (66 animals). Thus, the positive trade-off range without nest boxes begins at A\$20.5 million, since any NPV less than this would entail some commercial sacrifice with no compensating increase in final abundance. Apparently, the prolonged period of inadequate habitat followed by substantial growth of new habitat creates a large amount of “surplus” habitat that cannot be exploited by local populations within the 150-year time horizon. This allows for large timber harvests to take place without reducing maximum attainable final abundance (although such harvests might have a significant effect on abundance if random demographics were taken into account). In contrast, when nest boxes having a carrying capacity of 0.1 animals/ha are installed, trade-offs begin at the much lower NPV of A\$5.0 million. This partly reflects the fact that nest boxes artificially enlarge the habitat complex much earlier and reverse the decline in possums (compare nesting capacity and abundance over the first eight periods in Figs. 5a and 5b), reducing “surplus” carrying capacity.<sup>8</sup> It also reflects the positive impact of low levels of timber harvesting on abundance via an increase in food capacity, as illustrated in Fig. 5b. Food capacity is measured as  $\sum_t \sum_k K_k \sum_{m=1}^{M_{ik}} f_{ikmt} S_{ikm}$  from eq. 6, and only food within the Steavenson block is included (although some boundary populations also were supported by minor amounts of food from outside the block). In the absence of harvesting, surplus food capacity would exist until the 12th period, after which food capacity would begin to limit abundance. Thus, there is scope to increase final abundance by harvesting in one or more middle periods to expand food capacity in later periods when it would otherwise limit abundance. This appears to explain the large harvest in period 9 (Fig. 6a). Figure 5a implies that this beneficial effect of timber harvesting on final abundance would not exist when nest boxes are not installed, as populations are not capacity limited in any period.

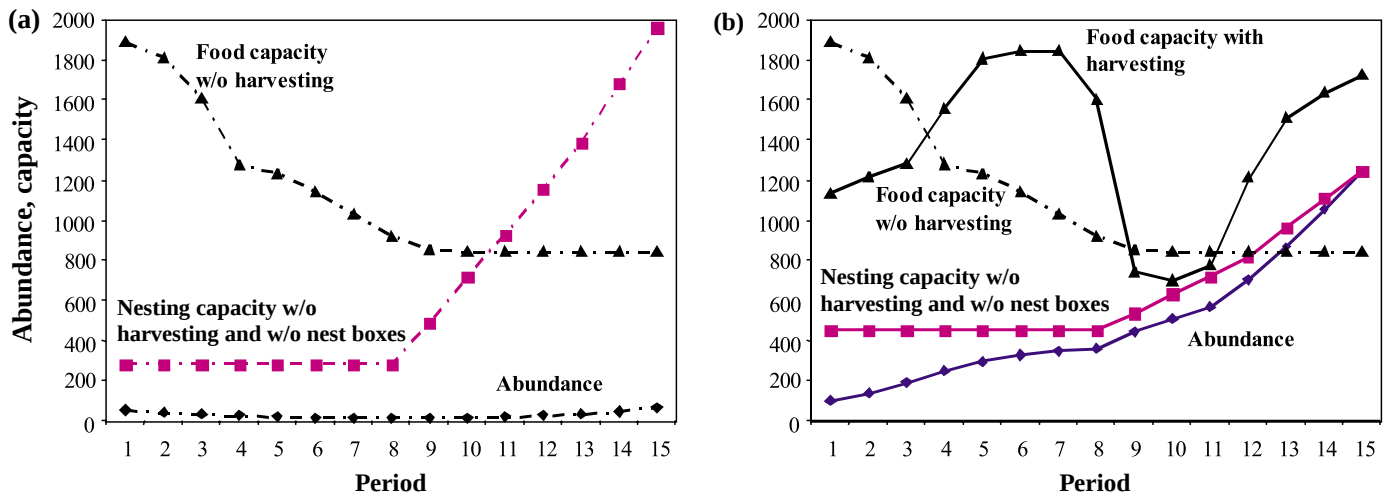
The optimal areal extent of nest-box installations and timber harvests, and their placement and timing, are sensitive to the mix of final abundance and NPV that is sought. This is illustrated in Fig. 6, which shows the timing of harvests at points A and B on PPF 1, and Figs. 7 and 8, which show the placement and areal extent of these harvests, together with details on nest-box installations.

Figure 6a illustrates that at point A on PPF 1, there is a large harvest in the first period followed by a larger harvest when regenerating stands reach 80 years (or eight periods) of age. The second harvest facilitates higher final abundance (as discussed above), while the first harvest has no impact on final abundance but a relatively large impact on NPV. Figure 6b shows that the higher NPV at point B on PPF 1 is partly achieved by a significantly larger first-period harvest. Also contributing to the higher NPV at point B is an increased use of more intensive harvest schedules, in which repeat harvests occur at four-period intervals rather than eight (not illustrated).

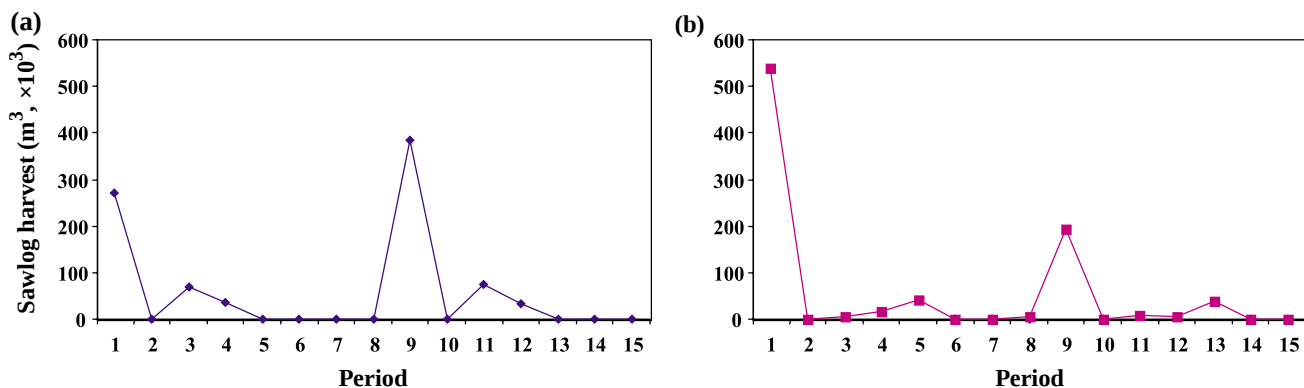
At point A on PPF 1, the areas selected for harvesting and nest-box installations in old-growth stands (within shaded

<sup>8</sup> Because of space limitations, we do not illustrate abundance and carrying capacities with optimal nest-box scheduling in the absence of timber harvesting.

**Fig. 5.** Abundance and carrying capacities through time associated with maximum final abundance (a) without nest boxes and without timber harvesting and (b) with optimally selected nest-box – harvest schedules (each nest box having a nesting capacity of 0.1 animals/ha).



**Fig. 6.** Sawlog harvests at points A (a) and B (b) on PPF 1 in Fig. 4.



cells in Figs. 7 and 8, respectively) typically are smaller than in stands having a lower initial age. This reflects the high nesting capacity of old-growth stands relative to that assumed of nest boxes. Most of the harvesting in old-growth stands is concentrated among perimeter cells, indicating clustering of habitat, which reduces its perimeter/area ratio and, thereby, minimizes dispersal losses (Bever and Flather 1999). Figures 7 and 8 also illustrate that the higher NPV at point B is partly achieved by some substitution of late nest-box installation schedules for schedules in which nest boxes are installed in all periods. At point A on PPF 1, this substitution is particularly evident in perimeter cells and cells that initially contain old-growth stands. Perimeter cells are colonized more slowly than interior cells because of their relative isolation, providing scope to economize on nest-box expenditures through later installation. At point B, late nest-box installation schedules are selected in virtually all cells.

Notably, the above results illustrate that extensive use is made of nest boxes over a wide range of abundance–NPV combinations and that it is efficient to economize on nest-box expenditures by limiting their timing and areal extent (particularly where a high NPV is sought). Similar findings were made after including eqs. 10 and 11, which impose the institutional requirement that DNRE provide an even flow of

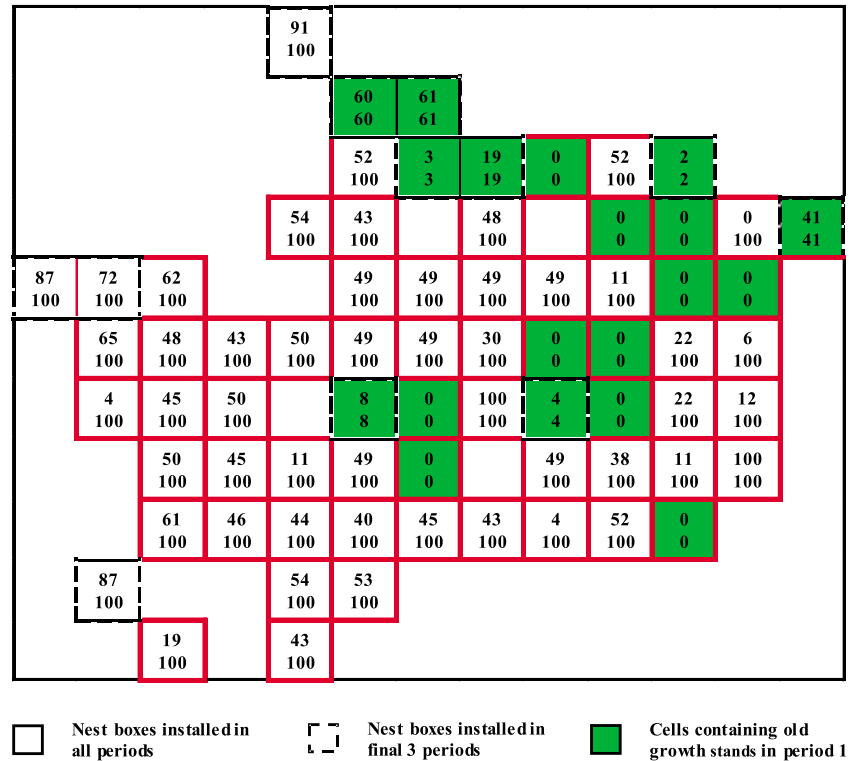
sawlogs and thereby limit its harvest timing flexibility. We set  $\psi$  to 0.10, causing sawlog flows to stabilize at between 80 000 and 90 000  $\text{m}^3/\text{year}$  (close to actual periodic harvest volumes in the study region). This resulted in an inward shift of the PPF (not illustrated). The fall in maximum attainable NPV is caused by a reduction in the initial harvest and increased use of relatively less profitable longer rotation harvest schedules. The fall in maximum final abundance is due to a reduction in harvest timing flexibility, which reduces the extent to which harvesting can be used to expand food abundance when required without reducing nesting and (or) food capacity in other periods. Notably, a larger area is selected for nest-box installations at maximum final abundance under sawlog-flow restrictions.

Our model is quite sensitive to assumptions about reproduction and dispersal, particularly when close to threshold conditions. Increasing reproduction rates and decreasing mean dispersal distances improves population outcomes, although this has not been illustrated because of space limitations.

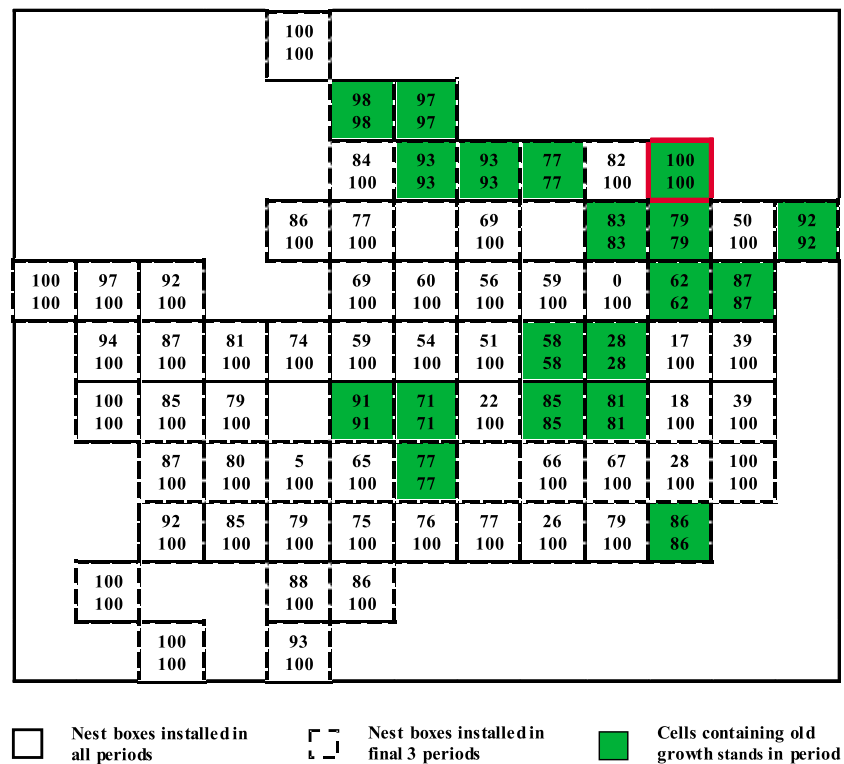
## Conclusion

Our results demonstrate the potential importance for efficient design of a nest-box program of the areal extent, place-

**Fig. 7.** The percentage of the area of each cell selected for harvesting (upper values in cells) and nest-box installation (lower values in cells) over all periods at point A on PPF 1 (Fig. 4). Percentages in cells that contain old-growth forest in the first period (shaded cells) refer only to the old-growth components of these cells.



**Fig. 8.** The percentage of the area of each cell selected for harvesting (upper values in cells) and nest-box installation (lower value in cells) over all periods at point B on PPF 1 (Fig. 4). Percentages in cells that contain old-growth forest in the first period (shaded cells) refer only to the old-growth components of these cells.



ment and timing of nest-box installations and timber harvests. This is particularly evident in the case analyzed above, in which natural nest sites appear to be critically low over the first half of the modeled time horizon. In these circumstances, nest boxes may allow for much larger population levels than would be possible when relying solely on reserving land. This finding highlights an important limitation of the approach used by ML to indicate whether to implement a nest-box program. ML compare the present value cost of a nest-box program with that of a logging ban over a long time horizon. Formulating the management problem in this way is inappropriate if populations of LBP in commercially productive montane ash forest are likely to go extinct because of a shortage of potential nest sites even in the absence of timber harvesting. In such cases, attention needs to be directed to artificial habitat enhancement opportunities and how these may be implemented in a cost-effective manner.

Although, where possible, data obtained from ecological studies of LBP were incorporated in our model, we do make a number of simplifying assumptions about habitat and population dynamics. For example, our model does not account for the potential decrease in foraging efficiency associated with increased local population levels. Capturing this effect would require nonlinear optimization techniques, which are likely to present major computational difficulties for models having a large spatial and temporal extent. Moreover, these more complex models would require more data on foraging behavior than currently exist for LBP. Secondly, our framework does not account for stochastic influences on abundance. The habitat of LBP is prone to large wildfires, and demographic stochasticity alone can add significantly to the risk of local extinction of this species (Lindenmayer and Lacy 1995). However, it is worth noting that, because of the risks imposed by wildfire, the flexibility of nest boxes (for example, they can be installed soon after a fire) may be advantageous relative to other population-recovery options.

The limited scope of our study also needs to be emphasized. We address the nesting requirements of only one species, LBP, in the montane ash forests of the Victorian Central Highlands, yet over 25 hollow-dependent species occur in these forests. It may not be feasible to provide nest boxes for all of these species. Moreover, the loss or delayed formation of hollow-bearing trees is only one of the impacts logging has on wildlife. Thus, the nest-box program considered here is best viewed as a highly targeted population recovery tool rather than a general tool of multiple-use forest management.

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## Appendix

### Habitat capacities and timber volumes

Discrete estimates of food capacity ( $f_{kmt}$ ) in period  $t$  are made using the following equation, which accounts for predicted acacia tree (*Acacia* sp.) abundance  $y$  years after clearfell harvesting:<sup>A1</sup>

$$[A1] \quad f_{(y+1)} = \begin{cases} 0, & 0 \leq y \leq 20 \\ \frac{(y-15)}{20}, & 20 \leq y \leq 35 \\ 1, & 35 \leq y \leq 60 \\ \frac{1-0.7(y-60)}{40}, & 60 \leq y \leq 100 \\ 0.3, & y \geq 100 \end{cases}$$

As in Lindenmayer and Possingham (1996), we assume that existing old-growth stands are at maximum nesting capacity (1 animal/ha) and remain at this value if unharvested. Discrete estimates of nesting capacity ( $a_{kmt}$ ) in period  $t$  in ar-

eas outside of existing old-growth stands are made using the following equation, which accounts for predicted nest tree abundance  $y$  years after harvesting:<sup>A2</sup>

$$[A2] \quad \begin{aligned} a_y &= 0, & 60 < y \leq 150 \\ a_{(y+1)} &= \frac{1.6(y-150)}{150}, & 150 \leq y \end{aligned}$$

Harvested stands are assumed to contain no retained trees, either because all trees were removed in the harvest or because any retained trees fall over soon after harvesting.<sup>A3</sup>

The assumption that harvesting occurs all at once at the beginning of the period results in systematic but conservative underestimation of abundance. For example, harvests are modeled at the beginning of a time step and remove capacity over the entire step, when in reality, harvests occur gradually and, thus, may allow for reproduction to occur over part of the time step. Sawlog and pulpwood volume yields at different stand ages are set out in Table A1.

**Table A1.** Timber volume yields (m<sup>3</sup>).

| Age<br>(years) | Sawlog | Pulplog |
|----------------|--------|---------|
| <20            | 0      | 148     |
| 30             | 0      | 347     |
| 40             | 30     | 466     |
| 50             | 84     | 509     |
| 60             | 171    | 488     |
| 70             | 269    | 456     |
| 80             | 371    | 414     |
| 90             | 462    | 380     |
| 100            | 516    | 379     |
| 110            | 576    | 373     |
| ≥120           | 628    | 371     |

**Note:** Values are from STANDSIM (Coleman 1989; settings used are available on request).

<sup>A1</sup>Based on eq. A1 in Lindenmayer and Possingham (1996, p. 104) to estimate food capacity after a wildfire. In the Lindenmayer–Possingham equation, food capacity begins to regenerate at 15 years after a wildfire. Our modification that food capacity regenerates at 20 years was made to ensure consistency with our 10-year time step. We also assume that acacia availability after coupe regeneration burning follows a similar pattern to that following wildfire in an unharvested stand.

<sup>A2</sup>Equation A2 is based on eq. A2 in Lindenmayer and Possingham (1996, p. 104).

<sup>A3</sup>Retained trees are likely to collapse soon after harvesting as many are burned in regeneration fires and face increased exposure to wind (S. Lawlor, Senior Forester, DNRE, personal communication).