The vegetation structure and condition of contracting lowland habitat for Leadbeater's possum (*Gymnobelideus leadbeateri*)

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Abstract. Lowland Leadbeater's possums are on a trajectory to extinction, with fewer than 40 individuals surviving in the wild. Quantification of the vegetation characteristics of their occupied habitat is urgently needed to inform strategies to conserve this genetically distinct population. We surveyed the canopy and midstorey vegetation at all remaining (nine) occupied territories and eleven abandoned territories in lowland swamp forest at the Yellingbo Nature Conservation Reserve. For each territory we quantified canopy and midstorey stem density, basal area (total and live) and vegetation condition (percentage live basal area, tree crown vigour and plant area index) within a 50-m radius of known den locations. The canopy at all locations was dominated by mountain swamp gum (*Eucalyptus camphora*), with most occupied sites supporting dense midstorey dominated by paperbarks, either *Melaleuca squarrosa* or *Melaleuca ericifolia*. Occupied territories had higher stem densities and better vegetation condition than abandoned territories. Stem density alone was able to predict occupancy vis-à-vis abandoned sites with a high (80%) degree of accuracy. Lowland Leadbeater's possums occupy swamp forests characterised by high stem density, particularly in the midstorey, structural complexity and healthy vegetation. These findings can help guide habitat restoration and translocation projects currently underway to expand the area of lowland habitat for this critically endangered species.

Introduction

Globally, anthropogenic land use is the major driver of biodiversity loss, with agriculture the leading contributor to deforestation, forest fragmentation and degradation (Chaudhary *et al.* 2016). Often, a species' ability to survive in a fragmented or degraded landscape is influenced by a combination of the: (i) ecological and demographic attributes of the species, such as population size, movement capacity and habitat requirements; and (ii) the suitability of the remaining environment for the species, such as the quality, size and connectivity of habitat, and the threatening process(es) acting upon it (Henle *et al.* 2004; Bennett and Saunders 2010; Ashman and Watchorn 2019).

Leadbeater's possum (*Gymnobelideus leadbeateri*) is one of ten mammal species in Australia listed as 'Critically Endangered' under the *Environment Protection and Biodiversity Conservation Act 1999*. The species has a restricted distribution confined to a

70 × 95 km area centred on the Central Highlands of Victoria, Australia. Across its range, the species occupies three distinct forest types spanning a broad elevation gradient (100–1500 m Australian Height Datum) (Harley 2004*a*; DEPI 2014). These include one outlying lowland population that is disjunct from highland populations. Approximately 96% of the remaining habitat known to support extant populations of Leadbeater's possum is montane ash forest (600–1300 m), typically dominated by mountain ash (*Eucalyptus regnans*) or alpine ash (*Eucalyptus delegatensis*). Subalpine woodland (1300–1500 m) dominated by snow gum (*Eucalyptus pauciflora*) accounts for ~4% of the remaining available habitat within the species' range. The third forest type occupied by the species is lowland swamp forest (100–120 m) dominated by mountain swamp gum (*Eucalyptus camphora*), which currently contributes <0.1% of available habitat. The vegetation floristics differ markedly between these

three forest types, albeit there are several features in common to each, including a predominance of gum-barked eucalypts and a cold, wet climate (Harley 2004*a*).

The type specimen of Leadbeater's possum was collected from lowland forest near Westernport Bay ~60 km to the south of the species' current range (McCoy 1867). Prior to extensive clearing for agriculture early last century, lowland swamp forest and shrub thicket (e.g. *Melaleuca ericifolia*) covered extensive areas within Leadbeater's possum's historic range (i.e. ≥10 000 ha; (Yugovic and Mitchell 2006). The widespread clearing of these floodplain forests for agriculture early last century (e.g. Spencer 1921) is the principal reason that Leadbeater's possums are now confined to a single lowland site, Yellingbo Nature Conservation Reserve, which protects 180 ha of remnant swamp forest along sections of the Cockatoo and Macclesfield Creek floodplains (McMahon and Franklin 1993; Harley *et al.* 2005).

Molecular analyses indicate that the extant lowland population of Leadbeater's possum at Yellingbo is genetically similar to historic, now-extinct lowland populations and distinct from extant highland populations (Hansen and Taylor 2008; Hansen *et al.* 2009). On this basis, the lowland population at Yellingbo represents the last remnant of the once extensive lowland distribution for the species. Research on population dynamics and demographic parameters on the extant lowland population has revealed a substantial population decline (~70%) since 2003, with the total wild population now comprising fewer than 40 individuals (Harley 2016). The risk of extinction for this population is extremely high without effective interventions, and it now constitutes the most threatened mammal population in Victoria, Australia.

Extensive research has investigated habitat attributes at sites occupied by highland populations of Leadbeater's possum. Part of the reason for this is tied to major disturbances from fire and timber harvesting across the species' highland range, both of which severely impact habitat quantity and quality (Lindenmayer and Sato 2018; Lindenmayer *et al.* 2012, 2020). In montane ash forest, Smith *et al.* (1985) and Smith and Lindenmayer (1988) found the basal area of *Acacia* species to be one of the strongest factors influencing the presence and abundance of Leadbeater's possum. Similarly, Lindenmayer *et al.* (1991*a*, 1991*b*) found the presence of Leadbeater's possum to be positively correlated with the basal area of *Acacia* species, and tree hollow occupancy to be associated with the quantity and proximity of vegetation surrounding denning locations. These findings highlight the importance of vegetation structure to Leadbeater's possum. In contrast to montane ash forest, quantitative data examining Leadbeater's possum's habitat requirements for the other two forest types occupied by the species are lacking.

Leadbeater's possum has three broad ecological requirements: hollow-bearing trees for diurnal denning, suitable plant species to support foraging and dense vegetation structure in the canopy or midstorey to facilitate movement (Harley 2004*a*). We examined two of these variables, floristics and vegetation structure, that are strongly tied to the quality of habitat for foraging and movement. Hollow-bearing trees for denning were not assessed in this study, as numerous nest boxes have been installed specifically for Leadbeater's possum throughout the study area since the mid-1990s, and therefore den availability was not considered a limiting resource (Harley 2004*b*).

Leadbeater's possum is an exudivore that supplements its diet with invertebrates (Goldingay and Jackson 2004). Our understanding of the species' diet in the wild is based on a single study of a highland population at a single locality. Based on faecal analysis, Smith (1984) identified the major dietary items as the gums of *Acacia* spp., manna, honeydew and arthropods. To date there has been no assessment of dietary breadth in relation to variables such as the dominant eucalypt, forest age class or elevation. Foraging observations have been made opportunistically for individuals being radio-tracked in lowland swamp forest at Yellingbo (Harley 2005). Most feeding observations involved possums licking, for short duration (typically <10 s), the trucks and major branches of *E. camphora*, and occasionally midstorey stems including scented paperbark (*Melaleuca squarrosa*), swamp paperbark (*M. ericifolia*) and woolly tea-tree (*Leptospermum lanigerum*) (D. Harley, unpubl. data). Possums were not observed feeding in canopy foliage, and foraging animals would frequently change trees in which they were feeding rather than spend prolonged periods in particular trees. Notably, there were no observations of possums feeding in wattles at Yellingbo, and wattle gum is not likely to form part of the species' diet in this forest type (Harley *et al.* 2005).

We characterised the vegetation at all currently occupied lowland territories as well as those abandoned by Leadbeater's possum since 2003 when population declines commenced, with two related aims: (i) to provide a quantitative description of the vegetation floristics and structure within occupied territories to guide habitat restoration and the identification of translocation sites; and (ii) to examine whether there were differences in vegetation structure and condition at these occupied territories compared to territories that have been abandoned. The results reported here provide the most detailed description of vegetation floristics and structure at sites occupied by the genetically-distinct lowland population of Leadbeater's possum.

Methods

Study area

This study was conducted at Yellingbo Nature Conservation Reserve (37°51′S, 145°29′E, ~110 m above sea level), which is located ~50 km east of Melbourne and supports the only extant lowland population of Leadbeater's possum (Fig. 1). The reserve comprises ~680 ha of remnant, riparian and swamp forest stretching along four watercourses, the Woori Yallock, Sheepstation, Macclesfield and Cockatoo Creeks. The area receives an average of ~1100 mm of rainfall annually, and experiences mean daily maximum temperatures ranging from 13.6°C in winter to 25.6°C in summer.

Previous research has found that within Yellingbo, the Leadbeater's possum population is confined to low-lying flood-plains with a canopy dominated by mountain swamp gum with, in places, a dense midstorey of tea-tree (*Leptospermum* spp.) or paperbark (*Melaleuca* spp.) (Harley *et al.* 2005). This forest type, and hence the possum's distribution within the reserve, was previously restricted to a narrow, linear section of flood-plain, ~6 km long and rarely exceeding 120 m in width when monitoring commenced in the mid-1990s (Harley *et al.* 2005).
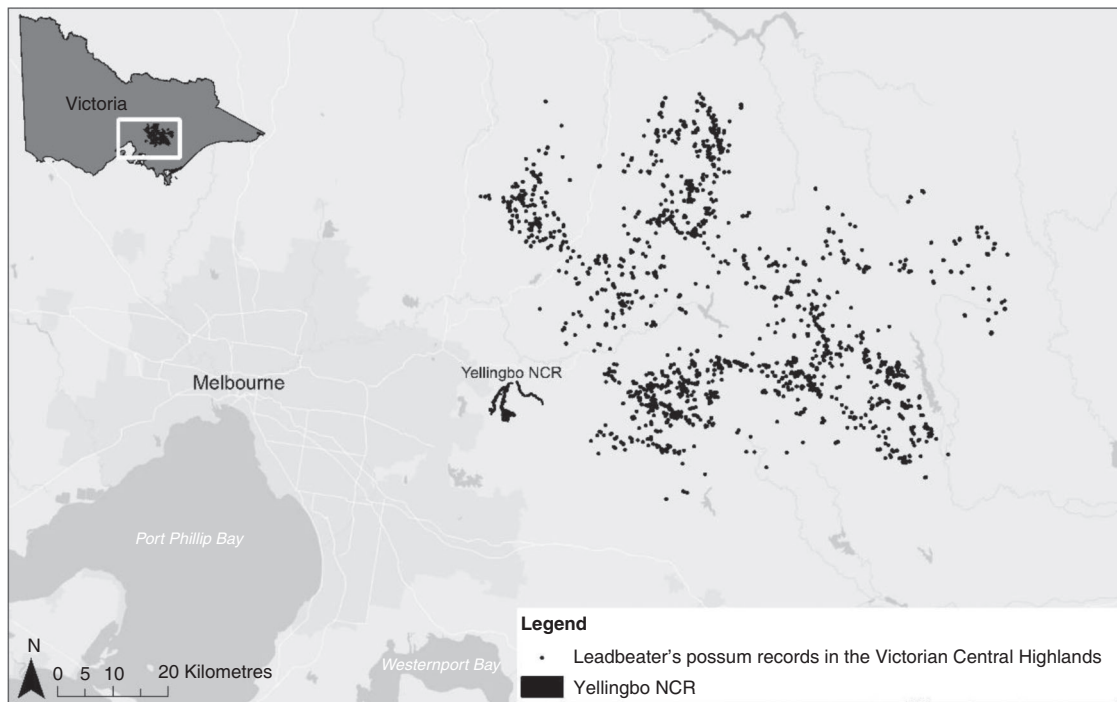
Fig. 1.   The distribution of the critically endangered Leadbeater's possum in Victoria, Australia, based on Victorian Biodiversity Atlas (VBA) records. Montane forest and sub-alpine woodland habitats within the Victorian Central Highlands comprise the vast majority of extant populations of Leadbeater's possum (VBA records indicated with small black circles). Lowland populations of Leadbeater's possum, once extensive, are now confined to a single site, Yellingbo Nature Conservation Reserve (black area).

At the time of this study, this distribution had contracted to ~4 km of this floodplain (D. Harley, unpubl. data).

Large areas (>30%) of *E. camphora* swamp forest at Yellingbo are dieback-affected, putatively due to impeded drainage and prolonged flooding/waterlogging resulting from erosion-derived sedimentation following land clearing and stream channelisation upstream of the reserve (McMahon and Franklin 1993; Greet 2016; Zacks *et al.* 2018). Drier forests dominated by messmate (*Eucalyptus obliqua*), green scentbark (*Eucalyptus fulgens*) and narrow-leaved peppermint (*Eucalyptus radiata*) occur on the well-drained slopes adjacent to the floodplain where tree cover remains. However, this is limited in extent as the reserve is surrounded by extensively cleared farmland.

Study sites

We surveyed 20 locations within the reserve, comprising all nine territories currently known to be occupied by lowland Leadbeater's possums, and 11 formerly occupied territories that have been abandoned in the years since 2003. The location and status of territories at Yellingbo were determined from annual surveys conducted since 1996 (Harley *et al.* 2005; Harley and Lill 2007; D. Harley, unpublished data). All the suitable foraging habitat in the reserve has been surveyed using a combination of camera traps, nest boxes, stag-watching and call imitation surveys (i.e. multiple survey techniques applied) and sampling is thought to comprise the total wild population.

The social organisation of Leadbeater's possum is based around a single monogamous breeding pair and multiple generations of their young (Smith 1984; Harley 2005). This group of individuals, typically referred to as a 'colony', den together each day and represent a stable social unit (Harley 2005). Each colony occupies a defined territory that does not overlap with that of neighbouring colonies (Smith 1984; Harley 2005; Harley *et al.* 2005; D. Harley, unpubl. data). For the purposes of this study, each occupied territory supports a resident colony. Abandoned territories previously supported resident colonies.

Given past difficulties in trapping Leadbeater's possum at highland locations, nest boxes were installed at Yellingbo as an alternative capture technique to support population monitoring. During the mid–late 1990s, large numbers of nest boxes (~160) were installed throughout potential foraging habitat and were readily colonised by the species (Harley 2004b). This included targeted provision of nest boxes for colonies that were identified through stag-watching and call imitation (Smith *et al.* 1989; Harley *et al.* 2005; Harley 2015). Leadbeater's possum colonies use multiple dens within their territory, periodically shifting between them, albeit the frequency at which this occurs is highly variable (Lindenmayer and Meggs 1996; Harley 2005). Multiple nest boxes (≥3) were installed for each colony that was identified, providing animals with multiple denning options. Nocturnal radio-tracking indicates that individuals typically forage within a 100-m radius of the den (D. Harley unpubl. data).

Vegetation surveys

All vegetation assessments were completed in 2019, including for abandoned territories irrespective of when they were abandoned (i.e. after 2003). This meant that the interval between site abandonment and vegetation assessment was variable. This shortcoming

arose from the lack of sustained vegetation monitoring to accompany the long-term possum population monitoring.

We assessed the floristics, structure and condition of the canopy and midstorey vegetation in which lowland Leadbeater's possums forage at Yellingbo (Harley *et al.* 2005). Vegetation sampling was conducted within a 50-m radius of preferred den locations within territories that were currently occupied or had been previously occupied and were subsequently abandoned. Preferred denning locations (nest boxes) were selected based on several criteria, including: (i) the presence of a large Leadbeater's possum nest having been constructed in the nest box, (ii) a high frequency of possum denning records in that nest box relative to neighbouring nest boxes, and (iii) for occupied territories, nest boxes that showed a recent pattern of usage. A 50-m radius was selected to cover the core area of each colony's territory, including both the movement pathways surrounding den locations and key foraging areas, whilst avoiding overlap with neighbouring colonies.

Within the 50-m radius circular plot at each territory, six random sampling locations were selected. At each sampling location, all midstorey plants were identified to species level within a subplot of radius 2.5 m, and all canopy trees identified within a subplot of radius 5 m (the larger subplot size due to the sparser distribution of canopy trees). For each woody plant surveyed, the diameter at breast height (DBH) of each stem >1.3 m in height was measured, and its status recorded as dead or alive, based on whether it supported live foliage. Also, for each canopy tree, we visually assessed crown vigour (percentage of existing branch structure supporting live foliage) to the nearest 5% (*sensu* Cunningham *et al.* 2007).

At each location we took a fish-eye lens photograph of the canopy, with the camera mounted atop a tripod at 1.3 m above the ground, to measure plant area index (PAI). All hemispherical images were processed in ImageJ using the Hemispherical 2.0 plugin. This plugin applies the minimum threshold algorithm to the blue colour plane, which has been found to be the most accurate for separating sky and vegetation (Glatthorn and Beckschäfer 2014). All binary images were then processed in Gap Light Analyser to calculate plant area index (PAI) using a consistent image mask.

Average vegetation structure and condition measures were calculated for each territory. To characterise the vegetation structure, we calculated stand density (density of stems) and basal area (cross-sectional area of woody stems), including both live and dead stems. To account for the different sized subplots used to survey canopy and midstorey plants, we first converted stem density and total basal area to a per hectare measure. For each subplot we then calculated the numbers of woody stems and basal area for canopy trees, and midstorey, separately, and combined. To characterise vegetation condition, we determined percentage live basal area (percentage of basal area accounted for by live stems), tree crown vigour and plant area index, all of which have been shown to be reliable, objective measures of floodplain stand condition (Cunningham *et al.* 2007, 2009).

Data analyses

To compare vegetation measures between occupied and abandoned territories, we used generalised linear models assuming either log-normal, beta or negative binomial error, with status (occupied or abandoned) as the sole predictor. We used logistic regression implemented under leave-one-out cross validation (Sammut and Webb 2010) to test the capacity of our vegetation measures to predict occupancy. In principle, we considered that site occupancy would vary according to stem density, live basal area, and vegetation condition (i.e. percentage live basal area, tree canopy vigour and PAI). However, we could not include all the predictors together because there were insufficient data (numbers of occupied and abandoned territories) to estimate their parameters. We thus assessed support for candidate single- or two-predictor models according to Akaike information criteria corrected for small sample size (Burnham and Anderson 2002) and the classification error rate from cross-validation. The models with two predictor variables failed to converge in the cross-validation context, thus we deemed them unsuitable.

All analyses were conducted in R (R Core Team 2020). Generalised linear models of vegetation measures were fit using the *glmmTMB* package (Brooks *et al.* 2017) for ease of implementation of models assuming beta and negative binomial distributions. Cross validation was implemented using the *rsample* (Kuhn and Wickham 2019) and *broom* (Robinson and Hayes 2019) packages. All data and code used for analyses are freely available via an Open Science Foundation project page: osf.io/ecfht.

Results

Floristic composition

Eucalyptus camphora was by far the dominant canopy tree across both occupied and abandoned territories. All other canopy trees combined, *E. fulgens*, *E. obliqua*, *E. ovata* and *E. radiata*, comprised <16% of all trees recorded (Table 1). Greater numbers of *E. camphora* trees were recorded at occupied than abandoned territories (785 c.f. 538 stems/ha; Table 1). Furthermore, a mean of 78% of *E. camphora* trees recorded at occupied territories were alive compared to 50% at abandoned territories.

Melaleuca squarrosa accounted for more than half (53%) of all midstorey trees and shrubs recorded across all territories. The second most common midstorey species was *M. ericifolia* (18%), with *Coprosma quadrifida*, *Kunzea leptospermoides*, *Leptospermum scoparium* and *L. lanigerum* also commonly occurring, but typically at lower densities. Similar percentages of midstorey plants recorded were alive at occupied and abandoned territories. However, stem densities of the dominant *Melaleuca* spp. were several times greater at occupied territories than abandoned territories, with this difference typically attributable to dense paperbark thickets (*M. squarrosa*, and sometimes *M. ericifolia*; Table 1).

Vegetation structure and condition

Occupied territories had 2.6 times higher mean total stem densities (canopy and midstorey plants combined) per hectare compared with abandoned territories: fitted means 11 414 stems/ha (95% CI: 8039–16 206) c.f. 4389 stems/ha (2696–7143); Fig. 2*a*. The estimated mean density of canopy trees, 892 stems/ha (631–1231) c.f. 728 stems/ha (515–1031); and midstorey trees and shrubs, 9765 stems/ha (4569–20 869) c.f. 4279 stems/ha (1730–10 589) were both higher in occupied than abandoned

Table 1.   Floristic composition of occupied and abandoned territories

Mean number and range of stems per hectare and percentage of stems recorded that were alive for canopy trees and midstorey trees and shrubs within territories that were either occupied ($n = 9$) or abandoned ($n = 11$) by lowland Leadbeater's possums at Yellingbo Nature Conservation Reserve

Species	Mean stems/ha (range)		Percentage alive	
	Occupied	Abandoned	Occupied	Abandoned
	Canopy			
Eucalyptus camphora	785 (149–1613)	538 (0–1464)	78	50
Eucalyptus fulgens	45 (0–149)	48 (0–276)	88	91
Eucalyptus obliqua	0	2 (0–21)	–	100
Eucalyptus ovata	0	19 (0–149)	–	96
Eucalyptus radiata	64 (0–573)	54 (0–382)	100	58
	Midstorey			
Acacia dealbata	0	9 (0–85)	–	100
Acacia melanoxylon	0	424 (0–1698)	–	75
Allocasuarina sp.	11 (0–85)	0	100	–
Cassinia aculeata	0	19 (0–170)	–	100
Coprosma quadrifida	1050 (0–3650)	924 (0–6706)	98	91
Kunzea leptospermoides	244 (0–1273)	632 (0–5687)	100	91
Leptospermum lanigerum	117 (0–424)	198 (0–1358)	100	73
Leptospermum scoparium	32 (0–255)	358 (0–1698)	100	27
Melaleuca ericifolia	2493 (0–12 308)	434 (0–3905)	93	98
Melaleuca squarrosa	7629 (0–23 937)	981 (0–6366)	66	66

territories, but with substantially overlapping confidence intervals (Fig. 2*b, c*).

The disparity in mean stems per hectare did not translate into clear differences in average live basal area. While occupied territories tended toward greater average live basal area of canopy trees, 25 m^2/ha (95% CI: $\pm$ 8) c.f. 17 m^2/ha ($\pm$7), midstorey trees and shrubs, 10 m^2/ha ($\pm$6.3) c.f. 7 m^2/ha ($\pm$5.6), and canopy and midstorey plants combined, 35 m^2/ha ($\pm$10.6) c.f. 24 m^2/ha ($\pm$9.6), than abandoned territories, the confidence intervals around the fitted means overlapped considerably in each case (Fig. 2*d–f*).

Vegetation condition at occupied territories compared to abandoned territories was higher on average (Fig. 2*g–i*). Average crown vigour of canopy trees in occupied territories was around 2.4 times higher, 52% (95% CI: 38–66%) c.f. 22% (14–35%). Similarly, the average proportion live basal area, 77% (63–87%) c.f. 55% (41–69%) was significantly higher in occupied territories. Plant area index, 79% (69–87%) c.f. 66% (56–75%), was higher on average but with considerable overlap in confidence intervals.

Predictors of occupancy

Logistic models of lowland Leadbeater's possum occupancy which included either combined stem density (AICc = 21.31), midstorey stem density (22.59) or average tree crown vigour (23.00) were equally the most plausible single-predictor models (i.e. had AICc values <2 different; null model AICc = 29.75) and all were statistically clear predictors ($P < 0.05$). Combined stem density was the best predictor of occupancy with an error rate of 0.2, so it correctly predicted occupancy 80% of the time. Models using midstorey stem density and crown vigour were equally plausible on AICc values but had less favourable cross validation error rates of 0.25. All territories surveyed with >10 000 stems/ha were occupied, whereas territories with a mean crown vigour of <36% were all abandoned (Fig. 3).

Discussion

Our study presents the first quantitative data detailing the vegetation at sites inhabited by lowland Leadbeater's possums. There were clear differences in the stem density and condition of vegetation in territories currently occupied by the species at Yellingbo compared to territories that have been abandoned. Abandoned locations had relatively poor stand condition indicated by lower percentage live basal area, tree crown vigour and plant area index scores. Currently occupied territories had higher stem densities, particularly of midstorey plants, with more than three times the number of midstorey stems at occupied territories. Our findings suggest that high stem density is a critical component of lowland Leadbeater's possum habitat, and stem density alone was able to predict occupancy *vis-à-vis* abandoned sites with a high (80%) degree of accuracy. The functional role of high stem density is likely to be twofold, both facilitating the possum's arboreal movements through the forest and increasing the substrate available for foraging.

The key finding of this study, that lowland Leadbeater's possums occupy sites supporting high stem densities, corresponds with extensive nocturnal observations of the possum's habitat use made at the study locality over two decades (D. Harley, pers. obs). Given that the possum is unable to glide and rarely descends to the ground, dense vegetation structure greatly facilitates the movement of this species through the forest. This finding concurs with our broader ecological understanding of this species from highland montane ash forest, where the presence and abundance Leadbeater's possum is positively correlated with basal area of *Acacia* spp. in the midstorey (Smith *et al.* 1985; Smith and Lindenmayer 1988; Lindenmayer *et al.* 1991*a*). Investigations are underway to see if this finding also applies to populations of Leadbeater's possum inhabiting subalpine woodland.
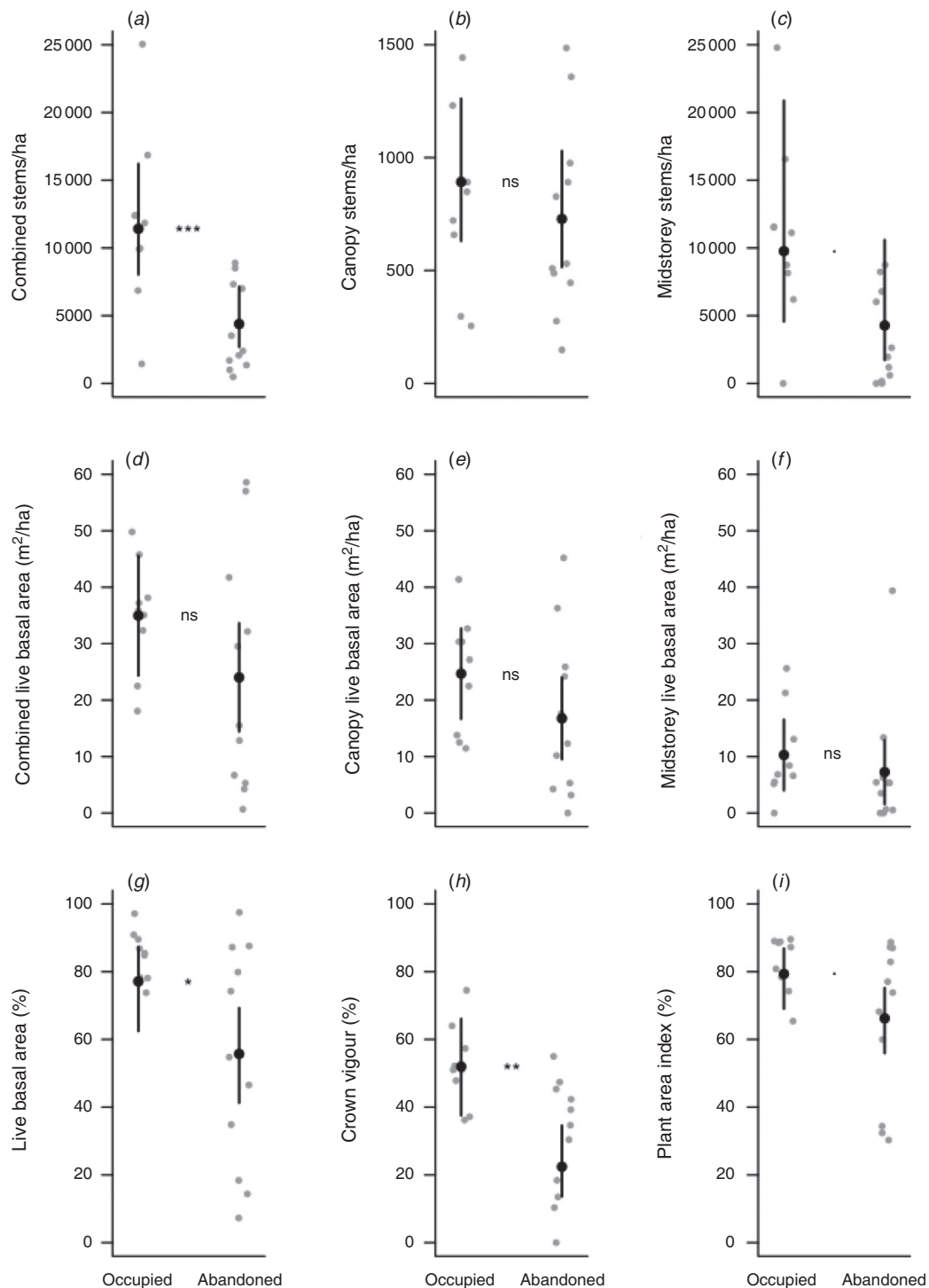
Fig. 2. Comparisons of stem density (*a–c*), live basal area (*d–f*) and vegetation condition (*g–i*) between territories occupied (*n* = 9) and abandoned (*n* = 11 sites) by lowland Leadbeater's possums at Yellingbo Nature Conservation Reserve. Jittered grey circles indicate the observed means at the site level, and superimposed are fitted group means and their 95% confidence intervals. The *P*-value for the difference in means is indicated on each plot according to the following thresholds: 0> *** <0.001> ** <0.01> * <0.05> · <0.1> ns <1.

Previous studies conducted in montane ash forest occupied by highland populations of Leadbeater's possum indicate that *Acacia* spp. provide an important food resource and movement pathways for the possum (Smith 1984; Lindenmayer *et al.* 1991*a*). *Acacia* spp. are virtually absent from the floodplain forest inhabited by lowland Leadbeater's possums at Yellingbo,
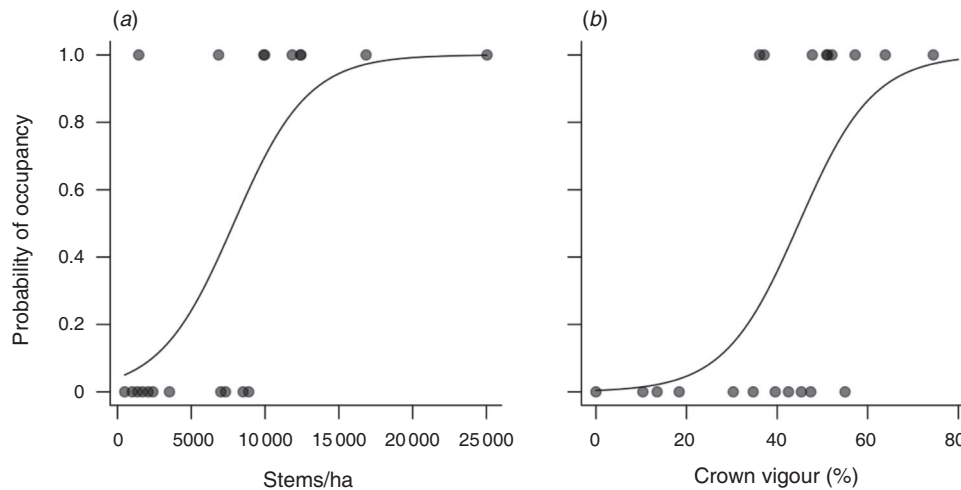
Fig. 3.   Prediction curves from logistic regression models with (*a*) combined canopy and midstorey stem density or (*b*) tree crown vigour as sole predictors of occupancy by lowland Leadbeater's possum. Grey translucent circles represent observed data.

indicating that the species does not rely on *Acacia* spp. as a food resource in lowland forests. Many of the occupied territories at Yellingbo are characterised by high stem density of *Melaleuca* spp. in the midstorey, and it is likely that they provide important foraging substrate (Harley *et al.* 2005). A consistent pattern observed across lowland and highland sites within the possum's range is that high rates of site occupancy coincide with the presence of dense stands of *Acacia* spp., *Melaleuca* spp., or *Leptospermum* spp. in the midstorey (Lindenmayer *et al.* 1991*a*; D. Harley, unpubl. data), suggesting these plants may provide an important source of exudates and/or invertebrate prey. Similarly, Goldingay *et al.* (2020) observed higher rates of nest box occupancy by the brush-tailed phascogale (*Phascogale tapoatafa*) in areas with greater stem densities, potentially reflecting the increased area of foraging substrate.

The differences in vegetation condition between occupied and abandoned territories at Yellingbo suggest that deteriorating vegetation condition has been a major driver of Leadbeater's possum population decline there. The majority of the 180 ha floodplain at Yellingbo Nature Conservation Reserve does not currently provide suitable habitat for foraging and movement by lowland Leadbeater's possum owing to the open vegetation structure and/or poor stand condition (Harley 2016). The possum's area of occupancy in the reserve has contracted by more than half, and its population size has declined by ~70% since 2003 (D. Harley, unpubl. data). In this forest type, nest boxes can provide adequate den sites (Harley 2004*b*), so suitable habitat is largely determined by the structural density and health of the canopy and midstorey vegetation to support foraging and movement. Quantifying food availability, as a means of determining site quality and carrying capacity, has not yet been possible owing to uncertainty surrounding specific dietary items and their relative contributions in lowland swamp forest, coupled with difficulties in reliably measuring the production of certain exudates such as honeydew. In the absence of such resolution, the floristic composition and stand density are considered to provide suitable surrogates to inform assessments

of site suitability for Leadbeater's possum. Previous research on another critically endangered species at Yellingbo, the helmeted honeyeater (*Lichenostomus melanops cassidix*), found similar preferences for structurally complex forests characterised by high stem density (Pearce *et al.* 1994).

One of the major threats to forest condition at Yellingbo is altered flooding regimes (Greet 2016; Zacks *et al.* 2018). Within the reserve, progressive dieback of *E. camphora* has been documented since the early 1990s at sites now subject to near permanent inundation and waterlogging (McMahon and Franklin 1993; Greet 2016). Many of the abandoned possum territories that we surveyed were in or adjacent to these dieback-affected areas and were dominated by standing and fallen dead trees that presumably provide little or no exudate food resources for possums. Conversely, in other areas of the reserve, floodplains have been disengaged via levee banks or stream channelisation, and now flood infrequently. At these sites, reduced flooding appears to be promoting a more open forest structure less suitable for Leadbeater's possum (Harley 2016). This may be partly attributable to reduced swamp forest regeneration in the absence of flood disturbance.

Implications for lowland Leadbeater's possum conservation

The Leadbeater's possum population at Yellingbo is the last remnant of a once extensive lowland range for this species. There are no detailed habitat descriptions from other lowland sites historically inhabited by Leadbeater's possum, and notably, *E. camphora* is absent from these locations. Based on remnant vegetation, these are considered likely to have supported a canopy of swamp gum (*E. ovata*) with a dense midstorey of *M. ericifolia* (Yugovic and Mitchell 2006), thus bearing strong similarities to the habitat currently occupied by the possum at Yellingbo. The current lack of high-quality swamp forest dominated by *E. camphora* and/or *E. ovata* and *Melaleuca* shrub thickets due to historic clearing is the key impediment to recovering populations of lowland Leadbeater's possum.

Habitat restoration, with the specific intent of increasing the area of available habitat for the possum and a sympatric threatened species with overlapping habitat requirements, the helmeted honeyeater, is currently underway at sites within Yellingbo Nature Conservation Reserve and several locations beyond Yellingbo. This study provides estimates of stem densities that can inform revegetation programmes aiming to provide suitable habitat for the possum at lowland sites. Our results are also being used to inform the selection of translocation sites for this critically endangered species, with an emphasis on stem density.

Based on vegetation dynamics and trajectory, the extent and condition of habitat available for Leadbeater's possums at Yellingbo are likely to continue to decline without appropriate intervention. Sites that remain occupied by the possum may be at an earlier stage of decline than those that have become abandoned. Interventions to reinstate appropriate flooding regimes are likely required to arrest further dieback of swamp forests and reconnect disengaged floodplain areas to promote vegetation regeneration. Hydrological interventions led by Melbourne Water are currently underway to assess the potential for such actions to promote habitat recovery. We suggest regular but variable flooding is essential for maintaining vegetation health and appropriate habitat structure for swamp-adapted fauna such as the lowland Leadbeater's possum (Greet *et al.* 2020).

Urgent interventions are also required to address the small population size and loss of genetic diversity. Evidence of inbreeding depression in this population has recently been documented (Zilko *et al.* 2020). A genetic rescue strategy is currently being implemented, whereby mixed pairs of lowland and highland individuals will be established in captivity and subsequently translocated to the wild in order to achieve outbreeding.

Our case study of Leadbeater's possum at Yellingbo exemplifies limitations that often beset research on critically endangered wildlife species, including (1) restricted sample sizes and study locations (in this case, there is only one study location available given a single extant lowland population), (2) data collection that commenced after the population decline commenced, and (3) vegetation data from a single point in time. The last remaining occupied habitat may not be a good guide to a species' realizable niche (Kerley *et al.* 2012; Simmonds *et al.* 2017; Lentini *et al.* 2018), and it is possible that Leadbeater's possums occupied a broader suite of lowland vegetation associations previously, however, appropriate historic baseline data are lacking (e.g. McClenachan *et al.* 2012).

Despite the inherent limitations of our study, we consider the data presented here provide insights into the key vegetation variables influencing site occupancy by Leadbeater's possum at this location, information that should be useful to managers. The alternative is to make management decisions in the absence of such data, which is not an outcome we support. Rather we encourage threatened species programmes to invest in well-designed monitoring programmes and use insights from those data to inform decision-making. Initiating the collection of habitat condition data early in any recovery programme is strongly recommended.

This study also highlights a more general management challenge faced by conservation practitioners – simply reserving land for conservation will not always ensure the persistence of threatened species (e.g. Françoso *et al.* 2015). Active management may also be necessary to maintain or restore ecosystem structure and function and/or address threatening processes (e.g. climate change, altered hydrology, novel predators, browsing pressure).

Conclusion

Our findings highlight that vegetation structure and condition are strongly associated with territory occupancy by lowland Leadbeater's possum. The limited and contracting extent of high-quality lowland habitat (i.e. characterised by dense, healthy vegetation) is the major threatening process for lowland Leadbeater's possum, historically at a landscape scale and currently within Yellingbo Nature Conservation Reserve. The extent of suitable habitat is so restricted that extinction of Leadbeater's possum from lowland habitats, and the loss of this unique gene pool, is highly likely without effective management intervention.

Conflict of interest

The authors declare no conflicts of interest.

References

Ashman, K. R., and Watchorn, D. J. (2019). Quantifying landscape change as a consequence of plantation forestry expansion: a case study of the Koala Zone in south-west Victoria. *Australian Forestry* **82**, 116–122. doi:10.1080/00049158.2019.1621728

Bennett, A. F., and Saunders, D. A. (2010). Conservation Biology for All. *Conservation biology for all* **93**, 1544–1550.

Brooks, E., Kristensen, K., Benthem, J., Magnusson, A., Berg, W., Nielsen, A., Skaug, J., Mächler, M., and Bolker, M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal* **9**, 378–400. doi:10.32614/RJ-2017-066

Burnham, K. P., and Anderson, D. R. (2002). 'Model selection and multimodel inference: a practical information-theoretic approach', 2nd edn. (Springer-Verlag: New York).

Chaudhary, A., Pfister, S., and Hellweg, S. (2016). Spatially explicit analysis of biodiversity loss due to global agriculture, pasture and forest land use from a producer and consumer perspective. *Environmental Science and Technology* **50**, 3928–3936. doi:10.1021/ACS.EST.5B06153

Cunningham, S. C., Read, J., Baker, P. J., and Mac Nally, R. (2007). Quantitative assessment of stand condition and its relationship to physiological stress in stands of *Eucalyptus camaldulensis* (Myrtaceae). *Australian Journal of Botany* **55**, 692–699. doi:10.1071/BT07031

Cunningham, S. C., Mac Nally, R., Read, J., Baker, P. J., White, M., Thomson, J. R., and Griffioen, P. (2009). A robust technique for mapping vegetation condition across a major river system. *Ecosystems* **12**, 207–219. doi:10.1007/S10021-008-9218-0

DEPI (2014). Action statement no. 62: Leadbeater's possum *Gymnobelideus leadbeateri*. (Department of Environment and Primary Industries: Melbourne).

Françoso, R. D., Brandão, R., Nogueira, C. C., Salmona, Y. B., Machado, R. B., and Colli, G. R. (2015). Habitat loss and the effectiveness of protected areas in the Cerrado Biodiversity Hotspot. *Natureza and Conservação* **13**, 35–40. doi:10.1016/J.NCON.2015.04.001

Glatthorn, J., and Beckschäfer, P. (2014). Standardizing the protocol for hemispherical photographs: accuracy assessment of binarization algorithms. *PloS One* **9**, e111924. doi:10.1371/JOURNAL.PONE.0111924

Goldingay, R. L., and Jackson, S. M. (2004). A review of the ecology of the Australian Petauridae. In 'The biology of Australian possums and gliders'. (Eds R. Goldingay and S. Jackson) pp. 376–400. (Surrey Beatty & Sons: Sydney)

Goldingay, R. L., Quin, D. G., Talamo, O., and Mentiplay-Smith, J. (2020). Nest box revealed habitat preferences of arboreal mammals in box-ironbark forest. *Ecological Management and Restoration* **21**, 131–142. doi:10.1111/EMR.12412

Greet, J. (2015). The marked flooding tolerance of seedlings of a threatened swamp gum: implications for the restoration of critical wetland forests. *Australian Journal of Botany* **63**, 669–678. doi:10.1071/BT15128

Greet, J., Fischer, S., and Russell, K. (2020). Longer duration flooding reduces the growth and sexual reproductive efforts of a keystone wetland tree species. *Wetlands Ecology and Management* **28**, 655–666. doi:10.1007/S11273-020-09738-9

Hansen, B. D., and Taylor, A. C. (2008). Isolated remnant or recent introduction? Estimating the provenance of Yellingbo Leadbeater's possums by genetic analysis and bottleneck simulation. *Molecular Ecology* **17**, 4039–4052. doi:10.1111/J.1365-294X.2008.03900.X

Hansen, B. D., Harley, D. K. P., Lindenmayer, D. B., and Taylor, A. C. (2009). Population genetic analysis reveals a long-term decline of a threatened endemic Australian marsupial. *Molecular Ecology* **18**, 3346–3362. doi:10.1111/J.1365-294X.2009.04269.X

Harley, D. (2015). The use of call imitation to establish territory occupancy by Leadbeater's possum (*Gymnobelideus leadbeateri*. *Australian Mammalogy* **37**, 116–119. doi:10.1071/AM14014

Harley, D. (2016). An overview of actions to conserve Leadbeater's possum '*Gymnobelideus leadbeateri*'. *The Victorian Naturalist* **133**, 85.

Harley, D. K. P. (2004a). A review of recent records of Leadbeater's possum *Gymnobelideus leadbeateri*. In 'The biology of Australian possums and gliders'. pp. 330–338. (Surrey Beatty & Sons: Sydney).

Harley, D. K. P. (2004b). Patterns of nest box use by Leadbeater's possum *Gymnobelideus leadbeateri*: applications to research and conservation. In 'The biology of Australian possums and gliders'. pp. 318–329. (Surrey Beatty & Sons: Sydney).

Harley, D. K. P. (2005). The life history and conservation of Leadbeater's possum (*Gymnobelideus leadbeateri*) in lowland swamp forest. PhD thesis. Monash University, Melbourne.

Harley, D. K. P., and Lill, A. (2007). Reproduction in a population of the endangered Leadbeater's possum inhabiting lowland swamp forest. *Journal of Zoology* **272**, 451–457. doi:10.1111/JZO.2007.272.ISSUE-4

Harley, D. K. P., Worley, M. A., and Harley, T. K. (2005). The distribution and abundance of Leadbeater?s possum *Gymnobelideus leadbeateri* in lowland swamp forest at Yellingbo Nature Conservation Reserve. *Australian Mammalogy* **27**, 7–15. doi:10.1071/AM05007

Henle, K., Davies, K. F., Kleyer, M., Margules, C., and Settele, J. (2004). Predictors of species sensitivity to fragmentation. *Biodiversity and Conservation* **13**, 207–251. doi:10.1023/B:BIOC.0000004319.91643.9E

Kerley, G. I. H., Kowalczyk, R., and Cromsigt, J. P. G. M. (2012). Conservation implications of the refugee species concept and the European bison: king of the forest or refugee in a marginal habitat?. *Ecography* **35**, 519–529. doi:10.1111/J.1600-0587.2011.07146.X

Kuhn, M., and Wickham, H. (2019). rsample: general resampling infrastructure. R package version 0.0.4. Available at https://CRAN.R-project.org/package=rsample

Lentini, P. E., Stirnemann, I. A., Stojanovic, D., Worthy, T. H., and Stein, J. A. (2018). Using fossil records to inform reintroduction of the kakapo as a refugee species. *Biological Conservation* **217**, 157–165. doi:10.1016/J.BIOCON.2017.10.027

Lindenmayer, D., and Meggs, R. (1996). Use of den trees by Leadbeater's possum (*Gymnobelideus Leadbeateri*). *Australian Journal of Zoology* **44**, 625–638. doi:10.1071/ZO9960625

Lindenmayer, D. B., and Sato, C. (2018). Hidden collapse is driven by fire and logging in a socioecological forest ecosystem. *Proceedings of the National Academy of Sciences* **115**, 5181–5186. doi:10.1073/PNAS.1721738115

Lindenmayer, D. B., Cunningham, R. B., Tanton, M. T., Nix, H. A., and Smith, A. P. (1991a). The conservation of arboreal marsupials in the montane ash forests of the Central Highlands of Victoria, south-east Australia: III. The habitat requirements of leadbeater's possum *Gymnobelideus leadbeateri* and models of the diversity and abundance of arboreal marsupials. *Biological Conservation* **56**, 295–315. doi:10.1016/0006-3207(91)90063-F

Lindenmayer, D. B., Cunningham, R. B., Tanton, M. T., Smith, A. P., and Nix, H. A. (1991b). Characteristics of hollow-bearing trees occupied by arboreal marsupials in the montane ash forests of the Central Highlands of Victoria, south-east Australia. *Forest Ecology and Management* **40**, 289–308. doi:10.1016/0378-1127(91)90047-Y

Lindenmayer, D. B., Blanchard, W., McBurney, L., Blair, D., Banks, S., Likens, G. E., Franklin, J. F., Laurance, W. F., Stein, J. A. R., and Gibbons, P. (2012). Interacting factors driving a major loss of large trees with cavities in a forest ecosystem. *PloS one* **7**, e41864. doi:10.1371/JOURNAL.PONE.0041864

Lindenmayer, D. B., Foster, C. N., Westgate, M. J., Scheele, B. C., and Blanchard, W. (2020). Managing interacting disturbances: lessons from a case study in Australian forests. *Journal of Applied Ecology* **57**, 1711–1716. doi:10.1111/JPE.V57.9

McClenachan, L., Ferretti, F., and Baum, J. K. (2012). From archives to conservation: why historical data are needed to set baselines for marine animals and ecosystems. *Conservation Letters* **5**, 349–359. doi:10.1111/J.1755-263X.2012.00253.X

McMahon, A. R. G., and Franklin, D. C. (1993). The significance of mountain swap gum for helmeted honeyeater populations in the Yarra Valley. *The Victorian Naturalist* **110**, 230–237.

McCoy, F. (1867). On a new genus of Phalanger. *Annals and Magazine of Natural History* **20**, 287–288. doi:10.1080/00222936708694132

Pearce, J., Burgman, M., and Franklin, D. (1994). Habitat selection by helmeted honeyeaters. *Wildlife Research* **21**, 53–63. doi:10.1071/WR9940053

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at https://www.R-project.org/

Robinson, D., and Hayes, A. (2019). broom: convert statistical analysis objects into tidy tibbles package version 0.5.2. Available at https://CRAN.R-project.org/package=broom

Sammut, C., and Webb, G. I. (2010). Leave-one-out cross-validation. In 'Encyclopedia of machine learning'. pp. 600–601. (Springer US: Boston, MA)

Simmonds, J. S., van Rensburg, B. J., and Maron, M. (2017). Non-random patterns of vegetation clearing and potential biases in studies of habitat area effects. *Landscape Ecology* **32**, 729–743. doi:10.1007/S10980-016-0482-7

Smith, A. (1984). Diet of Leadbeaters possum, *Gymnobelideus leadbeateri* (Marsupialia). *Wildlife Research* **11**, 265–273. doi:10.1071/WR9840265

Smith, A., and Lindenmayer, D. (1988). Tree hollow requirements of Leadbeater's possum and other possums and gliders in timber production ash forests of the Victorian central highlands. *Wildlife Research* **15**, 347–362. doi:10.1071/WR9880347

Smith, A., Lindenmayer, D., Begg, R., Macfarlane, M., Seebeck, J., and Suckling, G. (1989). Evaluation of the stag-watching technique for census of possums and gliders in tall open forest. *Wildlife Research* **16**, 575–580. doi:10.1071/WR9890575

Smith, A. P., Lindenmayer, D., and Suckling, G. (1985). The ecology and management of Leadbeater's possum. Research report to World Wildlife Fund, University of New England, Armidale, NSW.

Yugovic, J., and Mitchell, S. (2006). Ecological review of the Koo-Wee-Rup swamp and associated grasslands. *The Victorian Naturalist* **123**, 323.

Zacks, G., Greet, J., Walsh, C. J., and Raulings, E. (2018). The flooding tolerance of two critical habitat-forming wetland shrubs, *Leptospermum lanigerum* and *Melaleuca squarrosa*, at different life history stages. *Australian Journal of Botany* **66**, 500–510. doi:10.1071/BT18039

Zilko, J. P., Harley, D., Hansen, B., Pavlova, A., and Sunnucks, P. (2020). Accounting for cryptic population substructure enhances detection of inbreeding depression with genomic inbreeding coefficients: an example from a critically endangered marsupial. *Molecular Ecology*. doi:10.1111/MEC.15540