

Assessing reserve effectiveness: Application to a threatened species in a dynamic fire prone forest landscape



Charles R. Todd^{a,*}, David B. Lindenmayer^b, Kasey Stamation^a,
Silvana Acevedo-Cattaneo^{a,c}, Stephen Smith^{a,d}, Linda F. Lumsden^a

^a Arthur Rylah Institute for Environmental Research, Department of Environment, Land, Water and Planning, P.O. Box 137, Heidelberg, Victoria 3084, Australia

^b Fenner School of Environment and Society, The Australian National University, Canberra, Australian Capital Territory 0200, Australia

^c School of Mathematical and Geospatial Sciences, RMIT University, GPO Box 2476, Melbourne, Victoria 3001, Australia

^d Department of Environment, Land, Water and Planning, 5 Binns McCraes Road, Alexandra, Victoria 3714, Australia

ARTICLE INFO

Article history:

Received 4 November 2015

Received in revised form 22 July 2016

Accepted 26 July 2016

Keywords:

Metapopulation model

Leadbeater's possum

Gymnobelideus leadbeateri

Population risk analysis

Risk assessment

Reserve adequacy

ABSTRACT

Reserve systems are part of biodiversity conservation planning. However, reserves are rarely assessed for their contribution to population persistence. Here we address knowledge gaps on reserve effectiveness by developing a new approach to model protected area efficacy as a function of habitat suitability and natural disturbance regimes. We demonstrate the utility of the model through a detailed case study of the critically endangered Leadbeater's possum (*Gymnobelideus leadbeateri*) in south-eastern Australia. We defined reserve effectiveness for the species to be when there was no more than 5% probability of populations falling to (or below) 500 adult females in 40 generations. A reserve system established specifically for Leadbeater's possum was found inadequate to ensure population persistence for the next 40 generations, given historical disturbance, habitat decline, and future fires. Simulation modelling of potential areas of reserve suggests that, depending on management risk tolerance, between 30% to 100% of current forest extent within the range of the species may be required to ensure population persistence. This study exemplifies the need to consider the size of reserves prior to their establishment to ensure an adequate reserve design that will be effective against future disturbance for conserving threatened species.

© 2016 Published by Elsevier B.V.

1. Introduction

Threatened species management can be fraught with uncertainty (Bottrill et al., 2011; Gregory et al., 2013; Salomon et al., 2013; Tempel et al., 2014). Natural disturbance and anthropogenic impacts can combine so that some threatened species require management intervention to ensure persistence (Reece et al., 2013). One of the goals of threatened species management is to promote conditions for a species to retain the potential for evolutionary change without intensive management (Akçakaya et al., 1997; Redford et al., 2011). The most widely applied approach for threatened species management is to set aside protected areas such as reserves (Rodrigues and Brooks, 2007; Watson et al., 2014; Butchart et al., 2015). Thirteen percent of the earth's landmass is in formal reserves (Le Saout et al., 2013). Reserves are credited with

conserving many species that might have otherwise succumbed to extinction (Rodrigues and Brooks, 2007; Le Saout et al., 2013). However, reserves and the species they aim to protect can remain vulnerable to natural disturbances such as wildfires (Baker, 1992; McCarthy and Lindenmayer, 2000; Watson et al., 2011a,b).

Notwithstanding that protected areas are considered a fundamental part of credible biodiversity conservation programs (Lindenmayer and Franklin, 2002) and conservation biology more generally (Sodhi and Ehrlich, 2010), they are rarely assessed a priori for their effectiveness in ensuring species persistence and viability (Cabeza and Moilanen, 2001; Barber et al., 2012; Bottrill and Pressey, 2012). Here we address knowledge gaps on reserve effectiveness for the protection of a threatened species by developing a new approach to model protected area efficacy as a function of habitat suitability and natural disturbance regimes. We demonstrate the utility of the model through a detailed case study of the critically endangered Leadbeater's possum (*Gymnobelideus leadbeateri*), across its entire range in south-eastern Australia.

* Corresponding author.

E-mail address: charles.todd@delwp.vic.gov.au (C.R. Todd).

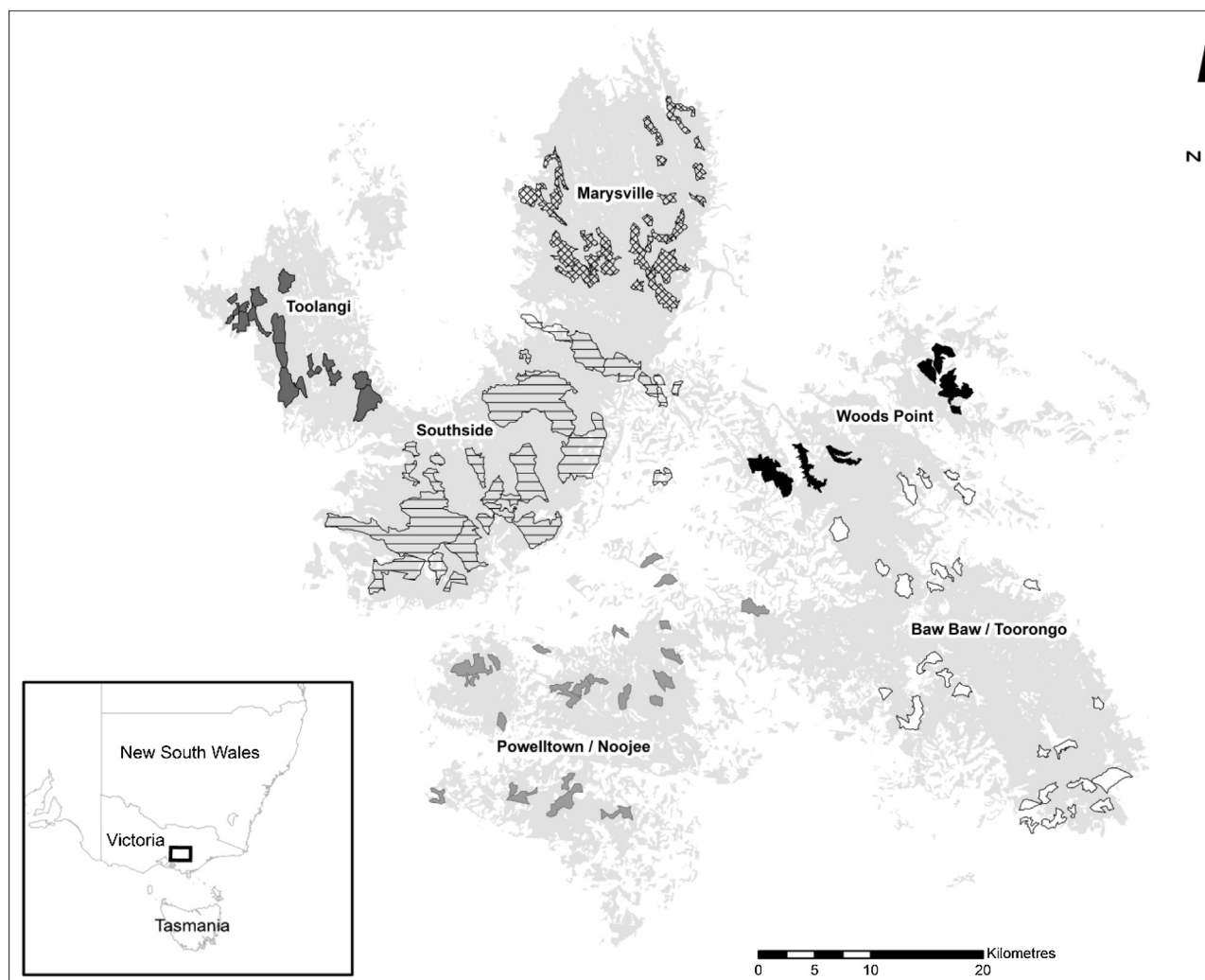


Fig. 1. Location of the reserve system for Leadbeater's possum in the Central Highlands of Victoria, south-eastern Australia with the reserve system regional groupings: 1 Toolangi (dark grey); 2 Marysville (hatched); 3 Southside (horizontal); 4 Woods Point (black); 5 Powelltown/Noojee (medium grey); and 6 Baw Baw/Toorongo (white), and the broader Central Highlands montane eucalypt forest in light grey.

The range-restricted species, Leadbeater's possum, is sensitive to the effects of wildfires, clear-cut logging, and post-fire salvage logging (Lindenmayer et al., 2013). A reserve system was established specifically for this species in 2008 and just one year later ~43% of this reserve was burned along with 34% of all potential forest habitat for the species (Lindenmayer et al., 2014). Bushfires remove the dense understorey required by this species for foraging and the dead hollow-bearing trees typically used as nesting sites (Lindenmayer et al., 2013). Field surveys following this fire indicate that previously suitable habitat burnt in 2009 was no longer occupied by the species, irrespective of the intensity of the fire (Lindenmayer et al., 2013; Lumsden et al., 2013). Given this, there have been increasing concerns about the medium to long-term persistence of Leadbeater's possum, in part because the effectiveness of the reserve system developed for the species is unknown.

The establishment of the Leadbeater's possum reserve system was one of the key strategies of the Leadbeater's Possum Recovery Plan with the aim of sustaining viable populations throughout the species' range (Macfarlane et al., 1997). Here we define effectiveness for the Leadbeater's possum reserve as ensuring no more than 5% probability of populations falling to (or below) 500 adult females in 40 generations to prevent inbreeding and applied to the whole population. Using the species generation time accords with more recent research on minimum viable population size and per-

sistence (Reed et al., 2003; Frankham and Brook, 2004; Sanderson, 2006; O'Grady et al., 2008). Additionally, 40 generations (200 years) reflects the time for trees to develop suitable nesting habitat (large hollows) for Leadbeater's possum (Smith and Lindenmayer, 1988). On this basis, we addressed two key questions.

- 1) What is the effectiveness of the current Leadbeater's possum reserve system for conserving Leadbeater's possum?
- 2) If the current reserve system is considered ineffective, what would be an effective sized reserve system for Leadbeater's possum, and how does this compare to the total area protected in national parks and reserves or through prescriptions in State forest?

To assess effectiveness, we synthesized parameters from several previously developed population models for Leadbeater's possum (Lindenmayer et al., 1993; Lindenmayer and Lacy, 1995a,b; Lindenmayer and Possingham, 1995a,b). We proportionally increased the size of the 'reserve' in each region in the model and tested it repeatedly using a simulation model until it was deemed adequate for supporting populations of Leadbeater's possum (as defined above). We tested reserve effectiveness in response to the long-term effects of past disturbances on habitat suitability,

Table 1
Life history and key parameters for the Leadbeater's possum metapopulation model and glossary of terms.

Survival rates ^a		Reserve regional areas	ha
0–6 months ^b	0.8367	1 Toolangi	2604
6–12 months and older	0.8367	2 Marysville	4471
Coefficient of variation in survival rates		3 Southside	14,741
0–6 months	20%	4 Woods Point	2005
6–12 months and older	10%	5 Powelltown/Noojee	3038
Fecundity schedule per female ^a		6 Baw Baw/Toorong	3660
Six month probability of 0 female young	0.56	Central Highland regional areas	ha
Six month probability of 1 female young	0.33	1 Toolangi	10,438
Six month probability of 2 female young	0.11	2 Marysville	14,790
(Equivalent to 2.2 offspring per year)		3 Southside	36,753
CV in fecundity	10%	4 Woods Point	14,903
Dispersal if regional pop ⁿ is \geq	70%	5 Powelltown/Noojee	20,216
Pop ⁿ model summary		6 Baw Baw/Toorong	31,456
Max age	8 years	Area required per colony ^a	3 ha
Growth rate (λ) six months	1.024	Model timing	t steps
Annual growth rate	1.048	p_1 : 1939 wildfire	100
Average female age	2.91	p_2 : 1983 fire	188
Average adult female age	3.35	p_3 : 1990 fire	202
Generation time (T)	5 years	p_4 : 2007 fire	236
Fire impacts ^a	t steps ^c	p_5 : 2009 fire	240
Time when understory recovery begins	30	p_6 : future fire 2020	262
Time when max understory achieved	70	p_6 : future fire 2030	282
Time when understory decline begins	120	p_6 : future fire 2040	302
Time when understory stops declining	200	Number of fires (<i>nfire</i>)	6
Time when hollows first form in trees	240		
Time when max no. of hollows formed	480		
Glossary of terms			
i	6 month age class	p_k	Time step when fire k occurs
s_i	survival rate for age class i	PB_j	Proportion of area burnt
N_{ij}	Females in age class i in region j	<i>nfire</i>	Maximum number of fires
$dens_j$	Density dependence factor in region j	H_{jk}^2	Live tree habitat in region j after fire k
N_{1dj}	Females in age class 1 females dispersing from region j	H_{j1}^2	Live tree habitat in region j after first fire
N_{1ej}	Females in age class 1 entering region j	BH_{jk}^2	Burnt live tree habitat in region j after fire k
$Pr(FY=1)$	Probability of a female adult producing one female offspring in her litter	NBH_{jk}^2	Non-burnt live tree habitat in region j after fire k
$Pr(FY=2)$	Probability of a female adult producing two female offspring in her litter	H_{jk}^3	Dead tree habitat in region j after fire k
ED_j	The expected density of colonies in region j	H_{j1}^3	Dead tree habitat in region j after first fire
H_{jk}^1	Food habitat in region j after fire k	BH_{jk}^3	Burnt dead tree habitat in region j after fire k
H_{j1}^1	Food habitat in region j after first fire	NBH_{jk}^3	Non-burnt dead tree habitat in region j after fire k
BH_{jk}^1	Burnt food habitat in region j after fire k	DL	Decline level
NBH_{jk}^1	Non-burnt food habitat in region j after fire k	AD_j	Additional decline in region j

^a Collated from Lindenmayer et al. (1993), Lindenmayer and Lacy, (1995a,b); and Lindenmayer and Possingham (1995a,b).

^b The equivalent annual survival rate is 0.7, i.e. 0.8367^2 .

^c Halve t steps (time steps) to calculate years.

Table 2
Historical fire regime impacts on the Leadbeater's possum reserve system, with the area burnt in each fire in hectares (ha).

Year	Toolangi	Marysville	Southside	Woods Point	Pow/Noo ^a	BB/Toor ^b
1939	2474.7	4247.6	14004.2	1904.7	2886.4	3476.6
1983	0	0	591.34	0	1036.65	0
1990	0	0	0	302.1	8.15	0.08
2007	0	0	0	718.23	0	0
2009	256.2	3444.7	7227.0	0	32.1	0

^a Pow/Noo – Powelltown/Noojee.

^b BB/Toor – Baw Baw/Toorong.

as well as the impacts of ongoing habitat decline (Lindenmayer et al., 2012) and future fires.

We illustrate, using Leadbeater's possum as a case study, how uncertainty about future habitat availability and natural and human disturbances can (and should) be incorporated into the design of effective reserve systems.

1.1. Reserve system for Leadbeater's possum

A permanent 30,500 ha reserve system for Leadbeater's possum was established in 2008 to protect patches of high quality habitat from the impacts of timber harvesting and fire (Fig. 1) (Smith

and Morey, 2001). The reserve system comprises areas in both national parks (58 per cent) and State forest Special Protection Zones (42 per cent) (Smith and Morey, 2001). Timber harvesting is not permitted in the reserve. Areas of forest were selected for the reserve system based on characteristics that constitute suitable habitat for Leadbeater's possum, namely a high density of hollow-bearing trees, connectedness to other reserves, and the presence of old growth forest with limited or no history of logging (and where hollow-bearing trees are most abundant). Within the range of the species, there is approximately 195,000 ha of potentially suitable habitat (based on the vegetation types used by the species), although not all of this potential habitat is likely to be cur-

Table 3
Scenarios modelled to explore the effectiveness of the Leadbeater’s possum reserve based on past and future disturbances. HBT – hollow-bearing trees.

Scenario no.	Parameters	Description
S1	Table 1 & Table 2	Historical fire regime
S2	12.5% decline in HBT	Decline in HBT and S1
S3	25% decline in HBT	Decline in HBT and S1
S4	50% decline in HBT	Decline in HBT and S1
S5	12.5% decline in HBT and 25% area burnt in 2020; 2030; or 2040	Moderate future fire in 2020; 2030; or 2040 combined with S2
S6	25% decline in HBT and 25% area burnt in 2020; 2030; or 2040	Moderate future fire in 2020; 2030; or 2040 combined with S3
S7	50% decline in HBT and 25% area burnt in 2020; 2030; or 2040	Moderate future fire in 2020; 2030; or 2040 combined with S4
S8	12.5% decline in HBT and 50% area burnt in 2020; 2030; or 2040	Large future fire in 2020; 2030; or 2040 combined with S2
S9	25% decline in HBT and 50% area burnt in 2020; 2030; or 2040	Large future fire in 2020; 2030; or 2040 combined with S3
S10	50% decline in HBT and 50% area burnt in 2020; 2030; or 2040	Large future fire in 2020; 2030; or 2040 combined with S4

rently occupied (Lumsden et al., 2013), it is reasonable to think of the reserve system as part of the continuum of habitat available for use by Leadbeater’s possum. Overall, 51% of the range of Leadbeater’s possum (98,500 ha) is currently reserved as national parks or Special Protection Zones in State forest. In addition, approximately 43,000 ha of State forest available for timber harvesting will not be harvested due to biodiversity, regulatory, operational or prescriptive reasons.

The increased risk of extinction of the species after the 2009 bushfires (Lindenmayer and Possingham, 2013) led to concerns about the adequacy of the current reserve system (Lindenmayer et al., 2014). Furthermore, the observed decline in Leadbeater’s possum habitat in addition to the fire impact (Lindenmayer et al., 2012) led to concerns about future habitat disturbance, such as continued habitat decline, and what role future wildfires would play in shaping Leadbeater’s possum persistence. This led to the important question of what is an effective reserve size to ensure species persistence given the uncertain future habitat state.

2. The model

There have been several previous modelling studies of Leadbeater’s possum investigating population viability (Lindenmayer et al., 1993; Lindenmayer and Lacy, 1995a,b; Lindenmayer and McCarthy 2006; Lindenmayer and Possingham 1995a,b), all prior to the 2009 bushfires (see Supplementary material for detail on the biology and ecology of Leadbeater’s possum). We extend this earlier work by explicitly developing a new stochastic metapopulation model to address questions about reserve effectiveness as a function of historical fire disturbance, habitat decline, and future fires.

2.1. Model construct

We constructed an age-based stochastic metapopulation model to simulate fecundity directly by specifying a six month time step, in which females can reach a maximum age of 8 years (Table 1) with the following matrix:

$$\begin{bmatrix}
 0 & 0 & 0 & s_{1f} & s_{1f} & \dots & s_{1f} & \dots & s_{1f} & s_{1f} & s_{1f} \\
 s_2 & 0 & 0 & 0 & 0 & \dots & 0 & \dots & 0 & 0 & 0 \\
 0 & s_3 & 0 & 0 & 0 & & 0 & & 0 & 0 & 0 \\
 0 & 0 & s_4 & 0 & 0 & & 0 & & 0 & 0 & 0 \\
 0 & 0 & 0 & s_5 & 0 & & 0 & & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & s_6 & & 0 & & 0 & 0 & 0 \\
 \vdots & & & & & \ddots & & & & & \vdots \\
 0 & 0 & 0 & 0 & 0 & & s_i & & 0 & 0 & 0 \\
 \vdots & & & & & & & \ddots & & & \vdots \\
 0 & 0 & 0 & 0 & 0 & \dots & 0 & \dots & s_{14} & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & \dots & 0 & \dots & 0 & s_{15} & 0
 \end{bmatrix}$$

where s_i is the survival rate for the given six month period and f the fecundity based on the schedule in Table 1.

Leadbeater’s possum single population model construct for each region $j, j = 1, \dots, 6$:

$$\begin{aligned}
 N_{ij}(t+1) &= Bin(N_{i-1j}(t), dens_j(t) \times s_{i-1}(t)) & i = 4, \dots, 16 \\
 N_{3j}(t+1) &= Bin(N_{2j}(t), s_2(t)) \\
 N_{2j}(t+1) &= Bin(N_{1j}(t) - N_{1dj}(t) + N_{1ej}(t), s_1(t)) \\
 N_{1j}(t+1) &= Poisson\left(\sum_{i=4}^{16} N_{ij}(t) \times s_0(t) \times (1 \times Pr(FY=1) + 2 \times Pr(FY=2))\right) \\
 dens_j(t) &= \begin{cases} ED_j(t) / \sum_{i=4}^{16} N_{ij}(t) & \sum_{i=4}^{16} N_{ij}(t) > ED_j(t) \\ 1 & \sum_{i=4}^{16} N_{ij}(t) \leq ED_j(t) \end{cases}
 \end{aligned}$$

where t is a six month time interval; $N_{ij}(t)$ is the number of female Leadbeater’s possums in the i th 6 month age class in the j th region, $N_{1dj}(t)$ are 6 month old females dispersing from the j th region and $N_{1ej}(t)$ is the total number of 6 month old females entering the j th region from other regions (dispersal matrix described below); $s_i(t)$ is a random variate describing environmental variation in survival rates of possums in the i th 6 month age class (Table 1) drawn from normal distributions transformed to the unit interval (Todd and Ng, 2001) with specified means and standard deviations properly constrained to the unit interval without loss of information (all survival rates are perfectly correlated across the regions); $dens_j(t)$ is the density-dependence factor for female adults and available colony sites; $Pr(FY=1)$ and $Pr(FY=2)$ are the probabilities that a single female young is born and two female young are born respectively and is drawn from a normal distribution: $Pr(FY=1) = FY \sim N(0.11, 0.011)$, and $Pr(FY=2) = FY \sim N(0.33, 0.033)$ (Table 1) (perfectly correlated across regions independent from survival rates); $ED_j(t)$ is the expected density of colonies and is derived from the fire history for each region (derivation below); $Bin(n, s)$ is a random variate representing demographic variation in transition from one age class to the next with a binomial distribution $Bin(n, s) = X \sim Binom(n, s)$; and $Poisson(m)$ is a random variate representing demographic variation in recruitment with a Poisson distribution $Poisson(m) = Y \sim Poi(m)$.

There is no direct measurement of survival for Leadbeater’s possum, and a range of values have been used previously for different ages. The age class 0–1 has three estimates: 0.5–0.6 (Lindenmayer et al., 1993); 0.9 (Lindenmayer and Lacy, 1995a,b); and 1.0 (Lindenmayer and Possingham, 1995a,b). For all ages greater than 1, 0.7 is the most frequently used survival rate for females (Lindenmayer and Lacy, 1995a,b; Lindenmayer and Possingham, 1995a,b). It is unlikely that 100% of 0–1 aged juveniles would survive to become 2 year olds as in Lindenmayer and Possingham (1995a,b), in fact Smith (1984) documents variation between years in the survival of post-weaned juveniles (0–6 months). A survival rate of 0.7 for 0–1 aged females was used (approximately the average of the Lindenmayer et al., 1993 and the Lindenmayer and Lacy, 1995a,b estimates) and converted to a six

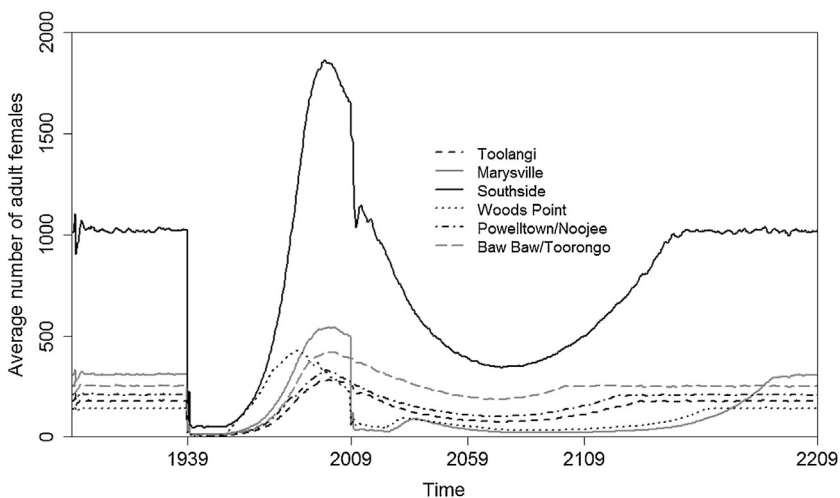


Fig. 2. The average number of adult females in each region of the Leadbeater's possum reserve, reflecting the impacts of the historical fire regime.

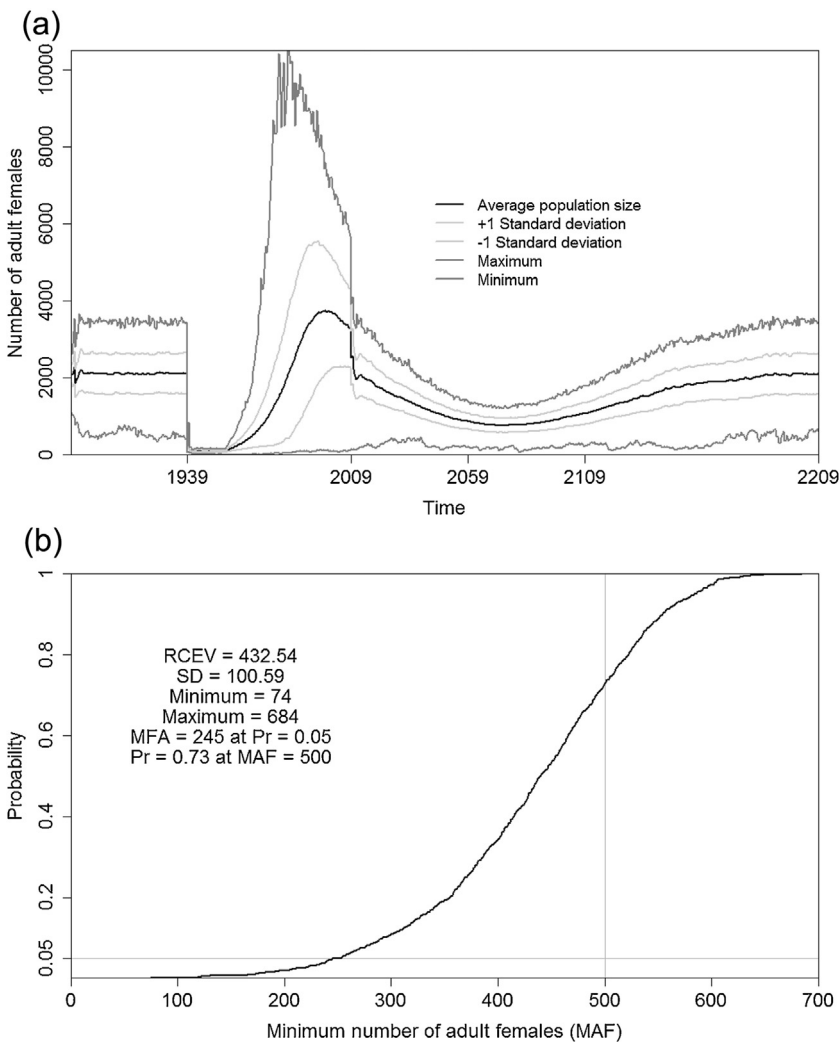


Fig. 3. The average number of adult females in the metapopulation within the Leadbeater's possum reserve showing ± 1 standard deviation as well as the maximum and minimum population sizes (a) and the associated minimum population size risk curve for adult females (b), where the minimum number of adult females is 245 when the probability threshold is set to 0.05 (the horizontal line) and the probability of being 500 adult females or less (the vertical line) is 0.73, when the minimum number of adult females is set to 500.

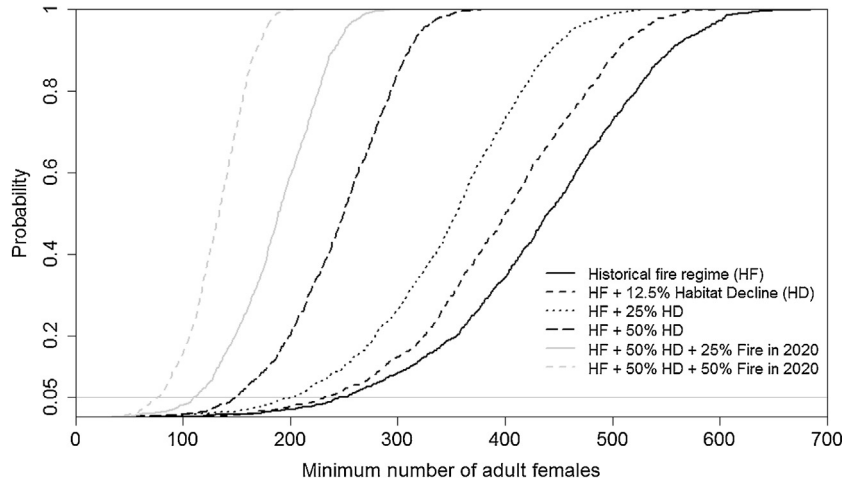


Fig. 4. Minimum population size risk curves for adult females, within the Leadbeater’s possum reserve, for scenarios S1–S4; S7 and S10 with a fire in 2020, the horizontal line shows the 0.05 probability threshold indicating that none of the risk curves are close to achieving the minimum population limit threshold of 500 adult females.

month survival rate 0.8367 (Table 1). The variable survival observed by Smith (1984) in post-weaned juveniles indicates greater variation in survival in the 0–6 months age class than older age classes (Table 1).

Annual fecundity was reported as 2.2 offspring per year (Lindenmayer et al., 1993), equivalently 1.1 offspring per six month period, although Lindenmayer and Possingham (1995a,b) used a lower fecundity 0.88 female offspring per female per year. Specifying a maximum of 2 female offspring per six months so that the annual fecundity rate was 2.2 and the annual female offspring per female was equivalent to 1.1 returns the fecundity schedule used in the model (Table 1). The fecundity schedule in Table 1 assumes an even sex ratio, Harley and Lill (2007) document litter composition as: single litter with males 42.5% and females 57.5% (n = 40); and dual litter with male/male 42.85%, male/female 42.85%, and female/female 14.3% (n = 49).

Model for food availability, $t = 6$ months, $j = 1, \dots, 6$ and $k = 1, \dots, n_{\text{fire}}$:

$$BH_{jk}^1(t+1) = \begin{cases} 0 & p_k \leq t \leq p_k + 30 \\ (H_{jk}^1(t) - 30)/40 & p_k + 30 < t \leq p_k + 70 \\ 1 & p_k + 70 < t \leq p_k + 120 \\ 1 - 0.7 \times (H_{jk}^1(t) - 120)/80 & p_k + 120 < t \leq p_k + 200 \\ 0.3 & t > p_k + 200 \end{cases}$$

$$NBH_{jk}^1(t+1) = 0.3 \quad t \geq 0$$

$$H_{j1}^1(t+1) = BH_{j1}^1(t) \times PB_j(t) + NBH_{j1}^1(t) \times (1 - PB_j(t))$$

$$H_{jk}^1(t+1) = H_{jk-1}^1(t+1) \times (BH_{jk}^1(t) \times PB_j(t) + NBH_{jk}^1(t) \times (1 - PB_j(t))) / 0.3$$

where $PB_j(t)$ is the proportion of the habitat burnt, given by Area of fire in region j /Area of region j (see Tables 1 and 2).

Model for availability of hollows in live trees with no salvage logging, $t = 6$ months, $j = 1, \dots, 6$ and $k = 1, \dots, n_{\text{fire}}$:

$$BH_{jk}^2(t+1) = \begin{cases} 1 & t < p_k \\ 0.15 \times H_{jk}^2(t) & t = p_k \\ 0 & p_k < t \leq p_k + 240 \\ 0.9975 \times H_{jk}^2(t) + 0.008 \times (t - 240)/240 & p_k + 240 < t \leq p_k + 480 \\ 0.9975 \times H_{jk}^2(t) + 0.008 & t > p_k + 480 \end{cases}$$

$$NBH_{jk}^2(t+1) = 1 \quad t \geq 0$$

$$H_{j1}^2(t+1) = BH_{j1}^2(t) \times PB_j(t) + NBH_{j1}^2(t) \times (1 - PB_j(t))$$

$$H_{jk}^2(t+1) = H_{jk-1}^2(t+1) \times (BH_{jk}^2(t) \times PB_j(t) + NBH_{jk}^2(t) \times (1 - PB_j(t)))$$

Model for availability of hollows in dead trees, $t = 6$ months and $j = 1, \dots, 6$ and $k = 1, \dots, n_{\text{fire}}$:

$$BH_{jk}^3(t+1) = \begin{cases} 0 & t < p_k \\ 5 \times H_{jk}^3(t) & t = p_k \\ 0.98 \times H_{jk}^3(t) + 0.01 \times H_{jk}^2(t) & t > p_k \end{cases}$$

$$NBH_{jk}^3(t+1) = 0.5 \quad t \geq 0$$

$$H_{j1}^3(t+1) = BH_{j1}^3(t) \times PB_j(t) + NBH_{j1}^3(t) \times (1 - PB_j(t))$$

$$H_{jk}^3(t+1) = H_{jk-1}^3(t+1) \times (BH_{jk}^3(t) \times PB_j(t) + NBH_{jk}^3(t) \times (1 - PB_j(t))) / 0.5$$

Using a similar rule to Lindenmayer and Possingham (1995a,b) that either food or hollows limit the available number of breeding sites, the expected density of breeding sites t years after a fire was:

$$AD_j(t) = \begin{cases} 1 & DL = 0 \\ 1 - DL / (1 + \exp(-0.07 \times (t - a))) & 100 \leq t \leq c \\ 1 - DL + DL / (1 + \exp(-0.1 \times (t - b))) & t > c \end{cases}$$

$$ED_j(t) = \text{Round}(CC_j \times AD_j(t) \times \min(H_{j\text{fire}}^1(t), (H_{j\text{fire}}^2(t) + H_{j\text{fire}}^3(t))))$$

where CC_j is given as the Area of the reserve/Area required per colony (Table 1); DL is the decline level modelled as 0, (no additional decline) 0.125, 0.25, and 0.5 (additional decline in section 2.4); $a = 100 + 2 \times (2020 - 1939)$, 100 is the model burn in time and 2020 is the year when half the decline occurs; $b = 100 + 2 \times (2059 - 1939) + 50$, 100 is the model burn in time and 2059 is the year when hollows are expected to increase (corresponds with time when hollows first form in trees Table 1), 50 lets the habitat decline equation match the habitat increase equation when $t = c$ (see for example Fig. SM2); $c = 100 + 2 \times (2059 - 1939)$, 100 is the model burn in time and 2059 is the year when hollows are expected to increase. See glossary of model terms in Table 1.

Dispersal was proportional to length of the source sub-population reserve boundary adjacent to the receiving sub-population, and occurs only if the source sub-population is greater than $0.7 \times ED$ and is only applied to 6 month old females transitioning to 1 year olds.

$$\text{Dispersal Matrix} = \begin{bmatrix} 0 & 0 & 0.008 & 0 & 0 & 0 \\ 0 & 0.014 & 0 & 0 & 0 & 0 \\ 0.003 & 0.038 & 0 & 0 & 0.02 & 0 \\ 0 & 0 & 0 & 0 & 0.012 & 0.007 \\ 0 & 0 & 0.009 & 0.007 & 0 & 0.004 \\ 0 & 0 & 0 & 0.006 & 0.003 & 0 \end{bmatrix}$$

Note that the equations for fire impacts on Leadbeater’s possum habitat were modified from Lindenmayer and Possingham (1995a,b), $BH_{jk}^2(t)$ and $NBH_{jk}^2(t)$ were rescaled to 1 with a

6 month time step, e.g. $0.995 \times H_2(t) + 1.6$ (Lindenmayer and Possingham, 1995b: eq. A2) became $0.9975 \times H_{jk}^2(t) + 0.008$. Also $BH_{jk}^3(t)$ and $NBH_{jk}^3(t)$ were rescaled to 0.5 with a 6 month time step, e.g. $0.96 \times H_3(t) + 0.02 \times H_2(t)$ (Lindenmayer and Possingham, 1995b: eq. A3) became $0.98 \times H_{jk}^3(t) + 0.01 \times H_{jk}^2(t)$. These scalings reproduced similar habitat quality response to Lindenmayer and Possingham (1995a,b).

2.2. Leadbeater's possum reserve system

We sub-divided the current reserve system for Leadbeater's possum into 6 regions based upon geological characteristics and historical fire disturbance: Region #1 Toolangi (2604 ha); Region #2 Marysville (4471 ha); Region #3 Southside (14,741 ha); Region #4 Woods Point (2005 ha); Region #5 Powelltown/Noojee (3038 ha); and Region #6 Baw Baw/Toorong (3660 ha) (Fig. 1). We modelled each region independently with a low level of dispersal between regions. Regions were modelled independently due to varying historical fire regimes between regions which drive tree hollow dynamics and thus the likely dynamics of Leadbeater's possum. Low levels of movement between regions were assumed, based on what is known about the dispersal of this species (Harley and Lill, 2007).

2.3. Modelling the impacts of wildfires

We used the method for modelling wildfire impacts developed by Lindenmayer and Possingham (1995a,b) to simulate the effects on existing habitat availability of fires in the five major fires over the last 80 years: 1939; 1983; 1990; 2007 and 2009 (Table 2). Lindenmayer and Possingham (1995a) assumed 100 per cent of the available habitat was impacted, which is not the case for the historical fire regime (Table 2). To model a multi-age forest structure (where stands support hollow-bearing trees that provide habitat for Leadbeater's possum) with each subsequent fire, fire was proportionally assigned to each stage of the forest in each region in a linear combination. Given the different fire history for each region, the available number of adult females varied between each region (for example, see Supplementary material: Fig. SM1; see section 2.7 for details).

2.4. Modelling the decline of suitable habitat

Lindenmayer et al. (2012) reported an increasing rate of decline in the number of hollow-bearing trees in recent decades, and no recruitment of any new large trees with cavities on any of the 156 monitored sites between 1997 and 2011. The observed increase in the rate of decline is an additional decline in habitat above that expected to occur through the modelling of wildfire impacts, as this was observed in areas not burnt in 2009. A significant increase in hollow-bearing trees is not expected to occur until the regrowth from the 1939 fires reaches 120 years old and older (Lindenmayer et al., 2012; Burns et al., 2015). To model an additional decline in habitat, a sigmoidal function was used where habitat declined to a preset level of hollow-bearing tree loss and then increased with the onset of hollow availability as the trees aged (Supplementary material: Fig. SM2; see sections 2.1 and 2.7 for details).

2.5. Initial conditions of the model

The model was applied to each region (including the impact of wildfire and dispersal) and simulations were run simultaneously as a metapopulation. Simulations were performed using *Essential* (Todd and Lovelace, 2014) where 1000 iterations were generated for each scenario. The initial population size of six month old females was set at half the carrying capacity, while the rest of the

ages were set to zero. The simulations were allowed to proceed for 100 time steps to ensure that the initial conditions did not influence the population dynamics when the historical fire regime was instigated. The time step used in the simulations was 6 months. Data for the risk analysis were collected 140 time steps after the initialisation of the impacts of the 1939 wildfires, equivalent to 2009, with a 200 year projection beyond 2009 equivalent to 40 generations. See Table 1 for key parameters used in the simulation.

2.6. Population risk analysis

Recording the minimum population size from each iteration or trajectory produces a distribution of minimum population sizes and is a summary of the extreme dynamics of populations (Burgman et al., 1993; Todd et al., 2008). Plotting the associated normalised cumulative frequency distribution produces a graph of probabilities versus population size called the minimum population size risk curve. Risk curves represents both the chance of extinction (probability of falling to zero) and the chance of falling below some non-zero population threshold or quasi-extinction (Burgman et al., 1993). Additionally, risk curves can be readily compared and assessed in terms of increasing or decreasing risk by a shift to the left or right respectively (Koehn and Todd, 2012; Todd et al., 2002). Calculating the expected value of the minimum population size risk curve provides a metric for scenario comparison (McCarthy and Thompson, 2001; Todd et al., 2005). The expected value of the minimum population size risk curve (RCEV) for adult females is used as a measure of risk.

2.7. Reserve assessment

To test the effectiveness of the Leadbeater's possum reserve system based on historical fire disturbance alone (no additional future threats), we applied the base metapopulation model using the parameters specified (Table 1 and 2). The purpose was to explore whether the design was effective, given the known fire disturbance. To explore sensitivity in reserve effectiveness to habitat loss, we tested a number of levels of future habitat decline (i.e. 12.5%, 25%, and 50% loss of hollow-bearing trees; see Table 3). To explore reserve system effectiveness in supporting Leadbeater's possum in the face of future fires, one fire was modelled to occur in 2020 or 2030 or 2040, with various proportion of the reserve burnt (i.e. 25%, and 50%) and various levels of habitat decline (i.e. 12.5%, 25%, and 50%) (see Table 3). The timeframes and sizes for the future fires were selected to simulate the equivalent of a moderate or large fire (similar to the size of the 2009 fire) occurring during the period of greatest shortage of hollow-bearing trees (i.e. over the next 5 decades before the 1939 regrowth commences hollow development).

Finally, we were able to assess how much habitat would be required to reduce the risk of extinction given these various habitat decline, future fire scenarios, and past disturbances. There is no spatial data on the density of hollow-bearing trees across the Central Highlands, and so for this part of the analysis we have assumed a sufficient density across the whole area to support a Leadbeater's possum colony every 3 ha (Table 1), and therefore dividing a region's area by 3 produces the maximum number of colonies for the region and, as a direct consequence, the maximum number of adult breeding females per region, as each colony has just a single breeding female (Harley and Lill, 2007). Historical timber harvesting was accounted for by removing the area clear-cut since 1978 (when this form of harvesting was introduced) as largely being unsuitable nesting habitat for Leadbeater's possum due to a lack of hollow-bearing trees. Future timber harvesting was not considered. The maximum total area of available habitat in the Central Highlands for Leadbeater's possum used in the model was

Table 4

Summary statistics of the minimum population size of adult females post 2009 for the scenarios modelled.

Scenario no.	RCEV ^a	Change in RCEV from S1	% Change in RCEV from S1
S1	432.54		
S2	394.9	-37.64	-8.70
S3	346.02	-86.52	-20.00
S4	245.15	-187.39	-43.32
S5 2020	299.02	-133.52	-30.87
S5 2030	298.48	-134.06	-30.99
S5 2040	307.79	-124.75	-28.84
S6 2020	265.88	-166.66	-38.53
S6 2030	268.19	-164.35	-38.00
S6 2040	274.01	-158.53	-36.65
S7 2020	187.02	-245.52	-56.76
S7 2030	192.75	-239.79	-55.44
S7 2040	196.48	-236.06	-54.58
S8 2020	206.39	-226.15	-52.28
S8 2030	209.7	-222.84	-51.52
S8 2040	217.85	-214.69	-49.63
S9 2020	185.31	-247.23	-57.16
S9 2030	208.47	-224.07	-51.80
S9 2040	212.99	-219.55	-50.76
S10 2020	131.34	-301.2	-69.64
S10 2030	147.57	-284.97	-65.88
S10 2040	152.73	-279.81	-64.69

^a RCEV – risk curve expected value.

177,280 ha of the potential 195,000 ha. This area was decreased proportionally across all regions until the criteria for an effective reserve was met, thus providing the minimum area necessary for an effective reserve. In addition to our defined effectiveness goal, we included lower and higher targets (2.5%, 10%) to produce tolerance bounds on the area required. This method was completed for all scenarios in Table 3, using the example of a future fire in 2020 and 2040. Scenarios without future fire were not considered, given the known fire history of the Central Highlands and the expectation that this will continue into the future. Although it is likely that there will be more than a one fire in the future in the Central Highlands, a single fire was modelled at three time periods for simplicity and to model the minimum likely fire impacts.

3. Results

3.1. Effectiveness of the current Leadbeater's possum reserve system

3.1.1. Historical impacts of fire

Modelling the fire history for each region (Table 2) indicates that all regional populations experience fluctuating dynamics largely as a result of the 1939 fires, and more recently for those regions impacted by the 2009 fires (Fig. 2). The metapopulation dynamics indicate the population remains in decline following the 2009 fires and is not expected to recover until after 2059, as hollows in 1939–regrowth trees begin to develop (Fig. 3a). The associated minimum population size risk curve for adult females, post 2009 (Fig. 3b), predicts the minimum number of adult females to range between 74 and 684 with an expected value of 432.54 (± 201.18) over the next 200 years (see Table 4). The chance of the Leadbeater's possum reserve system containing 500 adult females or less was 73% (significantly higher than the 5% threshold) and hence this reserve system does not meet our criteria of an effective reserve with respect to the historical fire regime.

3.1.2. Habitat decline and future fire

It is not known to what extent the observed accelerated rate of decline in the number of hollow-bearing trees (Lindenmayer et al., 2012) will continue (Burns et al., 2015). Scenarios S2–S4 (Table 3)

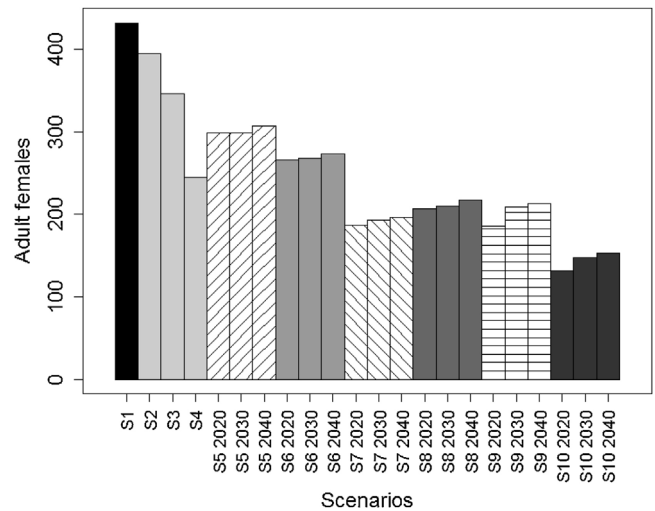


Fig. 5. The expected value of the minimum population size distribution (RCEV) for adult females post 2009 from each scenario modelled in Table 3.

explore a range of outcomes with increasing rates of decline producing higher risks for the metapopulation of Leadbeater's possum (Table 4, Figs. 4 and 5). The risks associated with habitat decline increase from a 9% decrease in adult females (approx., Table 4, Fig. 5) with 12.5% habitat decline to a 43% decrease in adult females (approx., Table 4, Fig. 5) with 50% habitat decline, until the number of hollow-bearing trees starts to increase again in 2059. While no extinctions were recorded (as the minimum population size: MPS > 0 in all habitat decline only scenarios in Fig. 4) the risk curves associated with habitat decline shift to the left with increasing habitat decline, leaving the metapopulation vulnerable to other threatening processes. The current reserve system does not achieve the definition of an effective reserve when accounting for habitat decline, as no risk curve is close to the threshold of 500 adult females when it crosses the 0.05 probability level (Fig. 4).

Modelling a future fire enables the assessment of the risk of fire (scenarios S5–S10: Table 3 and Fig. 5). Adding a future fire to the historical fire regime and habitat decline increases risk to the metapopulation (S5–S10: Table 4, Figs. 4 and 5). The risk curves of S7 2020 and S10 2020 (Fig. 4) are closer to zero than the other risk curves, indicating a higher risk of a small adult female population, with the larger fire producing the highest risk (Fig. 4). A fire in the near future (2020) appears to be more deleterious to the metapopulation than a later fire, as can be seen by comparing the year of fire in scenarios S5–S10 (Table 4 and Fig. 5), which is specifically due to the loss of food availability in the short term. Again, as the inclusion of a future fire increases risk, the current reserve system does not achieve the definition of an effective reserve when planning for potential future fires.

3.2. An effective sized reserve system

We tested reserve system effectiveness by estimating the area required to achieve the criteria of not more than 5% chance of falling to (or below) 500 adult females in 40 generations. Our results demonstrated that the smallest of threats (i.e. 12.5% habitat decline of hollow-bearing trees and 12.5% habitat burnt in a future fire in 2020) requires more than double the current Leadbeater's possum reserve (30,500 ha cf Table 5), at the 5% and 10% tolerance bounds, although this is less than the total area of reserved habitat in the Central Highlands in national parks or Special Protection Zones in State forest (98,500 ha). With increasing levels of threat, the area required for the reserve to support a viable population in the long term increases above the overall area of habitat currently protected

Table 5
The impact of future fires on the area (ha) of Leadbeater's possum habitat required for less than a 2.5%, 5% or 10% chance of the population in the Central Highlands falling below 500 adult females in 40 generations (200 year time frame), under differing levels of observed habitat decline (Lindenmayer et al., 2012). The columns show increasing rates of habitat decline (12.5%, 25% and 50%), while the rows show increasing areas of potential habitat burnt during future fires (12.5%, 25% and 50%). The final column shows the impact of a future fire in 2040 with a 50% habitat decline and increasing areas of potential habitat burnt during future fires (12.5%, 25% and 50%).

Probability of population falling below 500 females	Historical fire + 12.5% habitat decline	Historical fire + 25% habitat decline	Historical fire + 50% habitat decline	Historical fire + 50% habitat decline
	12.5% future fire, year 2020			12.5%, year 2040
2.5%	79,758	86,690	120,462	119,771
5%	67,473	74,640	104,595	101,404
10%	57,793	68,440	93,161	88,649
	25% future fire, year 2020			25%, year 2040
2.5%	87,577	100,305	159,785	156,071
5%	79,422	87,045	119,487	116,828
10%	67,367	73,240	105,746	102,557
	50% future fire, year 2020			50%, year 2040
2.5%	120,551	146,026	177,280	177,280
5%	108,166	122,855	171,345	163,463
10%	89,349	111,690	156,725	148,994

in formal parks and reserves, and the area in State forest excluded from harvesting due to biodiversity, regulatory, operational and prescriptive reasons, to almost the total area of available habitat in the Central Highlands (Table 3). More than 50% of the scenarios modelled (14:27) required an area larger than the total area of formally reserved habitat in the Central Highlands (98,500 ha cf Table 3). At the lower end of the tolerance bound of 2.5% for the scenario with the highest threat (i.e. 50% habitat decline and 50% of potential habitat burnt in future fires) the total area of suitable habitat across the Central Highlands was required to meet the goal of effectiveness.

4. Discussion

Around the world, reserve systems have been used extensively in an attempt to secure the persistence of threatened species (Rodrigues and Brooks, 2007; Beger et al., 2010; Watson et al., 2011a,b, 2014). However, habitat loss may still occur within reserves through deliberate human impacts, like illegal clearing (Mascia and Pailler, 2011), and the impacts of catastrophic natural disturbances such as wildfires (Turner et al., 2003; Spies et al., 2012). Design criteria for reserves in many parts of the world are built on the general CAR principles, that is, reserves should be comprehensive, adequate and representative (Anon., 1992; Sharafi et al., 2012). However, in many cases, the adequacy of a given reserve system is not subject to robust assessment and so there is a risk that a given protected area may be ineffective at achieving the conservation objective for which it has been set aside.

We have developed a metapopulation simulation approach for testing the effectiveness of reserve systems for one species and we demonstrated the use of our model with a detailed case study of the protected area network established specifically for the critically endangered Leadbeater's possum. Our analysis clearly indicates that the existing reserve for Leadbeater's possum is not adequate and there is a high likelihood of a critically low population size as a result of the lag effects of past disturbance, ongoing habitat decline and future fire. Even when factoring in all parks and reserves within the range of Leadbeater's possum, and areas in State forest excluded from harvesting, the area was considered insufficient under the scenarios of high levels of habitat decline and a single future fire. An assessment based on a single future fire is likely to be a conservative assessment, given the historic fire frequency, where it is probable that there will be multiple fires in this area during the modelled timeframe. Even without inclusion of additional fires, our analysis found that almost all of the remaining montane eucalypt forest, not harvested since 1978, would be required to have a reasonable prob-

ability of ensuring that populations of Leadbeater's possum did not fall below critical levels.

Reserve designs need to be robust in the face of uncertain future events (Mumby et al., 2011; Gillson et al., 2013; Kujala et al., 2013). Reserve design must take in to account systemic problems like ongoing habitat decline, as well as the risk of major disturbance such as wildfires. The only way in which reserve design can meet uncertain future outcomes is to include sufficient habitat to meet likely future disturbance, whether anthropogenic or natural. Typically reserve design attempts to capture a certain percentage of a given ecosystem (e.g. 10% Soulé and Sanjayan, 1998; James et al., 2001; Meir et al., 2004). Here we show that capturing parts of habitat can be inadequate when incorporating future uncertainties and that perhaps the entire ecosystem needs to be reserved to ensure that the reserve fulfils its design requirements; that is, to ensure persistence of threatened flora and/or fauna (see for example Cowling et al., 1999 and Santini et al., 2014).

While we modelled a single species, there are a suite of other species of cavity-dependent taxa in these same forests that are of conservation concern and require consideration in a management context. Two examples are the Greater Glider (*Petauroides volans*) and Yellow-bellied Glider (*Petaurus australis*), both of which are cavity-dependent and strongly associated with the abundance of large old trees (Lindenmayer, 2009). Populations of the Greater Glider are undergoing a rapid decline in montane ash forests (Lindenmayer et al., 2011). Earlier modelling analyses exploring the viability of various species of arboreal marsupials in Victorian forests (Lindenmayer and Lacy 1995a,b; Lindenmayer and McCarthy, 2006; Possingham et al., 1994) suggest there are important potential synergies between reserve strategies for different species of arboreal marsupials. These synergies are likely due to similarities in response to major disturbances such as clearfell logging (Lindenmayer, 1994) and high-severity wildfire (Lindenmayer et al., 2013) and, in turn, similar responses to management interventions like formal reservation and exemption of forest from logging.

We defined the effectiveness measure for the reserve of interest as no more than 5% probability of populations falling to (or below) 500 adult females in 40 generations. This definition allowed the model to be used to evaluate whether, or not, the reserve of interest was adequate to meet the design criteria. We also examined alternative risk tolerances to understand how sensitive our assessment of a reserve might be to capturing appropriate dynamics of both the population and habitat. In other words, if we are wrong, does it change how the system would be managed? Based on a single future fire 30%–100% of current forest extent within the range

of the species is required to ensure population persistence. If additional future fires were modelled the minimum increase required is expected to be higher than 30%. Our results indicate that regardless of the risk tolerance, a significant increase in the reserve was still necessary to ensure the reserve met the design criteria. This outcome is important on two levels. First, it highlights the utility in quantifying a target when designing reserves (Tear et al., 2005) by asking “what is the minimum population size we want our reserve to support?” Second, given likely uncertainties in the parameterisation of the model, the alternative risk tolerances, which all show the same pattern of the current reserve being insufficient in size, highlight that the results are robust.

The modelling process developed for this study is complex and could only be applied to a suite of species for which there is detailed biological data available. Regardless, it has general and significant implications for several aspects of conservation biology, particularly the design and establishment of protected areas which are the cornerstone of many conservation efforts for threatened species (Sodhi and Ehrlich, 2010). These generalities include the need to plan for disturbance on different spatial and temporal scales.

Acknowledgments

The authors gratefully acknowledge the assistance of M. Nicol, J. Nelson, M. Scroggie, M. White, and B. Brook. We also thank M. White for comments on the manuscript, A. Kitchingman for assistance with some figures, an anonymous reviewer for reviewing an earlier draft of the manuscript. This work was funded by the former Victorian Department of Primary Industries. The authors also thank the editor and journal reviewer for their constructive comments and suggestions. The authors dedicate this study to the memory of Professor David Choquenot who was instrumental in linking ecological processes and the management of wildlife through the use of modelling.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2016.07.021>.

References

- Akçakaya, H.R., Burgman, M.A., Ginzburg, L.R., 1997. *Applied population ecology*. In: *Applied Biomathematics*. Setauket, New York.
- Anon, 1992. National Forest Policy Statement: A New Focus for Australia's Forests. Australian Government Publishing Service, Canberra.
- Baker, W.L., 1992. The landscape ecology of large disturbances in the design and management of nature reserves. *Landsc. Ecol.* 7, 181–194.
- Barber, C.P., Cochrane, M.A., Souza, C. Jr., Verissimo, A., 2012. Dynamic performance assessment of protected areas. *Biol. Conserv.* 149, 6–14. <http://dx.doi.org/10.1016/j.biocon.2011.08.024>.
- Beger, M., Grantham, H.S., Pressey, R.L., Wilson, K.A., Peterson, E.L., Dorfman, D., Mumby, P.J., Lourival, R., Brumbaugh, D.R., Possingham, H.P., 2010. Conservation planning for connectivity across marine, freshwater, and terrestrial realms. *Biol. Conserv.* 143, 565–575. <http://dx.doi.org/10.1016/j.biocon.2009.11.006>.
- Bottrill, M.C., Pressey, R.L., 2012. The effectiveness and evaluation of conservation planning. *Conserv. Lett.* 5, 407–420. <http://dx.doi.org/10.1111/j.1755-263X.2012.00268.x>.
- Bottrill, M.C., Walsh, J.C., Watson, J.E.M., Joseph, L.N., Ortega-Argueta, A., Possingham, H.P., 2011. Does recovery planning improve the status of threatened species? *Biol. Conserv.* 144, 1595–1601.
- Burgman, M.A., Ferson, S., Akçakaya, H.R., 1993. *Risk Assessment in Conservation Biology*. Chapman and Hall, London.
- Burns, E.L., Lindenmayer, D.B., Stein, J.A., Blanchard, W., McBurney, L., Blair, D., Banks, S.C., 2015. An ecosystem assessment of Mountain Ash forest in the Central Highlands of Victoria, south-eastern Australia. *Aust. Ecol.* <http://dx.doi.org/10.1111/aec.12200>.
- Butchart, S.H.M., Clarke, M., Smith, R.J., Sykes, R.E., Scharlemann, J.P.W., Harfoot, M., Buchanan, G.M., Angulo, A., Balmford, A., Bertzky, B., Brooks, T.M., Carpenter, K.E., Comeros-Raynal, M.T., Cornell, J., Fisetola, G.F., Fishpool, L.D.C., Fuller, R.A., Geldmann, J., Harwell, H., Hilton-Taylor, C., Hoffmann, M., Joolia, A., Joppa, L., Kingston, N., May, I., Milam, A., Polidoro, B., Ralph, G., Richman, N., Rondinini, C., Segan, D.B., Skolnik, B., Spalding, M.D., Stuart, S.N., Symes, A., Taylor, J., Visconti, P., Watson, J.E.M., Wood, L., Burgess, N.D., 2015. Shortfalls and solutions for meeting national and global conservation area targets. *Conserv. Lett.* 8, 329–337. <http://dx.doi.org/10.1111/conl.12158>.
- Cabeza, M., Moilanen, A., 2001. Reserve design and the persistence of biodiversity. *Trends Ecol. Evol.* 16, 242–248.
- Cowling, R.M., Pressey, R.L., Lombard, A.T., Desmet, P.G., Ellis, A.G., 1999. From representation to persistence: requirements for a sustainable system of conservation areas in the species rich mediterranean-climate desert of southern Africa. *Divers. Distrib.* 5, 51–71.
- Frankham, R., Brook, B.W., 2004. The importance of time scale in conservation biology and ecology. *Ann. Zool. Fenn.* 41, 459–463.
- Gillson, L., Dawson, T.P., Jack, S., McGeoch, M.A., 2013. Accommodating climate change contingencies in conservation strategy. *Trends Ecol. Evol.* 28, 135–142. <http://dx.doi.org/10.1016/j.tree.2012.10.008>.
- Gregory, R., Arvai, J., Gerber, L.R., 2013. Structuring decisions for managing threatened and endangered species in a changing climate. *Conserv. Biol.* 27, 1212–1221.
- Harley, D.P.K., Lill, A., 2007. Reproduction in a population of the endangered Leadbeater's possum inhabiting lowland swamp forest. *J. Zool.* 272, 451–457.
- James, A., Gaston, K.J., Balmford, A., 2001. Can we afford to conserve biodiversity? *BioScience* 51, 43–52.
- Koehn, J.D., Todd, C.R., 2012. Balancing conservation and recreational fishery objectives for a threatened fish species the Murray cod, *Maccullochella peelii*. *Fish. Manage. Ecol.* 19, 410–425.
- Kujala, H., Moilanen, A., Araújo, M.B., Cabeza, M., 2013. Conservation planning with uncertain climate change projections. *PLoS One* 8, e53315. <http://dx.doi.org/10.1371/journal.pone.0053315>.
- Le Saout, S., Hoffman, M., Shi, Y., Hughes, A., Bernard, C., Brooks, T.M., Bertzky, B., Butchart, S.H.M., Stuart, S.N., Badman, T., Rodrigues, A.S.L., 2013. Protected areas and effective biodiversity conservation. *Science* 342, 801–805.
- Lindenmayer, D.B., Franklin, J., 2002. *Conserving Forest Biodiversity: A Comprehensive Multiscaled Approach*. Island Press, Washington.
- Lindenmayer, D.B., 1994. The impacts of timber harvesting on arboreal marsupials at different spatial scales and its implications for ecologically sustainable forest use and nature conservation. *Aust. J. Environ. Manage.* 1, 56–68.
- Lindenmayer, D.B., Lacy, R.C., 1995a. Metapopulation viability of arboreal marsupials in fragmented old-growth forests: comparison among species. *Ecol. Appl.* 5, 183–199.
- Lindenmayer, D.B., Lacy, R.C., 1995b. Metapopulation viability of Leadbeater's possum, *Gymnobelideus leadbeateri*, in fragmented old-growth forests. *Ecol. Appl.* 5, 164–182.
- Lindenmayer, D.B., McCarthy, M.A., 2006. Evaluation of PVA models of arboreal marsupials: coupling models with long-term monitoring data. *Biodivers. Conserv.* 15, 4079–4096.
- Lindenmayer, D.B., Possingham, H.P., 1995a. Modelling the viability of metapopulations of the endangered Leadbeater's possum in southeastern Australia. *Biodivers. Conserv.* 4, 984–1018.
- Lindenmayer, D.B., Possingham, H.P., 1995b. Modelling the impacts of wildfire on the viability of metapopulations of the endangered Australian species of arboreal marsupial, Leadbeater's possum. *For. Ecol. Manage.* 74, 197–222.
- Lindenmayer, D.B., Possingham, H.P., 2013. No excuse for habitat destruction. *Science* 340, 680.
- Lindenmayer, D.B., Lacy, R.C., Thomas, V.C., Clark, T.W., 1993. Predictions of the impacts of changes in population size and environmental variability on Leadbeater's possum, *Gymnobelideus leadbeateri* McCoy (Marsupialia: Petauridae) using population viability analysis: an application of the computer program VORTEX. *Wildl. Res.* 20, 67–86.
- Lindenmayer, D.B., 2009. *Forest Pattern and Ecological Process: A Synthesis of 25 Years of Research*. CSIRO Publishing, Melbourne, Australia.
- Lindenmayer, D.B., Wood, J.T., McBurney, L., MacGregor, C., Youngentob, K., Banks, S.C., 2011. How to make a common species rare: a case against conservation complacency. *Biol. Conserv.* 144, 1663–1672.
- Lindenmayer, D.B., Blanchard, W., McBurney, L., Blair, D., Banks, S., Likens, G.E., Franklin, J.F., Laurance, W.F., Stein, J.A.R., Gibbons, P., 2012. Interacting factors driving a major loss of large trees with cavities in a forest ecosystem. *PLoS One* 7, e41864. <http://dx.doi.org/10.1371/journal.pone.0041864>.
- Lindenmayer, D.B., Blanchard, W., McBurney, L., Blair, D., Banks, S.C., Driscoll, D., Smith, A.L., Gill, A.M., 2013. Fire severity and landscape context effects on arboreal marsupials. *Biol. Conserv.* 167, 137–148.
- Lindenmayer, D., Blair, D., McBurney, L., Banks, S.C., Stein, J.R., Hobbs, R.J., Likens, G.E., Franklin, J.F., 2014. Principles and practices for biodiversity conservation and restoration forestry: a 30 year case study on the Victorian montane ash forests and the critically endangered Leadbeater's possum. *Aust. Zool.* 36, 441–460.
- Lumsden, L.F., Nelson, J.L., Todd, C.R., Scroggie, M.P., McNabb, E.G., Raadik, T.A., Smith, S.J., Acevedo, S., Cheers, G., Jemison, M.L., Nicol, M.D., 2013. *A New Strategic Approach to Biodiversity Management—Research Component*. Arthur Rylah Institute for Environmental Research Unpublished Client Report for the Department of Environment and Primary Industries, Heidelberg, Victoria.
- Macfarlane, M.A., Smith, J., Lowe, K., 1997. *Leadbeater's Possum Recovery Plan*. Department of Natural Resources and Environment, East Melbourne.
- Mascia, M.B., Pailler, S., 2011. Protected area downgrading, downsizing, and degazettement (PADDD) and its conservation implications. *Conserv. Lett.* 4, 9–20.

- McCarthy, M.A., Lindenmayer, D.B., 2000. Spatially-correlated extinction in a metapopulation model of Leadbeater's possum. *Biodivers. Conserv.* 9, 47–63.
- McCarthy, M.A., Thompson, C., 2001. Expected minimum population size as a measure of threat. *Anim. Conserv.* 4, 351–355.
- Meir, E., Andelman, S., Possingham, H.P., 2004. Does conservation planning matter in a dynamic and uncertain world? *Ecol. Lett.* 7, 615–622.
- Mumby, P.J., Elliott, I.A., Eakin, C.M., Skirving, W., Paris, C.B., Edwards, H.J., Enriquez, S., Iglesias-Prieto, R., Cherubin, L.M., Stevens, J.R., 2011. Reserve design for uncertain responses of coral reefs to climate change. *Ecol. Lett.* 14, 132–140. <http://dx.doi.org/10.1111/j.1461-0248.2010.01562.x>.
- O'Grady, J.J., Reed, D.H., Brooks, B.W., Frankham, R., 2008. Extinction risk scales better to generations than to years. *Anim. Conserv.* 11, 442–451.
- Possingham, H.P., Lindenmayer, D.B., Norton, T.W., Davies, I., 1994. Metapopulation viability analysis of the Greater Glider *Petauroides volans* in a wood production area. *Biol. Conserv.* 70, 227–236.
- Redford, K.H., Amato, G., Baillie, J., Beldomenico, P., Bennett, E.L., Clum, N., Cook, R., Fonseca, G., Hedges, S., Launay, F., Lieberman, S., Mace, G.M., Murayama, A., Putnam, A., Robinson, J.G., Rosenbaum, H., Sanderson, E.W., Stuart, S.N., Thomas, P., Thorbjarnarson, J., 2011. What does it mean to successfully conserve a (vertebrate) species? *BioScience* 61, 39–48. <http://dx.doi.org/10.1525/bio.2011.61.1.9>.
- Reece, J.S., Noss, R.F., Oetting, J., Hctor, T., Volk, M., 2013. A vulnerability assessment of 300 species in Florida: threats from sea level rise, land use, and climate change. *PLoS One* 8, e80658. <http://dx.doi.org/10.1371/journal.pone.0080658>.
- Reed, D.H., O'Grady, J.J., Brook, B.W., Ballou, J.D., Frankham, R., 2003. Estimates of minimum viable population sizes for vertebrates and factors affecting those estimates. *Biol. Conserv.* 113, 23–34.
- Rodrigues, A.S.L., Brooks, T.M., 2007. Shortcuts for biodiversity conservation planning: the effectiveness of surrogates. *Annu. Rev. Ecol. Evol. Syst.* 38, 713–737.
- Salomon, Y., McCarthy, M.A., Taylor, P., Wintle, B.A., 2013. Incorporating uncertainty of management costs in sensitivity analyses of matrix population models. *Conserv. Biol.* 27, 134–144.
- Sanderson, E.W., 2006. How many animals do we want to save? The many ways of setting population target levels for conservation. *BioScience* 56, 911–922.
- Santini, L., Di Marco, M., Boitani, L., Maiorano, L., Rondinini, C., 2014. Incorporating spatial population structure in gap analysis reveals inequitable assessments of species protection. *Divers. Distrib.* 20, 698–707.
- Sharafi, S.M., White, M., Burgman, M., 2012. Implementing comprehensiveness, adequacy and representativeness criteria (CAR) to indicate gaps in an existing reserve system: a case study from Victoria, Australia. *Ecol. Indic.* 18, 342–352. <http://dx.doi.org/10.1016/j.ecolind.2011.11.023>.
- Smith, A., 1984. Demographic consequences of reproduction, dispersal and social interaction in a population of Leadbeater's possum. In: Smith, A., Hume, I. (Eds.), *Possums and Gliders*. Surrey Beatty & Sons Pty Limited, Chipping Norton, NSW, pp. 359–373.
- Smith, A.P., Lindenmayer, D.B., 1988. Tree hollow requirements of Leadbeater's Possum and other possums and gliders in timber production ash forests of the Victorian Central Highlands. *Aust. Wildl. Res.* 15, 347–362.
- Smith, S., Morey, J., 2001. Options for a Permanent Reserve System for the Conservation of Leadbeater's Possum. Central Highlands of Victoria. Flora and Fauna Program, Department of Natural Resources and Environment.
- Sodhi, N.S., Ehrlich, P.R., 2010. Conservation Biology for All. Oxford University Press, Oxford. <http://dx.doi.org/10.1093/acprof:oso/9780199554232.001.0001>.
- Soulé, M.E., Sanjayan, M.A., 1998. Conservation targets: do they help? *Science* 279, 2060–2061.
- Spies, T.A., Lindenmayer, D.B., Gill, A.M., Stephens, S.L., Agee, J.K., 2012. Challenges and a checklist for biodiversity conservation in fire-prone forests: perspectives from the Pacific Northwest of USA and Southeastern Australia. *Biol. Conserv.* 145, 5–14. <http://dx.doi.org/10.1016/j.biocon.2011.09.008>.
- Tear, T.H., Kareiva, P., Angermeier, P.L., Comer, P., Czech, B., Kautz, R., Landon, L., Mehlmán, D., Murphy, K., Ruckelshaus, M., Scott, J.M., Wilhere, G., 2005. How much is enough? The recurrent problem of setting measurable objectives in conservation. *BioScience* 55, 835–849.
- Tempel, D., Gutiérrez, R.J., Whitmore, S., Reetz, M., Stoelting, R., Berigan, W., Seamans, M.E., Peery, M.Z., 2014. Effects of forest management on California spotted owls: implications for reducing wildfire risk in fire-prone forests. *Ecol. Appl.* <http://dx.doi.org/10.1890/13-2192.1>.
- Todd, C.R., Lovelace, P.R., 2014. Essential 2.15. <http://livinglogic.com.au/Essential.html>.
- Todd, C.R., Ng, M.P., 2001. Generating unbiased correlated random survival rates for stochastic population models. *Ecol. Model.* 144, 1–11.
- Todd, C.R., Jenkins, S., Bearlin, A.R., 2002. Lessons about extinction and translocation: models for eastern barred bandicoots (*Perameles gunnii*) at Woodlands Historic Park, Victoria, Australia. *Biol. Conserv.* 106, 211–223.
- Todd, C.R., Ryan, T., Nicol, S.J., Bearlin, A.R., 2005. The impact of cold water releases on the critical period of post-spawning survival and its implications for Murray cod (*Maccullochella peelii peelii*): a case study of the Mitta Mitta River, southeastern Australia. *River Res. Appl.* 21, 1035–1052.
- Todd, C.R., Forsyth, D.M., Choquenot, D., 2008. Modelling the effects of fertility control on koala-forest dynamics. *J. Appl. Ecol.* 45, 568–578.
- Turner, M.G., Romme, W.H., Tinker, D.B., 2003. Surprises and lessons from the 1988 Yellowstone fires. *Front. Ecol. Environ.* 1, 351–358.
- Watson, J.E.M., Dudley, N., Segan, D.B., Hockings, M., 2014. The performance and potential of protected areas. *Nature* 515, 67–73.
- Watson, J.E.M., Evans, M.C., Carwardine, J., Fuller, R.A., Joseph, L.N., Segan, D.B., Taylor, M.F., Fensham, R.J., Possingham, H.P., 2011a. The capacity of Australia's protected-area system to represent threatened species. *Conserv. Biol.* 25, 324–332.
- Watson, J.E.M., Grantham, H.S., Wilson, K.A., Possingham, H.P., 2011b. Systematic conservation planning: past, present and future. In: Ladle, R.J., Whittaker, R.J. (Eds.), *Conservation Biogeography*. John Wiley & Sons, London, pp. 1956–1976. <http://dx.doi.org/10.1002/9781444390001> (ch6).