Tree Hollow Requirements of Leadbeater's Possum and Other Possums and Gliders in Timber Production Ash Forests of the Victorian Central Highlands

Andrew P. Smith[A] *and David Lindenmayer*[AB]

[A] Department of Ecosystem Management, University of New England, Armidale, N.S.W. 2351.
[B] Present address: Department of Forestry, Australian National University, P.O. Box 4, Canberra, A.C.T. 2600.

Abstract

This study models relationships between the density of tree-hollow dependent possums and gliders and the density of potential nest trees (PNT), in timber production ash forests of the Victorian Central Highlands, where PNT are defined as all living or dead trees with $\geqslant 0\cdot 5$ m diameter at breast height and $\geqslant 6$ m height. The total density of all possums and gliders was found to increase linearly with PNT density, in an approximately 1 : 1 ratio, then to plateau at an average maximum density of $11\cdot 3$ animals per 3 ha once PNT density exceeded 12 per 3 ha. Regression models predict that Leadbeater's possum will be absent from the majority of sites with fewer than $4\cdot 2$ PNT per 3 ha and will increase linearly in density to an average maximum of $7\cdot 8$ animals per 3 ha (or $3\cdot 1$ colonies per 3 ha) on sites with more than 10 PNT per 3 ha. The absence of Leadbeater's possums from sites with fewer than $4\cdot 2$ PNT per 3 ha was attributed to: competition for hollows by other species; use of more than one PNT by individual colonies; and unsuitability of hollows in up to two out of every three PNT. Regression models predict that current logging prescriptions in ash forests, that call for retention of a minimum of 15 trees for every 10 ha clearfelled, will result in elimination of Leadbeater's possum from the majority of clearfelled coupes, and will reduce the total number of hollow-dependent possums and gliders to less than one-eighth of their average maximum density in unlogged forest. The current decline in the availability of tree hollows caused by logging, fire and natural decay, is considered to be the most significant threat to the present and future survival of Leadbeater's possum. A range of forest management options are presented and discussed to ensure the continued availability of PNT for hollow-dependent arboreal mammals in timber production forests.

Introduction

The elimination of hollow-bearing trees during timber harvesting operations is one of the most significant threats to the survival of wildlife in timber production forests (Loyn 1985). Approximately 75% of arboreal marsupials use tree hollows as daytime refuges for shelter or reproduction (calculated from data in Strahan 1983). This problem is of particular significance for the conservation and management of Leadbeater's possum, *Gymnobelideus leadbeateri*, a rare and endangered species with a restricted distribution, centred on the Victorian Central Highlands. Leadbeater's possum is most widely distributed and most abundant in young, dense, moist stands of forest dominated by mountain ash (*Eucalyptus regnans*), alpine ash (*Eucalyptus delegatensis*) and/or shining gum (*Eucalyptus nitens*) with an understorey of gum-producing *Acacia* spp. that provide suitable feeding substrate, and an overstorey of large dead or living trees that provide hollows for shelter and reproduction (Smith 1982; Smith *et al.* 1985). Abundant habitat of this type was created in the Victorian Central Highlands after intense wildfires in 1939 burned approximately 65% of the State's ash forests, reverting them to young regrowth stands overtopped by large fire-filled trees and scattered living emergent trees. Many of these forests are now maintained at an early

regrowth stage by clearfelling for hardwood production. At present, approximately 77% of the total area of ash forest within 2 km of recorded Leadbeater's possum sighting localities is zoned for timber production (Smith *et al.* 1985). The number of large hollow-bearing overstorey trees in regrowth timber production forests is declining however, through a combination of natural decay, deliberate culling of dead trees, harvesting of large living trees, and incidental loss during post-logging, slash-burning operations. Unless existing hollow-bearing trees and a proportion of young living trees are protected from logging, Leadbeater's possum and other hollow-dependent fauna will eventually be severely reduced in number, or eliminated from clearfelled forest.

Current management prescriptions for the Central Highlands (Forests Commission of Victoria 1983) set maximum limits to the number of trees to be retained in logging coupes without any clear knowledge of whether they are adequate to ensure the continued survival of hollow-dependent wildlife. The number of retained trees in coupes is minimised on the grounds that retained mature overstorey trees suppress seedling germination and subsequent timber growth rates (see Incoll 1979; Rotheram 1983), even though there is little evidence that these processes affect timber production in ash forests.

In this study we determine the minimum and maximum density of potential nest trees, and some aspects of nest tree spacing, necessary to meet the tree hollow requirements of Leadbeater's possum and other hollow-dependent possums and gliders in logged forests. We also establish criteria for identification and selection of preferred potential nest trees for retention and protection within logged compartments.

Methods

Survey Sites

Eight survey regions were selected from throughout the present known range of Leadbeater's possum, within the Toolangi, Alexandra, Marysville, Powelltown and Neerim forestry districts. Within each region an average of four survey sites was selected to cover a range of habitat types. Selection was primarily on the basis of successional age, and *Eucalyptus* and *Acacia* spp. dominance. Sites were located to cover as wide a geographic range as possible to ensure that the study conclusions would be applicable throughout the ash dominated forests of the Central Highlands. The rarity of Leadbeater's possum and the fire history of its habitat suggest that it may have a patchy distribution, and that some areas of potentially suitable habitat currently remain unoccupied. To help ensure that possum density at each site reflected the true carrying capacity of each habitat type selected, we attempted to locate each site within 2 km of a prior Leadbeater's possum sighting locality. This was possible for all sites except those at Toolangi which averaged 3 km (range 2–6 km) from previously recorded sites because of the lack of previous sightings and apparent lack of suitable habitat in this district.

At each site a 3 ha (200 by 150 m) rectangular grid was marked out in a patch of relatively homogeneous vegetation by pacing along compass bearings. Each site contained not less than 4 and not more than 22 potential nest trees, where potential nest trees (PNT) were defined as those dead or living trees of $\geqslant 6$ m height and $\geqslant 0 \cdot 5$ m diameter at breast height (dbh). Some isolated living trees that met these specifications were excluded if they had no obvious hollows in the main trunk and no connectance of the tree crown with surrounding vegetation. It was assumed on the basis of prior observations (Smith 1984), that Leadbeater's possum would not descend to the ground to exit tree hollows. All PNT were mapped and numbered at each site.

Survey Method

The number of arboreal mammals in each tree was determined by an absolute count method (stag watching, see Smith 1984, Smith *et al.* 1985 and unpublished), which involved counting all animals emerging from tree hollows at dusk. Counts were carried out simultaneously at all PNT within each site with the assistance of numerous volunteer observers (see Acknowledgments). This method has two key assumptions: (1) that all individuals in a population den in tree hollows; and (2) that all individuals emerge from tree hollows at dusk while still detectable or visible in natural light. The method was developed specifically for Leadbeater's possum and was validated for resident, adult animals (Smith 1984). On two rare occasions non-resident, dispersing individuals of this species have been observed to emerge from temporary, overnight shelter in ground logs and debris (A. Smith,

unpublished observations). Stag watching provides a useful index of abundance for other species of arboreal mammals but may underestimate the number of sites occupied by greater gliders, *Petauroides volans*, and common ringtail possums, *Pseudocheirus peregrinus*, by 50% or more because of their late emergence or, in the case of ringtail possums, use of den sites in dense foliage as well as in tree hollows (A. Smith *et al.* 1985, Smith *et al.* unpublished).

Nest Tree Description

All PNT at each site were described by four variables: height, diameter at breast height (dbh), number of hollow branches and holes ($\geqslant 4$ cm diameter), number of fissures ($\geqslant 3$ cm length and $1 \cdot 5$ cm width), and access (to surrounding vegetation); and one attribute: tree form. The above ground heights and types of nest entrance, were also recorded for all actual nest trees. Form was determined by subjective classification into one of the seven forms and four groups illustrated in Fig. 1. These forms are intended to represent increasing senescence in mountain ash. Tree height was estimated visually, but checked periodically using a clinometer. The dbh was measured with a diameter tape. The numbers of hollow branches and holes were assessed visually for that portion of the tree trunk within and below the tree crown (in living trees) or within and below the tree canopy (in dead trees). Access to surrounding vegetation was calculated by scoring 1 point for every 3 m of tree height in contact with, or within 10 cm of, surrounding vegetation.
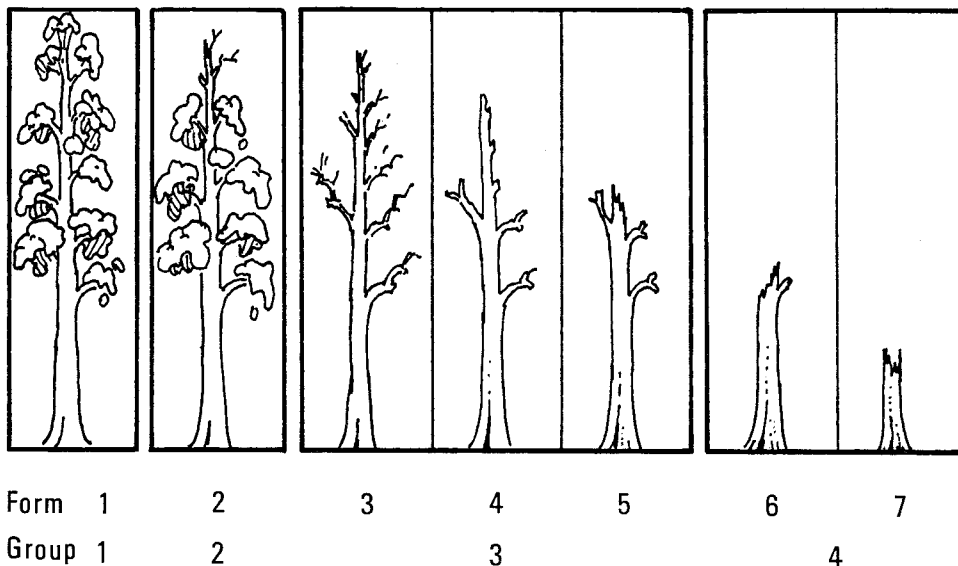

Fig. 1. The seven forms and four groups used for subjective classification of potential nest trees (all trees $\geqslant 0 \cdot 5$ m dbh and $\geqslant 6$ m height) in ash forest on the basis of increasing senescence, branch loss, and windthrow of the main stem.

Data Analysis

Preference for PNT of different form, diameter, height, access, and hollow and fissure numbers, were determined by Chi-square analysis, by comparing the total number of animals observed emerging from trees in each variable or attribute class with the expected number, after assuming random selection. Expected frequencies were calculated by summing the number of PNT in each variable or attribute class at all survey sites supporting at least one colony of Leadbeater's possum. Tree diameter, access, hole number and fissure numbers were tested for independence from tree form by analysis of variance.

Relationships between PNT density and animal density were determined by a modified (bent line) form of regression analysis. The relationship between PNT density and animal density in a habitat of uniform quality could theoretically be expected to take the form exhibited in Fig. 2*a*. The shaded area along line AB represents the expected distribution of data points when animal numbers are held below habitat carrying capacity by a shortage of nest sites. The shaded area reflects noise, sampling errors,

and variation caused by differences in the quality and spatial distribution of nest trees on sample sites. The shaded area along line BC represents animal density when PNT are present in excess, and population density is limited by other habitat parameters (e.g. food, foraging substrate structure, competition, and predators). When habitat is not uniform but varies from site to site, as in this study, a slightly different theoretical distribution of data points could be expected, as in Fig. 2b. In this situation the shaded area along line BC will become expanded below, to fill all space below lines AB and BC, to represent sample sites in poor habitat in which other factors became limiting before nest tree abundance.
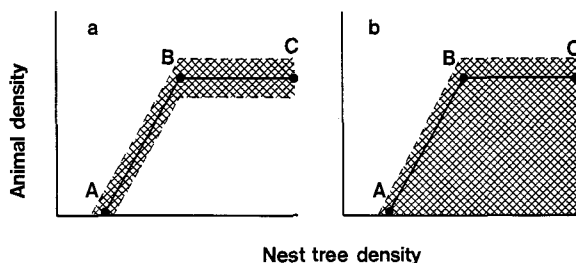

Nest tree density

Fig. 2. Theoretical relationships between the density of resource limited, hollow-dependent arboreal mammals and the density of potential nest trees in habitats of uniform (a) or variable (b) quality with respect to resources other than hollow availability (e.g. food availability). Line AB represents the linear relationships between animal density and potential nest tree density when only tree hollows are limiting. Line BC represents average maximum density when tree hollows are present in excess and other resources are limiting. Shading represents the expected distribution of data points determined by noise, sampling error and variations in potential nest tree quality (a), and also by site quality when other factors (food, competition) become limiting before tree hollow numbers (b).

In this study, the position of line AB was determined by least squares regression, by using only those data points from sites with optimal or near optimal feeding habitat in which PNT were limiting. Optimal feeding habitat was determined in a separate analysis of over 30 environmental variables and attributes at each site (see Smith et al. 1985). A preliminary analysis of relationships between Leadbeater's possum density and all measured environmental variables revealed that PNT density, the number of gum producing acacias, and tree and understorey canopy closure (connectance) explained the greatest variability in possum density. Furthermore, PNT availability was independent of (significantly uncorrelated with) all other measured habitat variables. The greatest r^2 for correlations between PNT density and all other measured variables was 0.08. For the latter reasons we are able to justify a univariate analysis of relationships between possum density and PNT availability, using only sites with suitable foraging habitat. Such sites include those dominated by ash eucalypt species (mountain ash, alpine ash or shining gum), with >20 individuals of *Acacia obliquinervia* and/or *Acacia dealbata* per 0.06 ha and with a combined canopy and understorey connectance rating >25. For justification of these criteria see Smith et al. (1985). The value of x (average maximum required PNT density) for the point of inflexion (B) in the bent line regression was determined by taking a series of trial values of x and calculating the resultant regression equation and residual sum of squares for line AB. The value of x leading to a minimum residual, before a trend of increasing residual sum of squares with increasing PNT density, was selected as the average maximum required PNT density. The resulting regression equation for line AB was then solved for this value to predict average maximum possum density in sites of optimal habitat with an excess of PNT.

Results

Nest Tree Quantity

Relationships between the number of Leadbeater's possums, the number of possum

colonies, the number of all possums and gliders, and the number of potential nest trees on each 3 ha survey site, are plotted in Fig. 3a–c. In general, the distribution of data points fitted the theoretically predicted pattern (Fig. 2b). However, possum density did not exhibit a strong tendency to plateau at high PNT densities. Most sites supported fewer than the 10–12 PNT per 3 ha required to sustain maximum possum and glider density. This pattern partly reflects our avoidance of sites with very high PNT densities because of the difficulty of organising sufficient volunteers to survey them. With only one or two exceptions, sites identified as suboptimal for Leadbeater's possum with respect to vegetation floristics and
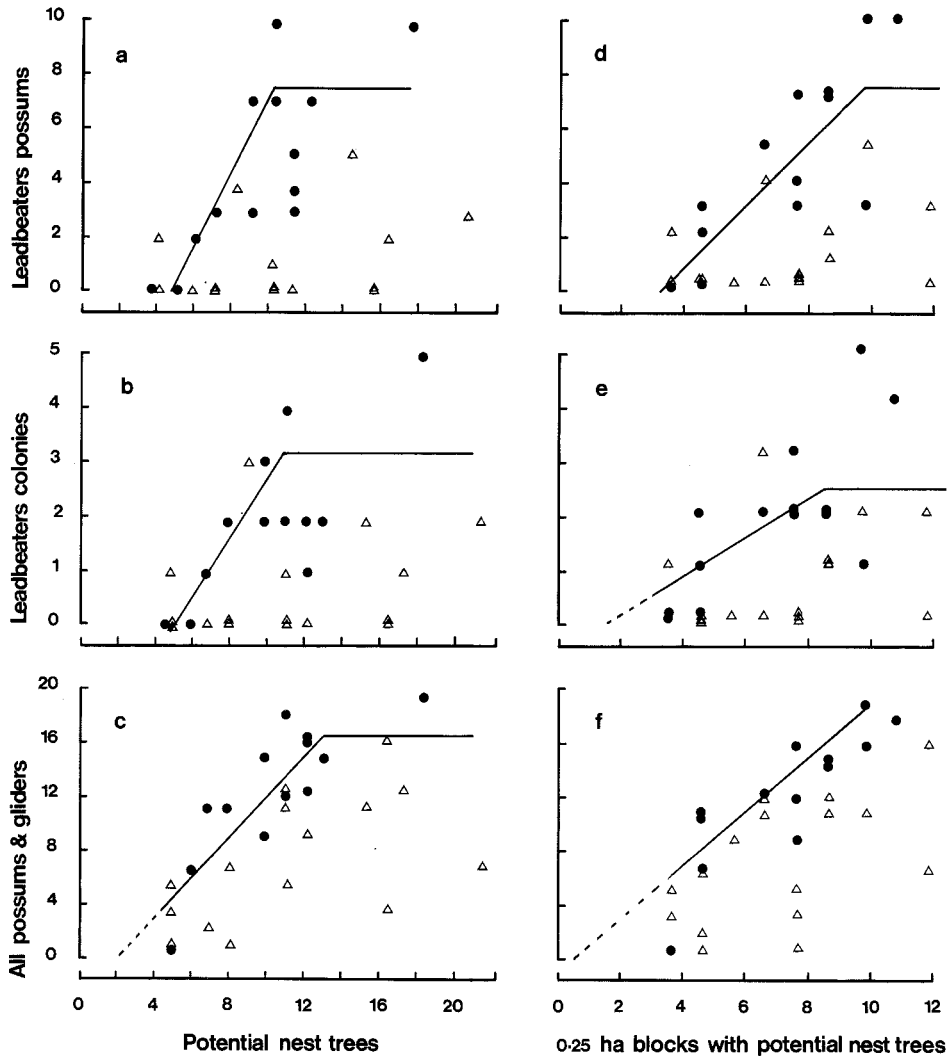

Fig. 3. Actual relationships between the number of hollow dependent arboreal mammals and the number of potential nest trees in 3 ha sites of uniform high quality for Leadbeater's possum (●) and in sites of low quality for Leadbeater's possum (△). Linear regression lines are shown for high quality sites only. Horizontal lines indicate average maximum animal numbers on the 3 ha survey sites as predicted from linear regression models (see Methods for further details). Nest tree densities are expressed both as PNT per 3 ha (a–c) and as the number of 0·25 ha blocks on each 3 ha site with at least one PNT (d–f).

structure, fell below the regression lines relating possum density to potential nest tree density (Fig. 2).

Significant linear relationships were established between the number of animals and the number of potential nest trees at each 3 ha site for those sites providing optimal or near optimal habitat with respect to parameters other than nest tree abundance. These relationships are listed in Table 1. These regressions predict that Leadbeater's possum density will average zero on sites with less than 4·2 PNT per 3 ha, and that Leadbeater's possum density will increase linearly to a maximum of 7·4 animals per 3 ha when the number of PNT is equal to or greater than 10 per 3 ha.

Table 1.   Linear regression relationships between the number of possums and gliders and the number of potential nest trees (large dead or living trees $\geqslant 0·5$ m dbh and $\geqslant 6·0$ m height) in a series of relatively homogeneous 3 ha patches of montane ash forest

A, predicted number of potential nest trees, or number of quarter ha blocks in each 3 ha site with potential nest trees, when animal density averages zero; B, predicted minimum number of potential nest trees, or quarter ha blocks with nest trees, necessary to sustain animal density at the average maximum; C, average maximum number of animals or colonies per 3 ha when number of potential trees is in excess

Regression variables		Regression equations	r^2	A	B	C
y	x					
Leadbeater's possums per 3 ha	Potential nest trees per 3 ha	$y = 1·39x - 6·46$	0·80***	4·7	10	7·4
Leadbeater's possum colonies per 3 ha	Potential nest trees per 3 ha	$y = 0·53x - 2·20$	0·78***	4·2	10	3·1
Leadbeater's possums per 3 ha	0·25-ha blocks with potential nest trees	$y = 1·25x - 3·47$	0·76***	2·8	9	7·8
Leadbeater's possum colonies per 3 ha	0·25-ha blocks with potential nest trees	$y = 0·39x - 0·64$	0·56**	1·6	8	2·5
All possums and gliders per 3 ha	Potential nest trees per 3 ha	$y = 1·08x - 1·62$	0·70***	1·5	12	11·3
All possums and gliders per 3 ha	0·25-ha blocks with potential nest trees	$y = 1·36x - 0·77$	0·74***	0·6	>10	>12·8

**$P < 0·01$, ***$P < 0·001$.

The slope of the relationship between the density of Leadbeater's possum colonies and the density of PNT indicates that PNT density exceeds the actual number of PNT used by Leadbeater's possum by a ratio of up to 3 : 1. Additional PNT are presumably used by other species of possums and gliders. These other species of possums and gliders included mountain brushtail possums, *Trichosurus caninus*, greater gliders, yellow-bellied gliders, *Petaurus australis*, common ringtail possums and sugar gliders *Petaurus breviceps*. A strong linear, almost 1 : 1, relationship occurred between the total number of all species of possums and gliders recorded emerging from tree hollows and the density of PNT on each site. The estimated maximum number of PNT required to satisfy the tree hollow requirements of all species (12 per 3 ha) was only marginally greater than the number required to satisfy the requirement of Leadbeater's possum alone (10 per 3 ha). This suggests that, if the PNT requirements of Leadbeater's possum are satisfied, at most only 20% more PNT will be required to satisfy the requirements of all other species of possums and gliders.

Nest Tree Spacing

The distribution of potential nest trees varied considerably between sites, from being relatively even, or random, to highly clustered on less than half the available area. Each 3 ha sample site was divided up into twelve 0·25 ha grid squares, such that the proportion of these squares containing potential nest trees, and the number of vacant squares adjacent to actual nest trees, provided indices of nest tree spacing as well density.

The numbers of Leadbeater's possums, Leadbeater's possum colonies, and the total numbers of possums and gliders per site, were significantly related to the number of 0·25 ha blocks on each site supporting PNT (Fig. 3*d, e, f* and Table 1). Leadbeater's possum density increased linearly from zero, when fewer than 1·6-2·8 of the 0·25 ha blocks contained potential nest trees, to a maximum density of 7·8 animals, or 2·5 colonies, per 3 ha when the number of blocks with potential nest trees exceeded 8-9. The total number of possums and gliders increased linearly from a predicted value of zero when the number of 0·25 ha blocks with PNT was 0·6, to an estimated maximum of >12·8 animals per 3 ha when the number of 0·25 ha blocks with PNT exceeded 10. Since the total number of possums and gliders did not exhibit any clear tendency to plateau as the number of 0·25 blocks with PNT increased, and since we did not sample any sites in which the number of 0·25 blocks with PNT exceeded 10 (see Fig. 3*f*), it is possible that maximum possum and glider density will only be reached on 3 ha sites in which all 0·25 ha blocks support PNT.

These regression relationships between possum density and the number of 0·25 ha blocks with PNT differed from previously established relationships between possum density and PNT density, largely only in passing closer to the origin when extrapolated to zero animal density. This result suggests that fewer PNT may be required to maintain a given animal density if PNT are more evenly spaced within the site.

The hypothesis that colony size increases in direct proportion to adjacent vacant space, was also investigated by regressing colony size against the number of vacant adjacent blocks (for sites of optimal or near optimal habitat only). The regression was non-significant. Regressions of mean colony size per site against the number of PNT and the number of 0·25 ha blocks with PNT, both also proved to be non-significant. These results suggest that colony size, and hence Leadbeater's possum density, may not increase in response to suitable adjacent PNT-free foraging habitat, which is consistent with the pair based territoriality documented for this species (Smith 1984).

New Tree Quality

Leadbeater's possums were observed significantly more frequently than expected in PNT of certain form, diameter, height, and access to surrounding vegetation (Table 2). They exhibited no significant preference for living trees over dead trees when trees of forms 1 and 2, and 3-7 (Fig. 1) were compared. Overall, they exhibited preference for living trees with broken or dead tops (form 2, Fig. 1), and avoidance of tall dead trees of forms 3-5 (Fig. 1). Leadbeater's possums were not found in dead trees of less than 1 m dbh, or greater than 2·5 m dbh, but exhibited a significant preference for those of 1·1-2·5 m dbh. In contrast, living trees less than 2·1 m dbh were strongly avoided while those greater than 2·5 m were preferred. Dead trees of 16-26 m height were preferred over all other height classes, with those greater than 46 m being least preferred, but this result may be an artefact of confounding between tree height and form (Table 3). In contrast, taller living trees (>46 m) were preferred to shorter living trees (36-45 m). Leadbeater's possum exhibited no apparent preference for trees with different numbers of fissures or holes.

The height of Leadbeater's possum nest entrances ranged from 2 to 46 m above ground, with a modal height of 10 m and a mean height of 16 m (Fig. 4). Nest entrances were significantly higher in living trees ($\bar{x}=22$ m) than dead trees ($\bar{x}=11$ m, Mann Whitney

Table 2. A comparison of the observed and expected (in parentheses) numbers of Leadbeater's possums nesting in trees of different form (see Fig. 1), diameter, height, and access to surrounding vegetation

Data are presented for living and dead trees combined, and for living trees (forms 1 and 2) and dead trees (forms 3–7) separately

| Variable	All trees	Dead trees	Living trees
Tree form			
1	10 (12)		
2	23 (15)		
3–5	21 (31)		
6–7	33 (29)		
χ^2	8·4		
P	<0·02		
Tree diameter (m)			
0·5–1·0	0 (6)	0 (6)	—
1·1–1·5	25 (24)	23 (19)	2 (6)
1·6–2·0	23 (22)	22 (17)	1 (6)
2·1–2·5	22 (21)	9 (7)	13 (11)
>2·5	17 (14)	0 (5)	17 (10)
χ^2	6·8	13·8	12·1
P	NS	<0·01	<0·03
Tree height (m)			
9–15	8 (12)	8 (10)	—
16–26	27 (19)	27 (17)	—
26–35	17 (20)	12 (15)	—
36–45	9 (16)	5 (6)	9 (15)
>45	26 (20)	2 (6)	24 (18)
χ^2	10·0	9·7	4·4
P	<0·05	<0·05	<0·05
Tree access		trees <30 m height only	
0–2	15 (22)	3 (10)	4 (7)
3	17 (15)	8 (8)	9 (7)
4	22 (18)	14 (11)	6 (5)
>5	33 (32)	11 (7)	14 (14)
χ^2	3·4	8·1	2·1
P	NS	<0·05	NS
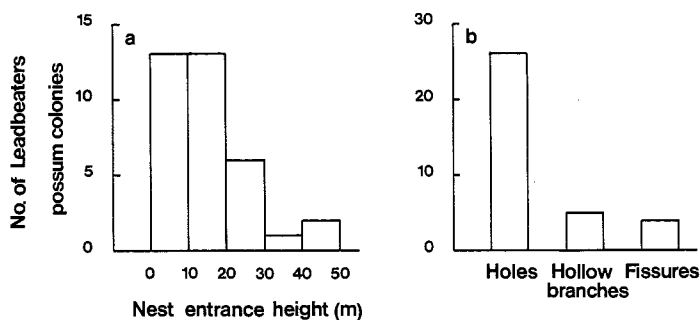
Fig. 4. (a) Frequency distribution of nest entrance heights for Leadbeater's possum colonies. (b) Relative number of Leadbeater's possum nest entrances through tree holes, hollow branches and fissures.

U-test $P<0.005$). The entrance height of nests in dead trees was significantly correlated with the height of the tree itself according to the following relationship:

$$\text{Entrance height} = 0.42(\text{tree height}) + 1.81 \qquad (r^2 = 0.41, \; P < 0.01).$$

No similar relationship was apparent for living nest trees.

Selection of nest trees by Leadbeater's possums did not appear to be significantly affected by the number of holes, hollow branches and fissures on potential nest trees. Most (73%) of nest entrances used by Leadbeater's possum were holes (holes excavated by possums themselves, natural decay sites in dead wood, and 'butt holes' left where large branches had been shed by the growing tree), followed by hollow branches (15%) and fissures (12%) (Fig. 4).

Access to nest trees, as determined by the number of 3 m trunk sections in contact with or within 10 cm of surrounding vegetation, was not significantly correlated with selection of dead or living trees. This result was initially unexpected. In retrospect however, the measure of nest tree access used may not have been appropriate because it was confounded by tree height and was difficult to assess in the crown of tall living trees. Notably when only dead trees of ⩽30 m height are considered (those that are almost entirely within or below the tree and shrub canopy), Leadbeater's possum exhibited a significant apparent preference for trees with an access score greater than 3 (Chi-square, test $P<0.05$).

Table 3. A sumary of interrelationships between potential nest tree form (from Fig. 1) and the mean (±95% confidence interval) values for tree height, tree diameter, hole and fissure number, and access to surrounding vegetation, as determined by analysis of variance

Form	1	2	3–5	6–7	P
Height (m)	47±4	44±4	40±3	22±4	<0·01
Diameter (m)	2·2±0·2	2·0±0·3	1·9±0·3	1·7±0·2	0·05
No. of holes	5·0±1·0	5·2±1·2	4·0±0·6	3·3±0·6	<0·05
No. of fissures	0·6±0·4	0·6±0·5	1·0±0·4	1·0±0·5	NS
Access	3·8±1·0	4·2±1·0	5·1±0·9	3·8±0·8	NS

Discussion

Relationships between Possum and Glider Density and PNT Density

Under conditions of resource limitation, the density of tree hollow dependent arboreal mammals should increase approximately linearly with tree hollow density and then plateau once tree hollows are present in excess and other resources such as food become limiting. Our objective was to model the relationships between tree hollow density and possum and glider density, and use these models to predict the minimum number of hollow-bearing trees needed to maintain a specified density of Leadbeater's possums and other species of hollow-dependent possums and gliders in clearfelled ash forests.

We were unable to measure tree hollow availability directly, but instead used the abundance of dead and living trees of ⩾0·5 m dbh and ⩾6 m height (PNT) as an index of potential tree hollow density. We found that the form of the relationships between total possum and glider density and PNT density (Figs 3a–f) conformed reasonably well with the expected pattern (Fig. 2). A strong linear, almost 1 : 1, relationship was found between the total number of possums and gliders and the total number of PNT. This relationship reached a plateau when the number of PNT exceeded 12 per 3 ha and the predicted average maximum density of possums and gliders was 11·3 animals per 3 ha. Relationships between Leadbeater's possum density and PNT density similarly conformed to the expected pattern, but differed from the relationships established for all species of possums and gliders in two

important respects. Instead of extrapolating through or close to the origin, the relationship between Leadbeater's possum density and PNT density predicts an average possum density of zero when the number of PNT falls below 4·2 per 3 ha or when less than 1·7, 0·25 ha blocks contain PNT. The relationship between Leadbeater's possum density and PNT density also indicates that on average approximately only one in three PNT are actually occupied by Leadbeater's possum colonies. The density of possum colonies increased linearly from an average of zero when the density of PNT was 4·2 to an average maximum of 3·1 when the number of PNT exceeded 10 per 3 ha.

We offer a number of plausible explanations for this apparent under-utilisation of PNT by Leadbeater's possum. It could result if: approximately only one in every three PNT contain suitable hollows for the species; Leadbeater's possum is excluded from potentially suitable hollows by other species of possums and gliders; or if each Leadbeater's possum colony requires access to more than one PNT. Available evidence suggests that all three of these factors may operate to some extent. Leadbeater's possum colonies have been recorded to use multiple nest sites and to move nest trees within their home ranges (Smith 1984). Additional data obtained in this study indicate that PNT are not selected at random but that certain sizes and forms are occupied more frequently than expected (see next section). Competition for tree hollows between species of possums and gliders is not well documented, but clearly when PNT occur at low densities some species must either be eliminated or must co-exist in the same tree as others, since over five species of possum and gliders are recorded in these forests. Some or all of these species will be disadvantaged once PNT density falls below 5 per 3 ha, particularly in areas with dead PNT in an advanced state of breakdown (forms 6, 7) that have fewer hollows. The species most likely to be disadvantaged are those of poor competitive ability (e.g. small size) with specialised hollow requirements. Leadbeater's possum may fall into this category, since it occupies large hollows (20–30 cm internal diameter) with small entrance diameters (4–8 cm diameter), and has been observed to be excluded from nest-boxes by similar sized sugar gliders in captivity (A. Smith, un-published observations). The abundance of sugar gliders in our survey sites was significantly negatively correlated with the abundance of Leadbeater's possum, and sugar gliders prevailed at survey sites in the Toolangi district that contained a near minimum density of PNT (Smith et al. 1985).

Our regression models predict negative densities of Leadbeater's possum for sites with less than 4 PNT for 3 ha or with less than 1·6, 0·25-ha blocks with PNT. Since it is not possible to measure negative animal densities, this result should be interpreted to indicate that Leadbeater's possum will be absent from sites with less than 4 PNT for 3 ha with increasing frequency as the number of PNT approaches zero. This result does not preclude the possibility that a portion of sites with low PNT densities will support Leadbeater's possum. This portion can only be determined with accuracy by further surveys of sites with low PNT densities.

PNT Preferences of Leadbeater's Possum

Actual nest trees utilised by Leadbeater's possum were not selected at random but could be distinguished from the range of available PNT on the basis of: form, height, diameter, and access to surrounding vegetation. Preferred dead nest trees were characterised by senescent form (forms 6 and 7, Fig. 1); a height of 16–25 m; a diameter of 1·1–2·5 m; and good access below 30 m height. Preferred living trees were those with dead or broken tops (form 2, Fig. 1); heights in excess of 46 m; and diameter in excess of 2·1 m. It is unlikely that possums discriminated between trees on the basis of height or diameter *per se*, but according to other, more functional characteristics associated or confounded with these variables, such as internal hollow development, or possibly hollow moisture content (not measured in this study). Hollow development has not been studied in living mountain ash but it may have some similarity to the pattern described for blackbutt, *Eucalyptus pilularis*, in moist forests of coastal northern New South Wales (Mackowski 1984). In this species

hollow development follows a logical sequence of decay and breakdown of internal heartwood by fungal and insect attack and excavation of heartwood by termites, followed by drainage of decomposed heartwood. Branch breakage is necessary to allow access to hollows and to enhance drainage of decomposed heartwood. Hollows suitable for use by wildlife are generally found in the upper regions of the tree and large hollows do not become available in the main trunk until trees reach an age of about 200 years (Mackowski 1984). The selection of living nest trees by Leadbeater's possum is consistent with a similar pattern of tree hollow ontogeny in mountain and allied ash species. Preference for living trees of $>2 \cdot 1$ m diameter (190–220 years in age) may reflect the availability of large hollows in the upper (narrower) trunk. Preference for form 2 trees with dead or broken tops may reflect improved access to hollows and improved hollow drainage. The mean nest entrance height (22 m) in living trees was significantly higher than that in dead trees (11 m), suggesting that hollows occur at greater height in living trees, which is consistent with the pattern of internal heartwood decay and drainage in living trees described by Mackowski (1984).

Patterns of tree decay and hollow development are less well studied in dead than living eucalypts, but observations of stag development and fall in the Cambarville region suggest that the pattern in dead trees is a continued process of internal decay and drainage followed by progressive windthrow of the main stem in sections of approximately $\frac{1}{4}$ to $\frac{1}{2}$ trunk length (Fig. 1). Remaining stems eventually fall completely, or become hollowed out (pipes) and decay in an upright position. Breakage of the main trunk by windthrow provides access to the large central hollow and probably accelerates hollow drainage. Leadbeater's possums preference for short (16–26 m) dead trees of forms 6 and 7, and the significant correlation between dead tree height and nest entrance height, suggests that possums are gaining access to hollows from above (at the point of breakage) at understorey or regrowth canopy height. Leadbeater's possums presumably nest on or above the undrained decayed heartwood, and excavate exit hollows themselves through the hard outer layer of dead wood, at or close to nest height level. If we surmise correctly, Leadbeater's possums using this type of PNT would be at risk of nest disturbance by larger species of possums and gliders, particularly mountain possums, that could easily gain access to the central trunk hollow and exclude smaller species.

Leadbeater's possums are accomplished gnawers which may explain why they apparently failed to favour dead trees with obvious natural hollows and holes. Of eight nest entrances examined closely in the Cambarville region, five had been excavated by possums at points of natural weakness, two consisted of natural fissures, and one was an apparently natural decay hole (A. P. Smith, unpublished observations). The preference for dead trees of narrower diameter $(1 \cdot 1–2 \cdot 5$ m) than living trees $(2 \cdot 1 +$ m), may reflect the greater dimensions of central hollows in the lower, relative to the upper, portion of the tree trunk. Narrow trees $(<1$ m dbh) may not become suitable for use until almost completely internally drained.

The Need for Tree Hollow Management

Present management prescriptions for the ash forests of the Central Highlands call for retention of a minimum 15 trees for every 10 ha clearfelled (Forests Commission of Victoria 1983), or retention of one tree cluster of at least five trees for every 5 ha felled (Wailes 1982). Assuming that all such retained trees are $\geqslant 0 \cdot 5$ m dbh and $\geqslant 6$ m height, our regression models predict that the total number of possums and gliders in logged coupes will be reduced to zero or one-eighth of the maximum, unless these criteria are altered. To assist in the appreciation of the significance of this statement to the future survival of Leadbeater's possum, we will briefly review the fire and logging history of Victorian ash forests.

Approximately 65% of Victorian ash forests were destroyed or damaged by wildfires in 1939 (Forests Commission of Victoria 1984). Mature and overmature trees that largely dominated these forests before the fire, were left standing as dead or living emergents above

a relatively uniform-aged regrowth ash forest. Salvage logging operations were initiated after this and earlier fires (1911, 1926) to harvest fire-killed or damaged mature trees, and these operations continued until approximately 1955 when damage to regenerating forest was becoming unacceptable. Logging of mature forests that survived the 1939 fires also commenced during this period and has continued until the present, providing the major source of ash timber while regrowth forests remained too young to be cut. Logging of mature and overmature forest has been so intensive during the past 40 years that now only approximately 8000 ha of mature ash remain in timber production zones, and approximately 80% of production forests are less than 60 years of age (Forests Commission of Victoria 1984).

The appearance of extensive tracts of regrowth forest with an overstorey of fire-killed mature trees provided abundant new habitat for Leadbeater's possum, which presumably increased greatly in abundance at around the time of the species 'rediscovery' in 1961 (Wilkinson 1961). The suitability of regrowth forests for Leadbeater's possum is now declining, for two main reasons: (1) natural fall and culling and logging of dead and living mature overstorey trees; and (2) progression of forest to a structurally less suitable successional age (Smith 1982, Smith *et al.* 1985). The second of these problems can be reversed by logging and future fires, but the first cannot, except possibly by supply of artificial nest sites, and will become the paramount problem over the coming 150 years before existing regrowth forests develop replacement hollows.

Ashton (1976) published a relationship between dbh and age [$\log_{10}$dbh (cm) $= 1 \cdot 02 \log_{10}$ age (years)] for mountain ash, which predicts a period of 190 years at $2 \cdot 1$ m dbh, before trees develop hollows suitable for Leadbeater's possum. Data of Piercy and Woodgate (1984) suggest a similar, but approximately 20% slower, growth rate for shining gum. Dead mature trees in ash regrowth forests are considerably less important than living mature trees in the long term because they appear to have a relatively short standing life after death (Smith 1982). Although the dynamics of stag fall have not been studied in any detail, it appears that stag losses have already exceeded critical levels in many 1939 regrowth forests. Estimation of stag densities from air photographs (including correction for below canopy stags) at one 28-km^2 site at Cambarville indicates that approximately 27% of mountain ash and 62% of alpine ash regrowth forests support less than two stags per ha. At the time of the 1939 fires these densities would have been approximately 10–80 trees per ha. Since Leadbeater's possum does not appear to favour use of living mature trees until the trees have >2 m dbh (approximately 200+ years of age), there is a high probablility that stag fall will render most existing regrowth forests, with an overstorey of dead mature trees, unsuitable for use by Leadbeater's possum during the next 0–150 years. This critical period could be reduced to approximately 60–80 years by careful management (see subsequent sections), but unless specific tree hollow management procedures are implemented, Leadbeater's possum may become restricted to those few scattered refuge areas with an overmature living overstorey and a regrowth understorey.

Suitable habitat could be created for Leadbeater's possum by selective logging of remaining mature ash forests. However, only about 8000 ha of mature forests (>80 years) remain in hardwood production areas, and these forests are also required in an unaltered state for conservation of mature-ash dependent wildlife. An additional 13 000 ha of mature forest ($\geqslant$80 years) occurs in water catchment areas. However, these forests are protected from logging, and most are currently unsuitable for Leadbeater's possum because they lack a regrowth understorey, have been poorly surveyed, and are spatially isolated from timber production forests (Forests Commission of Victoria 1984).

Tree Hollow Management

(i) Compatibility of clearfelling and Leadbeater's possum conservation

Results of this study indicate that a minimum of 10–12 PNT need to be retained in each 3 ha patch of ash forest to ensure maximum hollow availability for tree-hollow dependent

species of possums and gliders. In logged forests at least an equivalent number of younger trees will also be required to provide replacements for existing PNT in the event of natural or logging-induced PNT losses. Furthermore, replacement trees will need to be maintained in spatial isolation from existing living PNT to prevent their suppression and slowed hollow development. In other words, the retention of trees in small clusters does not allow for tree hollow replacement.

Maintenance of sustainable supply of PNT at the density required for maximum possum and glider conservation is feasible under low intensity (selective) logging regimes. Maintenance of PNT and provision for their future replacement is also compatible with clearfelling but requires the following modifications: more care during logging and slash burning to protect retained trees and filter strips; a slight reduction in the volume of timber harvested (equivalent to the harvestable volume of retained trees); and arguably some loss of future wood production through suppression of regrowth below or close to the crown of retained emergent living trees. It has been shown that retention of living overwood trees in regrowth hardwood forests can result in timber production losses that vary in magnitude with tree species, size and spacing (Incoll 1979; Rotheram 1983). This argument has been used to justify minimum tree retention in clearfelled ash forests. However, no research data are available for Central Highlands ash species which, because of their narrow crowns, high stocking densities and moist habitat preferences, may be less affected by overwood suppression than other species. In this study we found that multiage structured ash forest was not uncommon in the Central Highlands and, where it occurred, the basal area of understorey regrowth could be as high or higher than the area found in uniform stands of similar aged regrowth (Smith et al. 1985).

Rather than attempt to integrate and compromise wood production and wildlife conservation throughout the ash forests of the Central Highlands we suggest that all forests be categorised into three management zones with: (1) Leadbeater's possum (and other wildlife) conservation as a priority; (2) Leadbeater's possum conservation and timber production as joint priorities; and (3) timber production as a priority.

With respect to allocation of forests to these management zones we suggest that: (1) all remaining areas of mature and multiage structured forest (where the latter is forest with $\geqslant 12$ living mature, emergent PNT per 3 ha) be considered for allocation to zone 1; that all regrowth forest with $\geqslant 6$ living or dead PNT per 3 ha be considered for allocation to zone 2; and that remaining harvestable forest, with the exception of streamside connections, wildlife corridors, landscape corridors and other reserves, be allocated to zone 3. The specific location and relative extent of each zone would need to be negotiated after consideration of social and ecological as well as economic criteria. The principal ecological criterion would be the need to maintain minimum viable populations in all forest regions and isolates.

It is envisaged that mature-forest dependent wildlife would be conserved in the mature and multiage forests of zone 1. These forests would need to be classified as reserves or be protected from all types of timber harvesting other than low intensity selective logging. Leadbeater's possum would be conserved primarily in and along the edges of multiage forests in zone 1, in zone 2, and in and along the edges of those unlogged reserved corridor systems with a suitable density of PNT. Harvesting prescriptions for zone 2 would need to ensure active protection of existing PNT as well as their future ecological replacement. It would also be desirable in view of the anticipated massive decline in tree-hollow availability in regrowth ash forests over the coming 0–150 years to cease felling of any existing living PNT in zone 3.

A variety of harvesting options are available for integration of Leadbeater's possum conservation and timber production in zone 2. Our data suggest that 10 evenly scattered PNT, and at least an equivalent number of surviving younger trees will need to be retained in every 3 ha of clearfelled coupes in order to maintain an average maximum density of Leadbeater's possum. Should it be considered impractical or uneconomic to leave trees scattered within coupes, alternative prescription could include: (1) retention and protection

of retained trees in unlogged strips between long, narrow coupes (strip retention and logging); (2) retention of unlogged boundaries around small clearfelled coupes; or (3) retention of existing and replacement PNT in the outer half of logged coupes (the side adjoining stream-side reserves or wildlife corridors) and maximum utilisation in the centre of coupes. The ecological suitability of the above alternatives (1) and (2) depends on the extent to which Leadbeater's possums will extend their home range away from an edge and into PNT-free regrowth habitat. The maximum distance that Smith (1984) recorded Leadbeater's possums foraging away from a nest site was 150 m. By using this distance as a guide, approximately one half of an average sized (60 ha), clearfelled coupe, would be used as foraging habitat by Leadbeater's possums living in PNT in a circle of unlogged forest around the edges of the coupe. Further research should be carried out to validate this estimate before alternative methods (1) and (2) are used as a basis for management.

Potential nest trees require protection from timber harvesting, prescribed burning, post-logging burning, wildfire, windthrow, timber stand improvement and hazard control. Nest trees can be actively protected from post-logging fire by bulldozing fire breaks, using fire retardants or by situating trees or clusters in depressions or drainage lines or on rocky outcrops (Wailes 1982). Protection from windthrow and natural fall can be alleviated to some degree by protection of trees in rows or clusters and by selection of unusually sound, large diameter trees.

Nest trees selected for protection in logged coupes can be living or dead, but if living, should be $\geqslant 2 \cdot 1$ m dbh, with a fissured base and a dead or broken top. Dead trees should preferably be between 1 m and $2 \cdot 5$ m dbh and of broken senescent form (forms 6 and 7, Fig. 1). Suitability of living trees, particularly young narrow trees could conceivably be enhanced by fire scarring or topping with explosives. In view of the short life span of dead trees, living mature trees should be retained in preference to dead ones whenever possible. Selection for different tree forms by Leadbeater's possum is not particularly strong however, and in the event of nest tree scarcity any form greater than 1 m dbh should be protected.

(ii) *Use of artificial nest boxes*

The use of artificial nest boxes as a possible means of conserving Leadbeater's possum in areas from which natural hollows have been eliminated has yet to be adequately investigated. Leadbeater's possum has been recorded to occupy artificial hollows for short periods, in favourable habitats lacking potential nest trees, when they are placed in close proximity to established populations (M. Macfarlane, personal communication). However, it is possible that other species of hollow-dependent possums and gliders, bats or birds may colonise artificial hollows first and exclude Leadbeater's possum from areas in which they have been eliminated by logging. Our limited data suggest that sugar gliders may exclude Leadbeater's possum from artificial hollows when natural hollows are in short supply. Artificial hollows would have to be provided in sufficient density to meet the requirements of all potentially competing, hollow-dependent species.

Information is presently lacking on the insulative qualities, internal dimensions, and air flow characteristics of artificial nest boxes necessary to ensure continued occupation by free-living Leadbeater's possums and other hollow-dependent species in the natural environment. Even if these requirements are satisfactorily determined the cost of a widespread artificial nestbox program may prove a significant management constraint. Costing would need to consider: initial construction and installation costs, costs of regular monitoring for repair, replacement and relocation in response to changes in canopy height, and costs of road construction and maintenance for regular (5-yearly) access. We consider this approach to have greatest potential application in the reintroduction of captive-bred Leadbeater's possums to areas of local extinction, and in the restoration of wildlife corridors and refuge areas.

Acknowledgments

References

Ashton, D. H. (1976). The development of even aged stands of *Eucalyptus regnans* F. Muell. in Central Victoria. *Aust. J. Bot.* **24**, 397–414.

Forests Commission of Victoria (1983). 'Forest prescripions for hardwood harvesting and regeneration on state forests', Central Division. (Forests Commission of Victoria: Melbourne.)

Forests Commission of Victoria (1984). Assessment section forest inventory report No. 71. Internal report. (Forests Commission of Victoria, Division of Forest Management: Melbourne.)

Incoll, W. D. (1979). Effect of overwood trees on growth of young stands of *Eucalyptus sieberi*. *Aust. For.* **42**, 110–16.

Loyn, R. F. H. (1985). Strategies for conserving wildlife in commercially productive eucalypt forest. *Aust. For.* **48**, 95–101.

Mackowski, C. M. (1984). The ontogeny of hollows in blackbutt (*Eucalyptus pilularis*) and its relevance to the management of forests for possums, gliders and timber. In 'Possums and Gliders'. (Eds A. P. Smith and I. D. Hume.) pp. 553–67. (Surrey Beatty and Sons: Sydney.)

Piercy, K., and Woodgate, P. (1984). Eucalypt and understorey stand age survey, Erinundra Plateau. Internal report of Forests Commission of Victoria, Melbourne.

Rotheram, I. (1983). Suppression of growth of surrounding regeneration by veteran trees in Karri (*Eucalyptus diversicolor*). *Aust. For.* **46**, 8–13.

Smith, A. P. (1982). Leadbeater's Possum and its management. In 'Species at Risk: Research in Australia'. (Eds R. H. Groves and W. D. L. Ride.) pp. 129–47. (Australian Academy of Science: Canberra.)

Smith, A. P. (1984). Demographic consequences of reproduction dispersal and social interaction in a population of Leadbeater's Possum. In 'Possums and Gliders'. (Eds A. P. Smith and I. D. Hume.) pp. 359–73. (Surrey Beatty and Sons: Sydney.)

Smith, A. P., Lindenmeyer, D., and Suckling, G. (1985). The ecology and management of Leadbeater's possum. Report to World Wildlife Fund Australia, for Project 51, University of New England, Sydney.

Strahan, R. H. (1983). 'Complete Book of Australian Mammals.' (Angus and Robertson: Sydney.)

Wailes, K. (1982). Retention of habitat trees in logging coupes, part III: status and longevity of retained clusters as wildlife habitat. Internal report of Forests Commission of Victoria, Melbourne.

Wilkinson, M. E. (1961). The rediscovery of Leadbeater's Possums. *Vic. Nat.* **78**, 97–102.