Habitat characteristics of a threatened arboreal marsupial and its resource use in a degraded landscape: the brush-tailed phascogale (*Phascogale tapoatafa tapoatafa*) in central Victoria, Australia

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Abstract

   Context. Habitat loss and degradation has contributed significantly to the decline of many species worldwide. To address this loss, we first require a comprehensive understanding of habitat requirements and resource-use patterns of the species under threat.

   Aims. The study aimed to quantify variation in the habitat of a species threatened by habitat loss and degradation, the brush-tailed phascogale (*Phascogale tapoatafa tapoatafa*), by measuring several physical characteristics of trees and ground cover, as well as to determine potential foraging resource preferences using abundance data from a long-term monitoring study.

   Methods. Phascogale monitoring surveys were conducted over a 13-year period from 2000 to 2012. Habitat variables characterising tree communities, ground cover and coarse woody debris were used to develop explanatory models of phascogale abundance at the site scale. Tree species preference by foraging phascogales was evaluated by comparing usage (trees on which they were captured) and availability.

   Key results. The highest overall animal abundance was at sites characterised by associations of red stringybark, red box, grey box and broad-leaved and narrow-leaved peppermints. At these sites, red stringybark and grey box trees were of small diameter and tended to have small hollows. These sites also had low average tree height, low grass and/or herb and shrub cover and low volumes of coarse woody debris. From a resource-use perspective, phascogales foraged preferentially on certain species of *Eucalyptus*.

   Conclusions. Our study suggests that phascogale abundance is highly spatially and temporally variable, most likely as a response to heterogeneity in habitat and foraging resources operating at a range of spatial scales.

   Implications. This study has provided new information concerning spatial patterns of phascogale abundance and resource use within a forested area in central Victoria that has been subjected to multiple disturbances. Currently, the composition and age structure of tree communities and ground habitats are a response to severe disturbance due to past mining and harvesting activities. Successful conservation of this threatened species could be enhanced through active management of this forest to maintain the ongoing supply of nesting hollows and foraging resources.

Additional keywords: arboreal habitat, coarse woody debris, resource use, species abundance.

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Introduction

Land-use change and associated environmental degradation is a major driver of habitat loss globally, with rates likely to increase under climate change (Jantz *et al.* 2015; Segan *et al.* 2016). Habitat loss is arguably one of the most significant factors contributing to native species decline in Australia in recent times, particularly for hollow-using species (Gibbons and Lindenmayer 2002). Habitat loss and degradation is believed

to have contributed significantly to the decline of the brush-tailed phascogale (*Phascogale tapoatafa tapoatafa* Meyer, 1793) (Cuttle 1982; Menkhorst 1995; Soderquist 1995*a*; Strahan 1995), and its previously wide distribution has now contracted to drier Box and Ironbark forests of central and north-eastern Victoria (Traill and Coates 1993; van der Ree *et al.* 2001). Areas that this species previously inhabited have undergone extensive clearing and fragmentation, with removal of approximately half

of the suitable habitat (Woodgate and Black 1988; Menkhorst 1995; Robinson and Traill 1996). Many areas of remaining habitat have been subject to mining, grazing, intensive logging and firewood collection, culminating in forests and woodlands that are now dominated by small trees with limited hollow development (Robinson and Traill 1996; Soderquist 1999). As a consequence, the brush-tailed phascogale is listed in Victoria under the *Fauna and Flora Guarantee Act* 1988 with Conservation Status as Vulnerable (Advisory List), and considered to be Vulnerable in New South Wales under the *Threatened Species Conservation Act* 1995 and Western Australia under the *Western Australian Wildlife Conservation Act* 1950.

The brush-tailed phascogale (hereafter referred to as phascogale) is a small insectivorous dasyurid marsupial. It is an arboreal animal that spends 80–90% of its foraging time in trees using the base, trunk and all major limbs of the tree (Traill and Coates 1993; Soderquist 1995b; Scarff *et al.* 1998; Scarff and Bradley 2006), with occasional foraging on the ground around fallen logs (Traill and Coates 1993; Scarff *et al.* 1998; Lunt 1988; Scarff and Bradley 2006). As with any other native species, the phascogale has specific habitat requirements for shelter, nesting and feeding activities. This species typically prefers smaller sized den entrance hollows ranging from 24–100 mm in diameter (Soderquist 1993a, 1993b; Traill and Coates 1993; Rhind 1996), although they also utilise hollows with larger entrances, particularly during the breeding period. Cavity openings with smaller dimensions may limit the possibility for predation (Dickman 1991). Abundance of phascogales has been associated with trees displaying thicker bark and several studies have suggested that trees with diameters averaging 80 cm are preferred when they are available (van der Ree *et al.* 2001; Scarff and Bradley 2006), but there is no quantitative evidence to support this hypothesis. Den trees are typically from a range of species (including dead trees) according to their availability in the area (Scarff and Bradley 2006), but it is not known if phascogales prefer one tree species over another for denning, nesting or foraging.

Although the phascogale has been recorded as foraging on the ground, there is little evidence that it conforms to the expected patterns of ground habitat use as demonstrated by other species of dasyurid. For example, from what is known about species of *Antechinus* (Barnett *et al.* 1978; Moro 1991; Dickman 1991; Bennett 1993; Catling and Burt 1995; McElhinny *et al.* 2006b), it would be expected that the phascogale would exhibit a preference for a complex layer of vegetation with a deep and well established litter layer. Anecdotal evidence suggests otherwise, with known phascogale habitat consisting of a well-established litter layer with scattered tussocks of plants rather than continuous vegetation cover (Menkhorst and Gilmore 1979; Cuttle 1982; Tzaros 2005; Scarff and Bradley 2006). These studies have not quantified habitat resources in relation to the distribution or density of phascogales. There is also a lack of information concerning other ground cover variables, such as the abundance of coarse woody debris, which may be of importance to phascogales.

The need for effective management of forests to maintain suitable habitat, including hollow-bearing trees, and conserve this species as well as other threatened arboreal marsupials has never been more apparent. One of the objectives of the Action

Statement developed for the phascogale (Humphries and Seebeck 2003) was to establish a long-term (10+ years) monitoring study of populations to determine changes in distribution and density and to provide correlative information on habitat change and population vulnerability. As part of a larger study addressing this objective, phascogale populations have been monitored annually in the Hepburn–Wombat State Forest region since 2000 (see Holland *et al.* 2012). These surveys have provided valuable information about population size; however, there has been no accompanying study of habitat requirements or resource use of phascogales in this region. Following the recommendations of Holland *et al.* (2012), this study aimed to quantify the variation in habitat in the area included in monitoring surveys by examining: (1) the arboreal habitat – by measuring several physical characteristics of trees; (2) the terrestrial habitat – by measuring various features describing the ground cover; and (3) potential foraging resource preference. Using capture data from 2000 to 2012, this study develops explanatory models relating phascogale capture success to measured habitat variables in order to better describe habitat requirements and provide insight into resource use.

Materials and methods

Study area

The study area is located at the northern end of the Wombat State Forest and an adjoining section of Hepburn Regional Park in central Victoria (37°31′S, 114°9′E), and represents the 'Hepburn' monitoring site described in Holland *et al.* (2012). The landscape is distinguished by steep undulating terrain, with numerous ephemeral creeks and several man-made dams throughout the area. The mean air temperature reaches a maximum of 28.5°C in January (summer) and a minimum of 2.0°C in July (winter), and annual rainfall is 581 mm (data for Clunes; sourced from the Bureau of Meteorology (2014) (http://www.bom.gov.au/climate/data/). The majority of the vegetation in this area is Heathy Dry Forest Ecological Vegetation Class (EVC), but there are smaller areas of Grassy Dry Forest EVC and Valley Grassy Forest EVC. The dominant overstorey tree species include red stringybark (*Eucalyptus macrorhyncha* F.Muell. ex Benth.), red box (*E. polyanthemos* Schauer), broad-leaved peppermint (*E. dives* Schauer), long-leaved box (*E. goniocalyx* F.Muell. ex Miq.), grey box (*E. microcarpa* Maiden) and messmate stringybark (*E. obliqua* L'Hér.). The understorey vegetation is composed of sparse shrubs and grass tussocks.

Animal surveys

In 2000, five access tracks within the study area were selected for the first phascogale monitoring survey (see Holland *et al.* 2012). In total, 35 'trap stations' were established along these tracks (Seamond and Welcome Tracks with four stations each, Blowhole Track with five trap stations and Yandoit and Excelsior Tracks with eight and 14 trap stations respectively). In 2003, four additional stations were added to the Yandoit Track (Yandoit Track North), bringing the total to 39 trap stations. On each track, trap stations were 300 m apart with two traps deployed at each station on opposite sides of the track and at a distance of 50 m from the track (see Fig. 1).

Phascogale monitoring surveys were conducted in late March to early April of each year and data for 2000–12 are included here
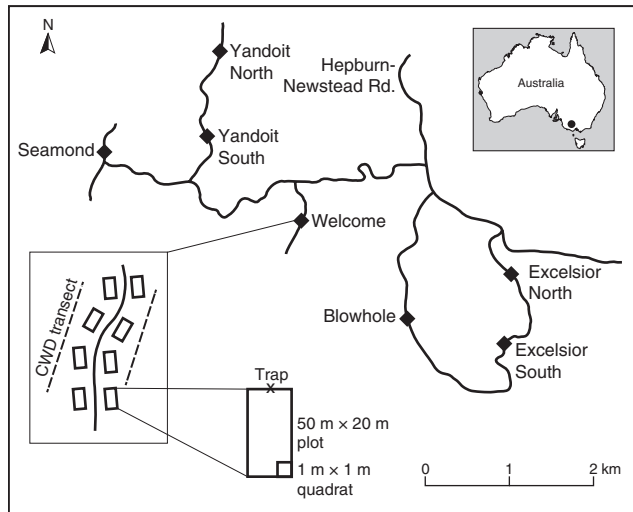
Fig. 1. The layout of the study area and location in Victoria (inset). Diamonds indicate the midpoint of each site. At each of eight trap points within each site, trees were assessed with a 50 m × 20 m plot, with 14 1 m × 1 m quadrats nested within the plots used to measure ground cover variables. Two 600 m transects adjacent to plots were used to estimate CWD.

(excluding 2002 when no sampling was undertaken). Traps were checked each morning over four consecutive days during each trapping year. The traps used were modified Elliot traps (48 cm × 15 cm × 16 cm) fitted with locking mechanisms so the door cannot be prised open from the inside (Elliot Scientific, Upwey, Victoria). Traps were fixed to T-shaped wooden brackets, nailed to the bole of trees at a height of ~2 m. Apart from conforming to the location of trapping stations described above, large trees (>10 cm diameter at breast height over bark (DBHOB)) were selected randomly for trap placement. A bait mixture of peanut butter, rolled oats and honey was placed in each trap and honey water solution sprayed down the trunk and ~1 m around the base of the tree as an attractant. Because of the establishment of four additional trap stations in 2003 (Yandoit North), there were 280 trap-nights in both 2000 and 2001 and 312 each year for the period 2003–12, totalling 3680 trap-nights.

Animal data collected annually included sex, mass and fat index. Animals were temporarily marked for identification in the event of recapture and ear clippings were taken for DNA sampling. Any scats found on or surrounding the traps were collected. The trap location and tree species on which the trap was positioned were recorded. Only the data concerning total animal abundance and tree species on which animals were trapped are presented here.

Habitat variables

In 2008, seven 'sites' were selected for detailed habitat assessment. Sites were coincident with groups of trap stations used for annual phascogale monitoring surveys, with the two longer tracks (Yandoit and Excelsior Tracks) divided into northern and southern sections, reflecting the nature of trap station placement on these two tracks (see Fig. 1). According to fire records and visual assessment, the majority of sites were long unburnt (>25 years since fire) with some evidence of more

recent low intensity fires at North and South Excelsior (11–25 years since fire) and Welcome Track (1–3 years since fire).

At each of the seven sites, eight 50 m × 20 m plots were established (four on each side of the track) for analysis of vegetation and ground cover. This particular plot size was chosen as it has been used effectively in studies conducted in similar environments and for similar purposes (see McElhinny *et al.* 2006*b*). For each plot the longest edge was oriented parallel to the track, with a trap site forming the midpoint of one of the short edges of the plot. Where there were more than four trap stations along a track, plots were located systematically to sample the greatest spatial range of the trap stations.

A suite of habitat descriptors were chosen which were both potential predictors of phascogale abundance and sufficiently stable over time to be robust estimates of resource availability. Within each plot the number and DBHOB of overstorey trees were measured and the species recorded, with data used to calculate plot basal area. Trees with a DBHOB smaller than 5 cm were not measured as Scarff and Bradley (2006) noted that phascogales do not forage on trees of this size. The total number of dead trees with DBHOB greater than 5 cm was also recorded. Tree height of the three tallest trees was measured and their 'form' was described by measuring the height to first branching point. Bark thickness was measured at four points around the circumference of each overstorey tree using a bark gauge. Bark roughness was subjectively categorised into three groups based on the presence or absence of flaking bark and depth of fissures (i.e. 1 = smooth bark, no flaking; 2 = rough bark, low amount of flaking, shallow fissures; 3 = rough bark, flaking and loose, deep fissures). Tree hollows (in living and dead trees) were observed from the base of the tree and scored according to two size categories of ≤10 cm (small) and >10 cm (large) diameter, similar to categories used in McElhinny *et al.* (2006*a*). The location of the hollow in the tree was also recorded (e.g. branch, basal, trunk, stump).

Understorey vegetation and ground cover was assessed in fourteen 1 m × 1 m quadrats nested systematically along the inside edges of each of the plots. In each plot, proportional cover (%) of understorey vegetation (categorised as shrub, grass/herb or moss/lichen) and ground cover (categorised as litter, rock or bare ground) was visually estimated. Data from the 14 quadrats within each plot were pooled for analysis.

Coarse woody debris (CWD) was assessed using two line intersect transects of 600 m, placed either side of the track starting at the first trap point and running parallel to the track towards adjacent trap points. A pilot study indicated that there were very few pieces of CWD with a diameter greater than 10 cm (data not shown), so pieces of CWD with diameter greater than 5 cm were included. The length and diameter at point of intersection was measured for each piece and density (pieces ha^{-1}) and volume (m^3 ha^{-1}) were calculated from these parameters (De Vries 1973; Bate *et al.* 2004). Each piece was assigned to a decay class of 1–5 (adapted from Pyle and Brown 1999) using characteristics that were common to the broad variety of logs found in the study site.

Analysis

Animal abundance and resource preference

Phascogale abundance data were first analysed using site as the experimental unit, as individual traps at trapping stations were not

independent. While there were some recaptures within sites in individual trapping periods, there were no recaptures between sites suggesting that they were effectively independent, although we acknowledge that this might not be the case due to the large home range of male phascogales (see Traill and Coates 1993; Soderquist 1995*b*). Data were standardised for trapping effort to create an abundance index taking into account unequal number of trap stations between sites and trap closures due to interference by other fauna (abundance index = number of animals captured/available trap-nights (2002–12)). Since overall capture rates were low and variability among years was high, patterns in the abundance index are presented graphically rather than statistically, as preliminary regression models proved unreliable due to the small sample size.

Because tree species was recorded for trap placement for each phascogale monitoring survey (2000–12), it was possible to associate capture data to tree species as a measure of resource preference during foraging. While the allocation of traps to trees was not completely random, the same suite of tree species occurred in both the area used for phascogale monitoring surveys (i.e. trap stations) and habitat assessment sites. For this analysis, and the habitat assessment (see below), we excluded uncommon trees (*Acacia* spp., *Exocarpos cupressiformis* Labill (cherry ballart), *Eucalyptus aromaphloia* subsp. *aromaphloia* L.D.Pryor & J.H.Willis (Creswick apple-box), *E. rubida* H. Deane & Maiden (candlebark) and, because of small numbers of individuals, combined the data for two similar eucalypt species (*E. radiata* Sieber ex DC. (narrow-leaved peppermint) and *E. dives* (broad-leaved peppermint)).

To explore foraging resource preference by phascogales, we first tested whether the tree species on which traps were placed were in similar proportions to those in which they occurred in the landscape (as recorded in habitat assessment plots), using a Wilcoxon signed-rank test. We subsequently evaluated phascogale tree species preference by comparing usage (trees on which they were captured) and availability. We achieved this by using a modified version of Johnson's (1980) rank-based resource selection index to determine if the number of phascogales trapped on a particular tree species differed to that predicted by a random model. This index is relatively insensitive to the choice of resource categories (tree species), and reflects relative rather than absolute differences in selection (Johnson 1980). The index is $u_i–a_i$ where u and a are the ranks of proportional use and availability values for tree species, respectively. Positive, negative and 0 values of the index indicate that phascogales were trapped on a species of tree more than, less than and in proportion to its availability, respectively. Use of a particular tree species was defined as the relative proportion of captures, and availability was defined as the relative proportion of that species in the study area based on counts in plots at each site.

Because capture rates were very low, animal abundance and tree species data from all years for each site were pooled for analysis. Due to the absence of site-based replication, 95% confidence limits for index values were generated using simulation. For each tree species, we used routines in PopTools 3.2 (Hood 2011) to simulate the raw data by drawing at random from a binomial distribution parameterised by the total sample size and the associated proportions. These data

were then used to calculate index values and the process was repeated 10 000 times, with the 2.5 and 97.5 percentiles of the resulting distribution forming 95% confidence limits.

Relationships between phascogale abundance at sites and measured habitat variables were explored with correlation analyses, as the small sample size precluded the building and comparison of multivariate regression models (see Harrell *et al.* 1996; Wintle *et al.* 2005). Principal Components Analysis (PCA) with varimax rotation was used to reduce the collinearity and number of environmental (predictor) variables measured at plots (Quinn and Keough 2002). Prior to PCA, data normality was visually assessed using histograms and Q-Q plots (IBM SPSS Statistics Ver. 20) and variables used were transformed as necessary. Single candidate variables to represent each axis were chosen based on high loadings (>0.7) and fidelity to that axis (see Table 1). Variables that loaded across several axes were independently included as predictor variables. The data reduction process led to identification of 11 candidate variables (plus CWD, which was assessed at the site scale) for consideration in subsequent bi-variate regression models.

Habitat assessment

To test for spatial differences in tree assemblage composition, tree data, using basal area as a measure of relative abundance, were analysed using PERMANOVA (Anderson 2001) with plot nested within site. An assessment of the contribution of species to differences among sites was undertaken using similarity percentages (SIMPER) analysis in PRIMER 6 (Clarke and Warwick 2001) with data log(x + 1) transformed before testing.

Differences in mean number of live and dead trees, bark thickness, dominant tree height and form, ground cover and CWD volume and density among sites were examined using one-way ANOVA followed by Student–Newman–Keuls (SNK) post-hoc analysis. Relationships among DBHOB and bark thickness, tree height and form, ground cover variables and CWD volume and density were explored using correlation analyses (Pearson's r and Spearman's ρ). Prior to analysis, percentage cover data for vegetation and ground cover were subject to arcsine-root transformation.

Categorical variables were analysed using cross-tabulation and Chi-square analysis. These included tree hollow size (small or large), tree size class (DBHOB categories: 1 = 5–15 cm; 2 = 16–25 cm; 3 = 26–35 cm; 4 = 36–45 cm; 5 = 46–55 cm; 6 = 56–65 cm; 7 = 66–75 cm; 8 = 76–85 cm), the location of hollow on the tree (branch, basal, trunk, stump), bark roughness index (categories 1–3) and CWD decay class (categories 1–5).

Results

Animal abundance and resource preference

For the period 2000–12, 114 animals were caught (93, excluding recaptures within years) representing a 3.2% capture success. Only two recaptures (females) were recorded between successive years over this period. Overall, the abundance of phascogales was consistently higher at some sites (Seamond, Yandoit South and Yandoit North) compared with others (Blowhole, Welcome, Excelsior South and Excelsior North). However, this pattern was not consistent among years (Fig. 2). Abundance was not related (either directly or lagged; see Holland

Table 1.   Rotated component matrix from Principal Components Analysis showing loadings of measured habitat variables (plot-scale)
Loadings <0.4 suppressed for clarity of interpretation. LLB, long-leaved box; GB, grey box; RSB, red stringybark; PBPN, peppermints; YB, yellow box; MM, messmate stringybark; RB, red box

	Principal component								
	1	2	3	4	5	6	7	8	9
LLB density	0.795								
LLB DBHOB	0.727								
LLB bark thickness	0.689								
GB density	−0.611								
GB bark thickness	−0.675								
% litter cover		−0.886							
% bare ground		0.721							
% shrub cover		0.604							
% log cover		0.563							
RSB bark thickness			0.749						
RSB DBHOB			0.579						
Dead tree density			−0.691						
RB density		−0.444	−0.610						
PBPN density				0.794					
PBPN DBHOB				0.900					
PBPN bark thickness				0.947					
YB density					0.575				
YB DBHOB					0.829				
YB bark thickness					0.875				
MM DBOH						0.910			
MM bark thickness						0.914			
Tree height							0.749		
1st branch height							0.786		
% grass/herb cover		0.487					0.578		
RB DBHOB								0.693	
RB bark thickness								0.748	
MM density								−0.634	
% cover moss/lichen									0.702
RSB density			−0.560						−0.596
GB DBOHOB	−0.558								0.589
% variance explained	19.5	11.2	10.2	8.6	6.2	6.1	5.1	4.7	4.4
% cum. variance explained	19.5	30.7	40.9	49.5	55.7	61.8	66.9	71.6	76.0

et al. 2012) to rainfall data available from a nearby weather station (Yandoit 37.21°S, 144.10°E; data not shown).

Overall, the same suite of tree species occurred in both the phascogale monitoring (trap stations) and habitat assessment sites in equivalent proportions ($Z = -0.296$, $P = 0.767$). An evaluation of the tree species preferred by phascogales, comparing usage (trees on which they were captured) and availability (relative abundance of each tree species at sites), indicated a non-random relationship. In this analysis, phascogales positively selected peppermints, red box and, to a lesser extent, long-leaved box, and negatively selected red stringybark, messmate stringybark and grey box. No pattern was evident for yellow box (*E. melliodora* A.Cunn. ex Schauer) (Fig. 3).

Habitat assessment

Overstorey trees

A total of 10 species of *Eucalyptus* were recorded in plots throughout the habitat assessment sites, with several species of *Acacia* scattered throughout the eastern part of the study area (Table 2, 'Tree characteristics'). The most abundant tree species

were red stringybark (124–208 trees ha⁻¹) and messmate stringybark (0–74 trees ha⁻¹), and the least abundant species were candlebark (0–11 trees ha⁻¹) and narrow-leaved peppermint (0–49 trees ha⁻¹). Messmate stringybark was the only tree species to be found consistently across all sites ($P = 0.419$). Total (live) mean tree density varied significantly across all sites ($P < 0.001$) and ranged from 831 ± 90 trees ha⁻¹ at the Blowhole site to 1554 ± 163 trees ha⁻¹ at Seamond. The mean density of dead trees was also significantly different across all sites ($P = 0.042$) and ranged from 104 ± 24 (Excelsior North) to 275 ± 73 trees ha⁻¹ (Seamond).

Live tree community composition differed significantly between sites (Pseudo-$F = 9.24$, d.f. $= 6.49$, $P = 0.001$) with pair-wise tests suggesting that Seamond, Yandoit North and Yandoit South were grouped according to their similarity, and Blowhole and Excelsior South were most similar to each other. Excelsior North was most similar to Yandoit North with Welcome remaining ungrouped. These patterns largely reflect geographic location (Fig. 1). SIMPER results indicated that, based on basal area, the first grouping reflects similarity due to dominance of stands of red stringybark, red box and peppermints, and to a lesser
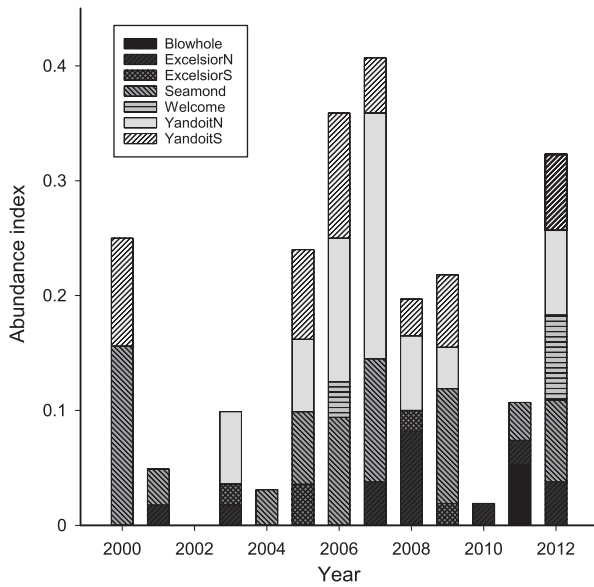
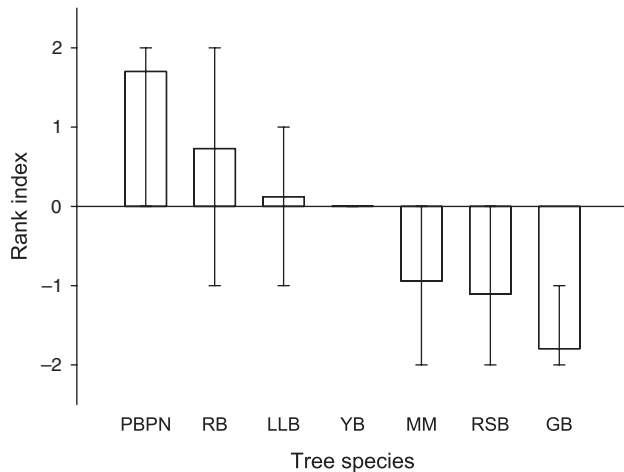**Fig. 2.**   Abundance of phascogales at each site over the trapping period (2000–12).

Fig. 3.   Tree resource use index derived from 13 years (2000–12) of phascogale trapping. Error bars indicate 95% confidence intervals. Positive, negative and 0 values of the index indicate that phascogales were trapped on a species of tree more than, less than and in proportion to its availability (see text for details). Tree species and sample size: PBPN = broad-leaved peppermint and narrow-leaved peppermint combined (peppermints) (10), RB = red box (222), LLB = long-leaved box (190), YB = yellow box (69), RSB = red stringybark (386), MM = messmate stringybark (19), GB = grey box (25).

extent, grey box. The second grouping reflected dominance of stands of red stringybark and long-leaved box. The Welcome site was characterised by having more yellow box and fewer red box (Table 3).

Tree attributes exhibited several patterns. Messmate stringybark and red stringybark were more likely to have flaking and loose rough bark with deep fissures than were other species ($\chi^2 = 1541.51$, d.f. = 12, $P < 0.001$). There was no clear association between tree species and hollow size ($\chi^2 = 3.079$,

d.f. = 4, $P = 0.545$), although there was a tendency for red and grey box to have a greater proportion of small hollows (56% and 57%, respectively) and for red stringybark to have a greater proportion of large hollows (57%). There was, however, an association between hollow size and tree size ($\chi^2 = 15.02$, d.f. = 4, $P = 0.005$), with trees with a DBHOB of 16–25 cm tending to have more small hollows (observed : expected 27 : 19) and those with a DBHOB of >45 cm having more large hollows (observed : expected 19 : 13). This pattern was most evident in grey box and red stringybark. Tree hollows were primarily located in a basal position in red box and red stringybark and in the tree trunk of grey box (data not shown).

Vegetation and ground cover

For the live ground vegetation, there was a greater proportion of grass/herb (8.2–16.4% cover) than shrubs (0.1–7.6% cover) at all sites but there was no significant difference among sites for each variable (Table 2, 'Vegetation and ground cover'). Sites differed in litter cover ($P < 0.001$), with Welcome (52.9% cover) having substantially less than other sites. Accordingly, Welcome had relatively higher proportions of bare ground (20.2% cover) and rock (13.4% cover).

The density of CWD was generally consistent across most sites (400–670 logs ha^{-1}; $P = 0.347$) but was highly variable within sites (i.e. standard errors representing up to 60% of mean value; Table 2, 'Coarse wood debris'). The volume of CWD was also consistent across all sites (8.4–21.5 m^3 ha^{-1}; $P = 0.159$), although there were greater levels of CWD decay at Yandoit South, followed by Blowhole, Yandoit North and Welcome ($\chi^2 = 66.57$, d.f. = 4, $P < 0.001$; data not shown).

Habitat predictors of phascogale abundance

Because several of the variables differed among sites creating broad-scale landscape variation, we investigated whether they could be used to explain phascogale abundance within the study area. Six habitat variables had significant pairwise correlations with overall abundance of phascogales, best described by linear relationships (Fig. 4). Four variables exhibited negative correlations with phascogale abundance: (1) CWD volume, $r = -0.932$, $P = 0.002$; (2) dominant tree height, $r = -0.859$, $P = 0.013$; (3) DBHOB, $r = -0.838$, $P = 0.018$; and (4) bark thickness of red stringybark, $r = -0.773$, $P = 0.041$. Two variables had positive correlations with phascogale abundance: (1) density of red box, $r = 0.884$, $P = 0.008$; and (2) density of grey box, $r = 0.800$, $P = 0.031$. There were two additional non-linear relationships with phascogale abundance: (1) grass/herb cover, $\rho = -0.857$, $P = 0.014$; and (2) density of yellow box, $\rho = 0.821$, $P = 0.023$.

As expected, and as identified in the PCA, several habitat variables were strongly intercorrelated. The volume of CWD was negatively correlated with density of two tree species (grey box, $r = -0.855$, $P = 0.014$; red box, $r = -0.918$, $P = 0.004$) and positively correlated with tree height ($r = 0.815$, $P = 0.026$), shrub cover ($r = 0.805$, $P = 0.029$) and DBHOB of red stringybark ($r = 0.767$, $P = 0.044$). DBHOB was positively correlated with bark thickness for red stringybark ($r = 0.873$, $P = 0.010$) and negatively correlated with the density of grey box ($r = 0.903$, $P = 0.005$). Tree height was negatively correlated with the density

Table 2. Summary of habitat variables (mean $\pm$ s.e.) measured at seven sites in the Wombat State Forest and Hepburn Regional Park

Lowercase letters in italics indicate homogeneous subsets as determined by one-way ANOVA and SNK post-hoc analysis. Tree species with low numbers of individuals and present at few sites are not shown (candlebark, cherry ballart and Creswick apple-box)

Variable	Blowhole	Excelsior North	Excelsior South	Seamond	Welcome	Yandoit North	Yandoit South	ANOVA	P value
				Tree characteristics					
Total tree density (ha^{-1})	831 ± 90^a	729 ± 84^a	1030 ± 119^a	1554 ± 16^b	791 ± 111^a	936 ± 91^a	1073 ± 154^a	$F_{6,49}=5.358$	<0.001
Tree species density (ha^{-1})									
Acacia species group	3 ± 3^a	21 ± 9^a	10 ± 9^a	0^a	0^a	0^a	0^a	$F_{6,49}=2.735$	0.023
Broad-leaved peppermint	189 ± 84^b	4 ± 4^a	15 ± 15^a	31 ± 17^a	70 ± 49^a	0^a	0^a	$F_{6,49}=3.262$	0.009
Candlebark	0^a	0^a	1 ± 1^a	0^a	11 ± 6^b	0^a	0^a	$F_{6,49}=3.500$	0.006
Grey box	0^a	66 ± 20^{ab}	1 ± 1^a	269 ± 89^b	104 ± 47^{ab}	118 ± 27^{ab}	511 ± 122^c	$F_{6,49}=8.888$	<0.001
Messmate stringybark	10 ± 9^a	52 ± 29^a	16 ± 10^a	0^a	78 ± 73^a	0^a	0^a	$F_{6,49}=1.027$	0.419
Long-leaved box	216 ± 39^{ab}	250 ± 91^b	598 ± 83^c	111 ± 72^{ab}	3 ± 3^a	44 ± 18^{ab}	30 ± 27^{ab}	$F_{6,49}=12.995$	0.001
Narrow-leaved peppermint	1 ± 1^a	1 ± 1^a	0^a	0^a	49 ± 43^a	0^a	0^a	$F_{6,49}=1.244$	0.301
Red box	126 ± 58^a	166 ± 37^a	50 ± 13^a	455 ± 94^b	80 ± 47^a	231 ± 27^a	135 ± 43^a	$F_{6,49}=6.933$	<0.001
Red stringybark	283 ± 53^{ab}	149 ± 45^a	329 ± 57^{abc}	625 ± 78^d	365 ± 50^{bc}	525 ± 55^{cd}	380 ± 49^{bc}	$F_{6,49}=7.759$	<0.001
Yellow box	4 ± 4^a	19 ± 7^a	10 ± 5^a	63 ± 15^b	33 ± 11^a	19 ± 9^a	16 ± 7^a	$F_{6,49}=4.689$	0.001
Dead tree density (ha^{-1})	116 ± 12^a	104 ± 24^a	180 ± 45^a	275 ± 73^a	228 ± 38^a	256 ± 45^a	181 ± 35^a	$F_{6,49}=2.383$	0.042
DBHOB (cm)									
Acacia species group	17.5 ± 1.0^b	6.9 ± 0.5^a	6.9 ± 0.4^a	–	–	–	–	$F_{2,24}=36.37$	<0.001
Broad-leaved peppermint	17.1 ± 1.2^a	12.3 ± 2.2^a	16.1 ± 1.8^a	12.0 ± 0.9^a	14.2 ± 1.5^a	–	–	$F_{4,155}=1.903$	0.113
Candlebark	–	–	22.0 ± 0.1^a	–	29.3 ± 4.6^a	–	–	$F_{1,8}=0.256$	0.626
Grey box	–	23.2 ± 1.8^b	17.0 ± 0.1^a	15.8 ± 0.6^a	15.1 ± 1.1^a	16.5 ± 0.8^a	15.1 ± 0.7^a	$F_{6,481}=7.012$	<0.001
Messmate stringybark	21.5 ± 3.6^a	25.0 ± 1.9^a	15.6 ± 1.1^a	–	21.6 ± 3.4^a	–	–	$F_{3,91}=1.845$	0.145
Long-leaved box	18.7 ± 1.1^a	16.4 ± 1.3^a	15.6 ± 0.8^a	11.9 ± 0.7^a	11.7 ± 0.9^a	13.7 ± 1.2^a	15.5 ± 2.1^a	$F_{6,489}=2.765$	0.012
Narrow-leaved peppermint	16.5 ± 0.1^a	13.4 ± 0.1^a	–	–	13.0 ± 1.3^a	–	–	$F_{2,24}=0.136$	0.873
Red box	14.2 ± 1.1^{ab}	19.1 ± 1.1^d	16.3 ± 1.6^{abc}	13.0 ± 0.7^a	15.0 ± 1.4^{abc}	18.6 ± 0.8^{bc}	17.8 ± 1.2^{bc}	$F_{6,656}=6.605$	<0.001
Red stringybark	25.0 ± 1.3^d	23.8 ± 1.1^{cd}	21.0 ± 1.1^{bc}	13.6 ± 0.5^a	19.8 ± 0.9^b	16.2 ± 0.6^a	14.3 ± 0.8^a	$F_{6,1045}=21.772$	<0.001
Yellow box	9.5 ± 1.7^a	21.8 ± 2.6^{ab}	16.8 ± 2.7^{ab}	15.9 ± 1.6^b	30.0 ± 3.4^b	19.2 ± 2.0^{ab}	20.6 ± 3.0^{ab}	$F_{6,144}=4.208$	<0.001
Dominant height (m)	18.8 ± 1.1^{ab}	18.0 ± 1.0^{ab}	18.8 ± 1.2^{ab}	16.6 ± 0.8^{ab}	21.0 ± 1.6^b	15.7 ± 1.1^a	16.1 ± 1.1^a	$F_{6,49}=2.678$	0.025
Height first branch (m)	8.4 ± 0.8^{ab}	7.2 ± 0.8^{ab}	8.4 ± 0.7^{ab}	9.7 ± 0.9^b	7.8 ± 1.2^{ab}	6.2 ± 0.4^a	5.6 ± 0.8^a	$F_{6,49}=3.017$	0.014
Bark thickness (cm)									
Acacia species group	0.6 ± 0.1^c	0.2 ± 0.1^a	0.4 ± 0.0^b	–	–	–	–	$F_{2,24}=20.404$	<0.001
Broad-leaved peppermint	1.1 ± 0.1^b	0.7 ± 0.1^a	0.8 ± 0.1^{ab}	0.9 ± 0.1^{ab}	1.0 ± 0.1^{ab}	–	–	$F_{4,155}=3.566$	0.008
Candlebark	–	–	1.3 ± 0.1^a	–	1.2 ± 0.2^a	–	–	$F_{1,8}=0.008$	0.932
Grey box	1.2 ± 0.1^c	1.1 ± 0.1^b	1.8 ± 0.1^{bc}	1.0 ± 0.1^{bc}	0.9 ± 0.1^a	1.0 ± 0.1^a	1.3 ± 0.1^c	$F_{5,481}=8.716$	<0.001
Messmate stringybark	2.1 ± 0.4^c	1.5 ± 0.1^b	0.9 ± 0.1^a	–	1.6 ± 0.2^b	–	–	$F_{3,91}=5.670$	0.010
Long-leaved box	1.2 ± 0.1^b	1.1 ± 0.1^b	1.2 ± 0.1^b	0.1 ± 0.1^a	0.8 ± 0.1^b	0.8 ± 0.1^b	1.1 ± 0.1^b	$F_{6,489}=53.588$	<0.001
Narrow-leaved peppermint	1.3 ± 0.1^a	0.7 ± 0.0^a	–	–	0.8 ± 0.1^a	–	–	$F_{2,24}=0.601$	0.556
Red box	1.0 ± 0.1^{bc}	1.0 ± 0.1^{bc}	1.1 ± 0.1^c	0.6 ± 0.1^a	0.8 ± 0.1^b	1.9 ± 0.1^b	1.1 ± 0.1^c	$F_{6,656}=19.379$	<0.001
Red stringybark	1.6 ± 0.1^c	1.6 ± 0.1^c	1.6 ± 0.1^c	0.9 ± 0.1^a	1.3 ± 0.1^b	1.1 ± 0.1^b	1.2 ± 0.1^b	$F_{6,1045}=34.215$	<0.001
Yellow box	1.1 ± 0.2^a	1.0 ± 0.1^a	0.9 ± 0.1^a	1.0 ± 0.1^a	1.1 ± 0.1^a	0.9 ± 0.1^a	0.9 ± 0.1^a	$F_{6,144}=0.779$	0.587
				Vegetation and ground cover					
Shrub (%)	2.2 ± 0.5^a	0.5 ± 0.1^a	7.6 ± 4.2^a	0.1 ± 0.1^a	6.7 ± 3.8^a	0.9 ± 0.5^a	1.7 ± 0.6^a	$F_{6,49}=1.976$	0.087
Grass/herb (%)	16.4 ± 3.6^a	7.4 ± 1.3^a	8.2 ± 3.3^a	8.1 ± 2.4^a	9.5 ± 4.4^a	8.6 ± 3.4^a	8.2 ± 1.0^a	$F_{6,49}=1.067$	0.395
Litter (%)	71.7 ± 1.5^a	81.3 ± 1.6^a	68.7 ± 4.2^a	72.5 ± 5.2^a	52.9 ± 6.0^b	74.8 ± 4.3^a	74.1 ± 2.1^a	$F_{6,49}=5.01$	<0.001
Rock (%)	7.4 ± 1.9^{ab}	4.5 ± 0.7^{ab}	5.4 ± 1.4^{ab}	3.3 ± 0.8^a	13.4 ± 5.7^{ab}	5.1 ± 1.8^{ab}	12.6 ± 2.5^b	$F_{6,49}=2.324$	0.047
Moss/lichen (%)	7.9 ± 1.6^{ab}	13.8 ± 2.3^b	9.6 ± 2.2^{ab}	2.8 ± 0.9^a	7.4 ± 2.9^{ab}	4.7 ± 2.4^a	6.5 ± 2.3^{ab}	$F_{6,49}=2.666$	0.026
Bare ground (%)	10.2 ± 1.6^a	8.2 ± 1.3^a	9.6 ± 1.8^a	10.4 ± 2.5^a	20.2 ± 5.0^a	6.1 ± 1.7^a	9.9 ± 1.9^b	$F_{6,49}=3.036$	0.013
				Coarse woody debris					
Density (logs ha^{-1})	619 ± 51^a	674 ± 34^a	982 ± 464^a	400 ± 36^a	394 ± 230^a	440 ± 25^a	392 ± 239^a	$F_{6,7}=1.167$	0.347
Volume (m^3 ha^{-1})	20.2 ± 0.1^a	12.5 ± 1.7^a	21.5 ± 1.6^a	6.9 ± 3.5^a	18.8 ± 7.9^a	8.4 ± 3.6^a	10.4 ± 4.3^a	$F_{6,7}=2.227$	0.159

of red box ($r=-0.782$, $P=0.038$) and positively correlated with the density of candlebark ($r=-0.780$, $P=0.039$) and density of narrow-leaved peppermint ($r=-0.766$, $P=0.045$). Grass/herb cover was positively correlated with the density of broad-leaved peppermint ($r=0.920$, $P=0.003$), while density of red box was negatively correlated with shrub cover ($r=-0.864$, $P=0.012$).

In summary, for the 13 years spanning phascogale surveys (2000–12) in the Hepburn–Wombat State Forest region, the highest overall animal abundance occurred at sites

Table 3. Mean basal area values (cm^2) and percentage contribution to differences between site tree assemblages derived from Similarity Percentages (SIMPER) analysis

Narrow-leaved peppermint and broad-leaved peppermint data combined (peppermints). Data for candlebark and *Acacia* species group omitted due to low numbers. C%, percentage contribution to site

	Blowhole		Exelsior North		Exelsior South		Seamond		Welcome		Yandoit North		Yandoit South	
	Mean	C%	Mean	C%	Mean	C%	Mean	C%	Mean	C%	Mean	C%	Mean	C%
Red stringybark	12 187	35.2	6873	20.5	10 306	31.5	3594	23.4	8323	41.7	5362	23.1	4738	24.3
Red box	1992	15.3	5377	20.3	1423	16.9	3723	23.4	1362	9.2	6484	23.3	3940	23.2
Long-leaved box	6988	33.6	3821	13.7	5455	29.4	693	2.7	27	0	827	7.9	757	0.4
Peppermints	1992	15.3	5377	20.3	1423	16.9	3723	23.4	1362	9.2	6484	23.3	3940	23.2
Grey box	0	0	4124	14.1	28	0	3655	16.0	2174	14.5	3371	15.7	4102	24.3
Yellow box	28	0	1047	5.6	261	3.2	1842	11.1	3018	23.8	1611	6.8	679	4.6
Messmate stringybark	1744	0.1	6259	5.5	878	2.1	0	0	6916	1.5	0	0	0	0

characterised by associations of red stringybark, red box, grey box and broad- and narrow-leaved peppermints. At these sites red stringybark and grey box trees were, on average, of smaller diameter, and tended to have smaller hollows. Overall, red stringybark trees were more likely to have rough bark, flaking and loose, with deep fissures compared with other species. These sites also had trees of lower average height, lower grass/herb and shrub cover and lower volumes of CWD.

Discussion

Trapping data collected in the same area over an extended period (>10 years) suggests that phascogale abundance is highly spatially and temporally variable, most likely as a response to heterogeneity in habitat and foraging resources. Our results are consistent with those reported by Holland *et al.* (2012), although the overall downward trend the authors described appears to have reversed since 2010 (see Fig. 2). Anecdotal evidence from previous studies indicated the habitat preference of phascogales for a low level of ground cover with a well-developed litter layer (Menkhorst and Gilmore 1979; Cuttle 1982; Tzaros 2005; Scarff and Bradley 2006). Such preferences have been confirmed and extended by this study, with areas of greatest abundance of phascogales associated with multiple environmental variables including relatively small trees (i.e. overall tree size including both height and DBHOB), high litter cover, low volume of CWD and a low level of live ground cover. High phascogale abundance was also associated with certain tree species, particularly red stringybark, red and grey box, and both broad- and narrow-leaved peppermints. A detailed analysis of capture data from a resource-use perspective indicated that, within these locations, phascogales forage preferentially on broad- and narrow-leaved peppermints and red box and, to a lesser extent, long-leaved box, and infrequently select red stringybark, messmate stringybark and grey box. These results suggest that there is a secondary set of drivers, probably associated with food availability, that operate at smaller spatial scales. While it is possible that phascogale capture was enhanced by the use of baits and attractants, traps were randomly allocated to trees of all species so there is a clear pattern of preferential tree usage.

Anecdotal evidence from related studies suggested that sites which have trees with a larger diameter would provide preferred habitat due to an increased foraging area, as well as being typically associated with the largest number of invertebrate communities (Recher *et al.* 1996; van der Ree *et al.* 2001). In our study, as phascogales were more abundant in areas with a large number of small trees, their abundance may be a response to the distribution of suitably sized hollows rather than food resources alone. Soderquist (1993*b*) found that phascogales generally use hollows for maternal nests that have a relatively small entrance diameter, generally ranging from 2.4–5.5 cm. Mackowski (1984) noted that small hollows are more numerous in small trees compared with large trees. We were able to confirm this observation as, across all sites, we found that smaller trees (16–25 cm DBHOB) had a higher proportion of small hollows (≤10 cm) than large hollows. Over the 13 years of our study, the highest overall phascogale abundance was at the Seamond and Yandoit North sites, where populations of red stringybark and grey box were, on average, smaller, and tended to have larger numbers of small hollows.

Phascogales are known to utilise alternate hollow sources making use of coppice hollows, tree stumps and ball-shaped stick nests of white-browed babblers (*Pomatostomus superciliosus*) (Traill and Coates 1993). Hollows are formed through a complex pattern of branch shedding and hollow occlusion and are therefore highly variable in abundance (Mackowski 1984; Lindenmayer *et al.* 1993; Gibbons and Lindenmayer 2002). The formation of hollows is typically a long and complex process that requires several factors to align for success to occur, with the size of the tree playing a large role in hollow formation (Gibbons and Lindenmayer 2002). Several studies have shown evidence for this with number, size and diversity of hollows typically increasing with age and tree diameter (Mackowski 1984; Lindenmayer *et al.* 1993). However, there may be an optimum age for formation of hollows as the greatest number of hollow-bearing trees often occurs within the mid-range of diameter classes (Bennett *et al.* 1994; Gibbons *et al.* 2002). This pattern can also be explained by the absence of very large trees (>70 cm DBH; Gibbons and Lindenmayer 2002) in our study, which is unsurprising considering the extensive mining and logging history of the study area. Den selection by arboreal marsupials
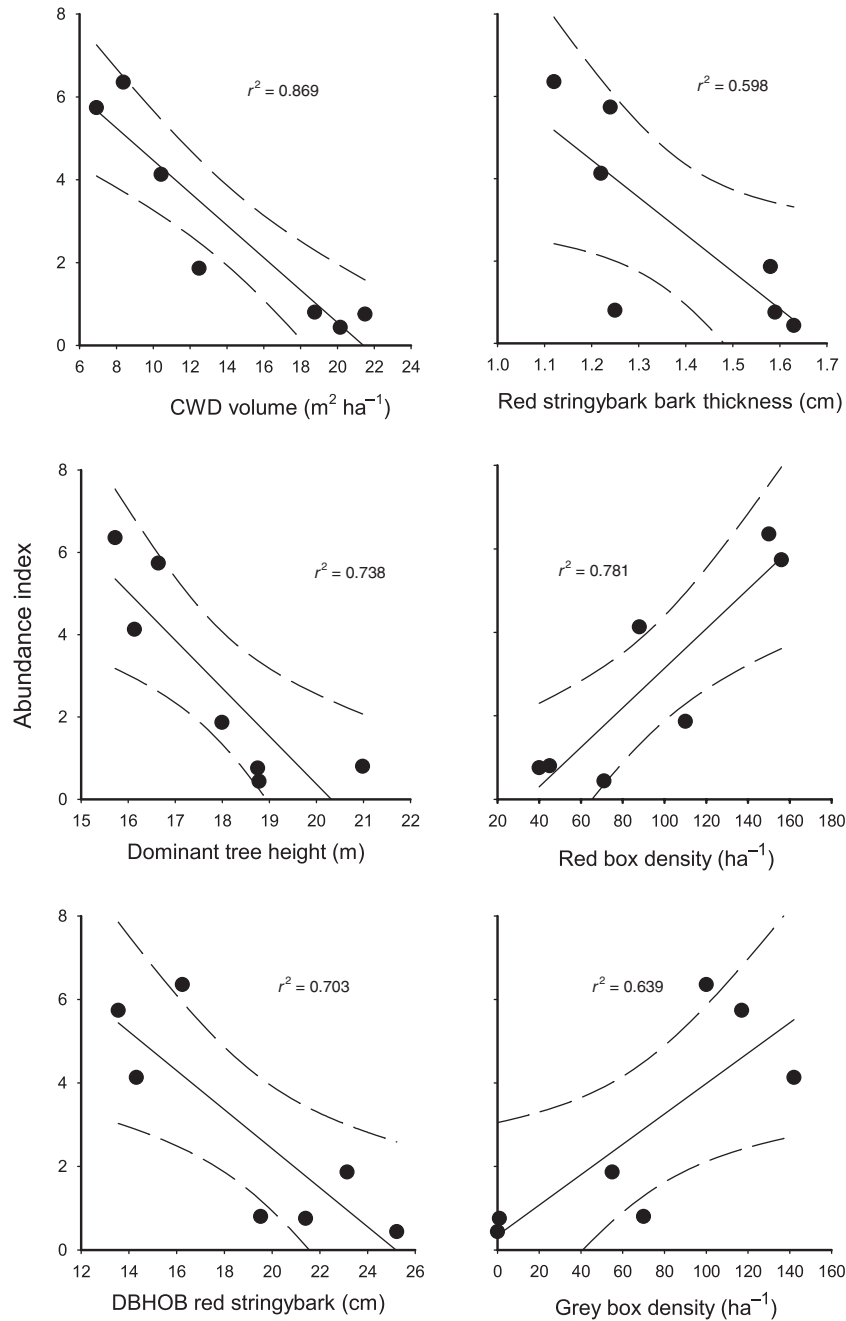
Fig. 4. Relationship of selected habitat variables with abundance of phascogales. Linear regression lines with 95% confidence intervals are shown.

is influenced by differences in the type and entrance height of tree hollows rather than simply by number of hollows (Lindenmayer *et al.* 1991), demonstrating that the quality of a resource can be more important than the abundance of the resource itself.

While earlier studies have provided some insight into foraging behaviour of the phascogale (e.g. Traill and Coates 1993; Soderquist 1995*b*; Scarff and Bradley 2006), little is known concerning specific tree usage. This study reports important new data suggesting that, in this area, phascogales forage on

certain species of *Eucalyptus* in preference to other species. Phascogales are generalist invertebrate feeders and forage by taking large insects such as spiders and centipedes off the surface of the bark or by reaching into deep crevices with their forepaws (Traill and Coates 1993). Bark type is important in determining bark-dwelling invertebrate diversity (Noske 1985; Majer *et al.* 2006; Croft *et al.* 2012) and bark complexity is often thought to be a good predictor of invertebrate abundance (Brawn *et al.* 1982; Noske 1985; MacFarlane and Luo 2009). However, in some

forests in south-western Australia, bark invertebrate diversity appeared to be greater on smooth-barked eucalypts (i.e. trees with relatively simple bark) than on their rough-barked counterparts (Majer *et al.* 2003). Box-type bark is often tessellated and tightly held but it may also be quite flaky, while peppermints are characteristically rough-barked (Boland *et al.* 2006). In this study, phascogales were negatively selecting for rough-barked trees (red stringybark, messmate stringybark and grey box) as a foraging resource, suggesting that bark complexity alone may not be the determining factor. Indeed, size (DBHOB) and bark thickness of red stringybark were important (negative) predictors of phascogale abundance in our study. Traill and Coates (1993) noted that saplings and tree limbs smaller than 10 cm in diameter were rarely used by phascogales, so it is likely that a combination of bark type and tree size determines the use of particular tree species as a food resource.

There is currently little information concerning relationships between phascogale abundance and activity and ground habitat resources, such as CWD. Phascogales have been observed to forage on the ground around fallen logs (Lunt 1988; Traill and Coates 1993; Scarff *et al.* 1998; Scarff and Bradley 2006) but this activity forms only a small part of feeding patterns. In this study there was a negative correlation between phascogale abundance and both CWD volume and grass/herb cover, although this may be in part due to confounding positive relationships between these variables and tree size, which is negatively correlated with phascogale abundance. A manipulative experiment would be required to untangle some of these relationships. Nevertheless, our findings concerning litter cover and more open understorey vegetation support observations made in other studies (Menkhorst and Gilmore 1979; Cuttle 1982; Tzaros 2005; Scarff and Bradley 2006). It may be that a simple ground layer is preferred to accommodate ease of movement for species that are primarily arboreal. This hypothesis can be supported by a study of the mountain brushtail possum (*Trichosurus caninus*), which was more likely to be found in trees that were surrounded by only a relatively small amount of dense vegetation (Lindenmayer *et al.* 1996).

There is the possibility that competition between the phascogale and other arboreal species occurs in the study area. The agile antechinus (*Antechinus agilis*) is found throughout the study area and has a similar diet to the phascogale (Lunney *et al.* 2001; Scarff and Bradley 2006). The common brushtail possum (*Trichosurus vulpecula*) has also been found to occur within the study area. These large and highly aggressive possums use large hollows in large trees (Wood and Wallis 1998; Gibbons *et al.* 2002), a characteristic of the study area, and it may be that phascogales are being outcompeted for these particular hollow resources. Feral cats (*Felis catus*) and, in particular, powerful owls (*Ninox strenua*) prey on phascogales and may also influence abundance (Van Dyck and Gibbons 1980; Tilley 1982; Traill and Coates 1993; Humphries and Seebeck 2003). In this respect, predation pressure may be used to explain the preference for smaller diameter hollows to restrict access of predators (Gibbons *et al.* 2002). Similarly, preference for low ground cover to ensure mobility between trees further supports the possibility of a high predator density and a need for an easy retreat to safety. However, a continuous layer of ground cover would also provide

increased protection from predators while phascogales are on the ground, so it is likely that there is a more complex explanation for the apparent preference for low ground cover than can be explained by this study.

This study has provided new information concerning spatial patterns of phascogale abundance and resource use within a multiple-use forest represented by the Hepburn–Wombat State Forest area in central Victoria. The current composition and age structure of tree communities are assumed to be a response to the severe disturbances of past mining and harvesting activities. Successful conservation of this threatened species could be enhanced through active management of this forest to, among other strategies, maintain nesting hollows and foraging resources and promote their ongoing supply. Appropriate silvicultural treatments could be applied to positively influence tree stand structure and hollow development, while in the shorter term, artificial nest boxes could enhance available nesting resources (Beyer and Goldingay 2006). Although not directly investigated in this study, management of fire regimes to manipulate the nature of the ground habitat, and control of feral animals and firewood collection are also likely to aid in conservation of the phascogale, and further studies of the effect of such strategies are encouraged.

Acknowledgements

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