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Relationships between tree size and occupancy by cavity-dependent arboreal marsupials

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Running Head: Hollow-bearing trees and animal occupancy patterns

Abstract

Hollow-bearing trees are keystone structures in many ecosystems worldwide and they play critical habitat roles for a vast array of fauna through providing denning and/or nesting sites. We quantified empirical relationships between the diameter of hollow-bearing trees and probability of occupancy of these trees by cavity-dependent arboreal marsupials in the Mountain Ash (*Eucalyptus regnans*) forests of the Central Highlands of Victoria, south-eastern Australia. We also quantified the effects of other variables such as stand age and elevation on tree occupancy. Finally, we compared the diameter of occupied and unoccupied hollow-bearing trees with non-hollow-bearing trees in 77-year old forest that regenerated after fires in 1939 and form the dominant age cohort of trees in our study region.

Hollow-bearing trees occupied by arboreal marsupials had a larger diameter than unoccupied hollow-bearing trees. The mean diameter of both occupied and unoccupied hollow-bearing trees was almost three times that of 1939-aged trees that did not contain hollows. Our analyses contained evidence of inter-specific differences in the diameter of hollow-bearing trees occupied by different species of arboreal marsupials. Beyond the influence on occupancy of tree-level factors such as diameter, we also found that the probability of occupancy of a hollow-bearing tree was affected by the age of the surrounding forest and landscape attributes such as elevation. The probability of occupancy of an individual hollow-bearing tree was highest when that tree was located in regrowth forest, most likely because of the scarcity of these critical nesting and denning resources in such stands.

Populations of large hollow-bearing trees, including those typically selected for occupancy by arboreal marsupials, are in rapid decline in Mountain Ash forests. This decline, coupled with the prolonged period until current cohorts of existing younger trees eventually reach an age (and therefore diameter) that are suitable for occupancy by arboreal marsupials, underscores the critical need to protect all existing hollow-bearing trees from practices that can otherwise destroy them, including industrial clearfelling operations. Better protection is important not only in the small remaining areas of old growth Mountain Ash forest but also in regrowth forest where such trees are scarce and have high marginal value as nesting sites, as reflected by high rates of per tree occupancy rates in stands of this age.

Keywords: Hollow-bearing trees, cavity trees, snags, forest management, Leadbeater's Possum, Mountain Ash forests, possums and gliders, large old trees, south-eastern Australia

1.1 Introduction

Large old trees are a critical structural feature of many ecosystems worldwide and they have several key characteristics not found in small young trees or small old trees (Lindenmayer and Laurance 2016). One of these characteristics is the presence of cavities that provide nesting and denning sites for a wide range of fauna globally (Fischer and McClelland 1983; Rose et al., 2001; Gibbons and Lindenmayer 2002; Remm and Lohmus 2011). Australia lacks primary cavity-excavating vertebrates such as woodpeckers, and trees on the continent develop cavities in several ways, for example through the activities of organisms such as fungi and termites (Perry et al., 1985; Remm and Lohmus 2011), disturbances such as fires (Inions et al., 1989), and age-related changes in tree physiology such as incomplete occlusion of wound tissue following damage such as stem wounding and/or branch breakage (Gibbons and Lindenmayer 2002). The effects of these processes can be both time and tree-size mediated, meaning that hollow-bearing trees should be the largest and longest-living individuals in most ecosystems. Those trees with large cavities suitable for occupancy by cavity-dependent species should be larger than unoccupied trees. We tested these simple premises in an investigation from the wet Mountain Ash (*Eucalyptus regnans*) forests of the Central Highlands of Victoria, south-eastern Australia.

Hollow-bearing trees in wet ash-type eucalypt forests can be recruited over prolonged periods of ontological development meaning that such trees are typically most abundant in old growth forests (Lindenmayer et al., 2000a). Hollow-bearing trees also may develop in pulses or cohorts as a result of major disturbance events such as wildfires (Gibbons and Lindenmayer 2002). For example, large numbers of hollow-bearing trees in Mountain Ash forests were created when old growth trees and stands were burned in high-severity, stand-replacing wildfires in 1939 (Lindenmayer et al., 1991b). In contrast, stands subject to clearfell logging commonly retain few or no live or dead large old trees, and new hollow-bearing trees will typically take over 120 years to form (Ambrose 1982). Importantly, hollow-bearing trees in Mountain Ash forests are critical nesting and denning sites for an array of species of cavity-dependent vertebrates including eight species of arboreal marsupials such as the Critically Endangered Leadbeater's Possum (*Gymnobelideus leadbeateri*) (Lindenmayer et al., 2015) and the nationally vulnerable Greater Glider (*Petauroides volans*) and regionally vulnerable Yellow-bellied Glider (*Petaurus australis*). Specifically, we posed four key questions in this study:

Q1: ***Are there relationships between tree occupancy by arboreal marsupials and the diameter of such trees?*** We predicted there would be strong positive relationships between the diameter of trees and the probability of them being occupied by arboreal marsupials. That is, occupied hollow-bearing trees would also be large diameter trees. This is because larger trees develop more and larger cavities (Mackowski 1987; Lindenmayer et al., 1993; Lindenmayer et al., 2000b) that are more likely to be suitable for occupancy by comparatively large cavity-dependent vertebrates such as arboreal marsupials and owls.

Animals require not only access to denning and sheltering sites, but also areas in which to forage. The suitability of foraging substrates may be influenced by the structure of the forest surrounding nesting sites that can vary in response to factors such as stand age. Our second key question was therefore:

Q2: Is the occupancy of hollow-bearing trees by arboreal marsupials influenced the age of the surrounding forest? At the outset of this study, we were agnostic about the kinds of relationships that might occur between tree occupancy and the age of the surrounding forest. Potentially, the proportion of hollow trees used per animal may vary with hollow tree availability (for instance, due to changes in resource sharing; (Banks et al., 2011) or due to resources other than the availability of hollow trees limiting animal occurrence (Banks et al., 2013). For example, the probability of occupancy of individual hollow-bearing trees may be reduced in old growth forests where animals have access to many alternative trees; that is, the marginal value of a given tree will be lower where there are already many hollow-bearing trees (Fischer et al., 2010). Conversely, the probability of occupancy of trees in old growth forest may be greater because of the suitability of surrounding areas as a food source for particular species (Lindenmayer et al., 1990b). In addition to test for the effects of stand age, we also sought to determine tree occupancy was influenced by factors such as the elevation of the site in which trees were located.

Q3. ***Are there inter-specific differences in the diameter of trees selected by different species of arboreal marsupials?*** Many species of animals select cavities in trees that are large enough to permit entry but with an entrance that precludes larger-bodied species that may be predators or competitors (Gibbons and Lindenmayer 2002). Given relationships between tree size and cavity size (Mackowski 1987; Lindenmayer et al., 1993), we postulated there would be positive relationships between the body size of particular species of arboreal marsupials and the diameter of trees they occupied.

The selection of trees for analyses of relationships between occupancy and diameter was based on those trees supporting obvious cavities (as determined using a pair of binoculars; see Section 2.1). However, it was important to determine if trees occupied by arboreal marsupials differed in diameter relative to other (non-hollow-bearing) trees in the remainder of the stand. We therefore posed a fourth question:

Q4: ***Are there differences in the diameter of hollow-bearing trees occupied by arboreal marsupials and the diameter of non-hollow-bearing trees?*** For this analysis, we focused on stands of trees that regenerated following the 1939 wildfires. We targeted this age class because it is the dominant age cohort in Mountain Ash forests and given the current lack of old growth forest in this ecosystem (< 1.16% of the estate (Lindenmayer et al., 2012a)), trees in these stands will be the next ones to develop into old growth if they are able to reach ecological maturity (Lindenmayer et al., 2015). Cavities in 77-year-old trees are very rare and typically lack the depth required for use by arboreal marsupials. As cavities typically develop in older and therefore larger Mountain Ash trees (Lindenmayer and Laurance 2016), we postulated that hollow trees would be significantly larger than other Mountain Ash trees that lacked cavities in the surrounding stand.

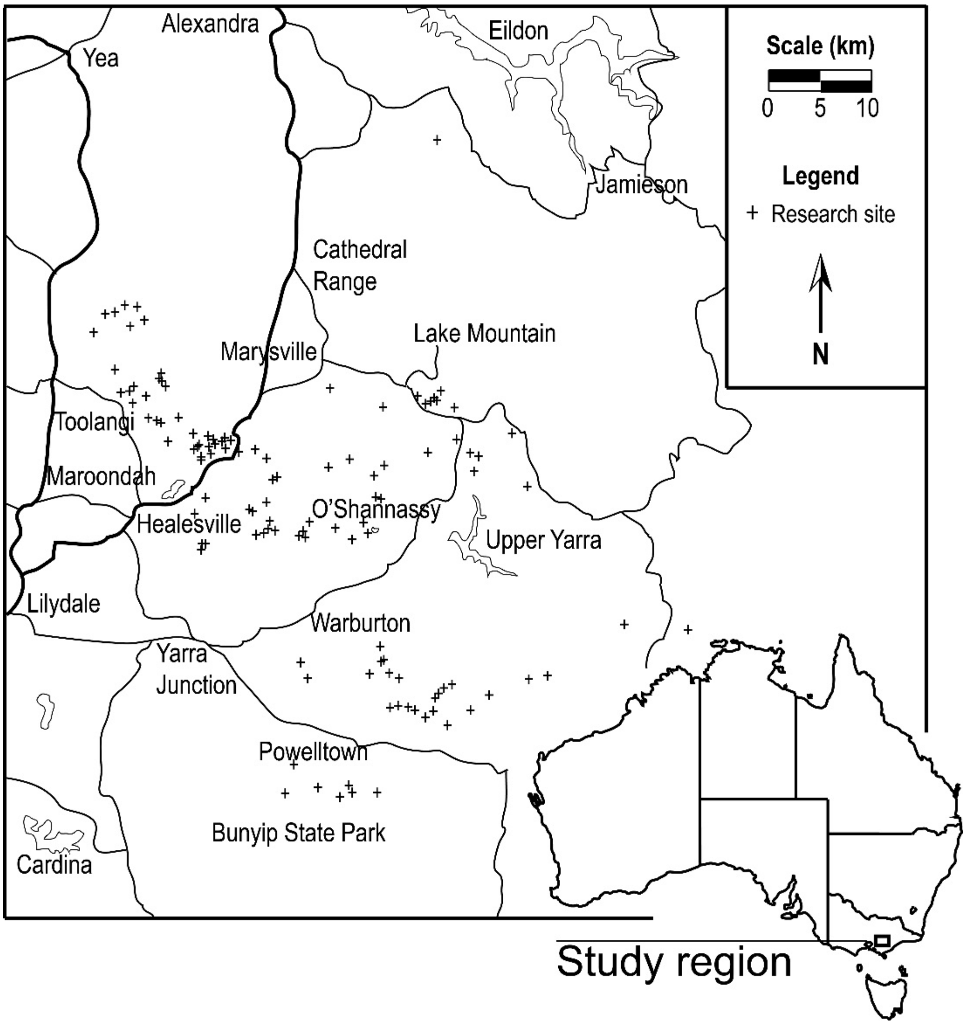
Populations of large old hollow-bearing trees are declining in many (although not all) ecosystems globally (Lindenmayer et al., 2012b; Lindenmayer and Laurance 2016). Such declines characterise Mountain Ash forests in the Central Highlands of Victoria (Burns et al., 2015). The loss of these trees will likely have corresponding negative conservation outcomes for an array of cavity-dependent species, including arboreal marsupials. Therefore, better understanding of the patterns of occupancy of trees of different sizes and contexts (i.e. relative to surrounding stand conditions) will have important implications for how to best manage ecosystems where hollow-bearing trees are keystone structures (sensu Tews et al., 2004).

2.1 Methods

2.1.1 Study area

We completed this study in the Mountain Ash forests of the Central Highlands of Victoria, south-eastern Australia (Figure 1). We established 119 long-term ecological research sites in the study region (Lindenmayer et al., 2003). Each of these sites measured 1 ha in size and were well distributed throughout the study region, covering a wide range of variation in environmental conditions. Our sites varied in slope (inclination: 2-38^{o}), elevation (220-1040 m), topographic position (gully, midslope, ridge) and aspect (assigned to one of the following categories: north, east, south, west). At the outset of this investigation (1997), we assigned our 119 field sites to one of four stand age classes: old growth (stands where the dominant age class of the overstorey had established pre-1900), stands that regenerated after the major wildfires in 1939, stands that regenerated after logging conducted between 1960-1990, and stands of overstorey trees of mixed age.

Figure 1. The location of the study region and research sites in the Central Highlands of Victoria, south-eastern Australia.



We completed three kinds of repeated surveys on our 119 field sites: **(1)** surveys of arboreal marsupials, **(2)** measurements of hollow-bearing trees, and **(3)** measurements of vegetation structure, primarily stand age. We briefly describe these surveys and associated measurements in Section 2.1.2. Notably, more than 50 000 ha of Mountain Ash forest was burned in wildfires in 2009 (Berry et al., 2015; Lindenmayer et al., 2015) and this demanded subsetting of some datasets for subsequent statistical analyses (see below).

2.1.2 Surveys of hollow-bearing trees

We defined a hollow-bearing tree as any live or dead tree containing an obvious cavity as determined from careful visual inspection using a pair of binoculars. The diameter of all hollow-bearing trees on each site was first measured in 1997 (measured with a diameter tape at 1.3 m above the ground). Each hollow-bearing tree was mapped and marked with a permanent metal tag with unique identifying number.

2.1.3 Occupancy of hollow-bearing trees by arboreal marsupials

Mountain Ash forests support eight species of arboreal marsupials. Of these, Leadbeater's Possum is listed as nationally Critically Endangered, the Greater Glider is listed as nationally Vulnerable and the Yellow-bellied Glider is listed as regionally Vulnerable. The other species of arboreal marsupials which occur in Mountain Ash forests are the Common Ringtail Possum (*Pseudocheirus peregrinus*), Mountain Brushtail Possum (*Trichosurus cunninghami*), Sugar Glider (*Petaurus breviceps*), Feathertail Glider (*Acrobates pygmaeus*) and Eastern Pygmy Possum (*Cercartetus nanus*) (Lindenmayer et al., 2015).

We counted arboreal marsupials on our field sites between December and March each year using the stagwatching method (sensu Lindenmayer et al., 1991a). Stagwatchingis the most reliable method for surveying arboreal marsupials (Smith et al., 1989; Lindenmayer et al., 2011) and has been carefully calibrated using radio-collared animals to test observer skill in Mountain Ash and other ecosystems. The field method involves counting the number of individuals of each species of arboreal marsupial emerging from every tree with a hollow on a given survey site (Lindenmayer et al., 1991a). All hollow-bearing trees on a given site are observed simultaneously by multiple, trained observers. Stagwatching surveys commenced an hour before dusk and continue until an hour after dusk to ensure the detection of both small- and large-bodied species that have different emergence times (Lindenmayer et al., 1991c).

2.1.4 Surveys of stand structure

We completed surveys of vegetation structure at each of our 1 ha sites. At each site, we established a central 100m long transect running perpendicular from the middle of the site's front edge. We established three 10m x 10m plots straddling the transect at 10-20m, 50-60m and 90-100m. The first plot (10-20m) was set back from the site's edge to reduce edge effects. On these plots, we recorded the height and diameter of each individual live and dead woody plant over 2m tall, of all species, including dominant overstorey eucalypt trees.

3.1 Statistical analysis

Q1 and Q2: Is tree occupancy by arboreal marsupials related to tree diameter and age of the surrounding forest, controlling for the elevation of the site?

To address our first two questions, we constructed a generalized linear mixed model for the presence in a tree of any species of arboreal marsupial. The model included the following terms: diameter, site elevation, and the age of the dominant tree cohort in the stand on the site (old growth, 1939 regrowth, 1960-1990 regrowth, mixed age). The response was modelled using a Bernoulli distribution (binary response, occupancy of a tree or not) with a logistic link function. To account for dependence among the trees at the site level, we included site as a random effect in the models.

Q3: Are there inter-species differences in the relationships between tree occupancy and tree diameter and age of the surrounding forest (after controlling for site elevation)?

We extended the model constructed to answer questions 1 and 2 to allow for potential differences in the relationships between tree occupancy and diameter and forest age in the following manner. We modelled data for the most commonly occurring species: Leadbeater's Possum, Greater Glider, Mountain Brushtail Possum, and Sugar Glider. The remaining four species did not occur frequently enough to facilitate further analysis. The response variable was the occupancy of a tree by an arboreal marsupial and the linear predictor contained the following terms: species (a four level factor), diameter, forest age, elevation, and the following interactions: species x diameter, species x forest age and species by elevation. We included two random effects in the analysis: site and tree. Site, as before, accounted for the dependence among the trees at a given site and the tree-level random effect accounted for the dependence among the species at a given tree.

We limited our analyses of relationships between tree occupancy and diameter to data gathered on our 119 field sites prior to the 2009 wildfires. This was because wildfire (irrespective of severity) has major negative impacts on animal occurrence with burned sites supporting almost no animals (Lindenmayer et al., 2013).

Q4. Are there differences in the diameter of hollow-bearing trees occupied by arboreal marsupials and the diameter of non-hollow-bearing-bearing trees?

We modelled the diameter of three different types of trees: **(1)** living and dead hollow-bearing trees with evidence of occupancy by arboreal marsupials emerging (i.e. occupancy), **(2)** hollow-bearing trees with no evidence of occupancy by arboreal marsupials prior to the 2009 wildfire, and **(3)** living 1939 regrowth trees that we measured in the three 10m x 10m plots (these trees showed no visible evidence of hollow development). We selected stands dominated by 1939 regrowth forest because the age class distribution in Mountain Ash forests means that these trees are now the next nearest cohort of large old trees in these ecosystems given the scarcity of the old growth estate (< 1.16% of forest cover in the Central Highlands region; (Lindenmayer et al., 2012a)). We restricted our analyses to 40 sites that remained unburned in the 2009 wildfires because measurements on burned sites would have included substantial regrowth and including these trees would have biased the results.

We assumed a Gaussian distribution for diameter and included elevation and a random effect of site to account for dependence among the trees observed at the site.

We employed Bayesian inference methods for all models and they were implemented in R (R Core Team 2015) using the brm function from brms package (Buerkner 2016). We employed non-informative priors on all model parameters and ran four parallel chains for 10 000 iterations, discarding the initial burn in of 2 000 iterations with a thinning factor of four, yielding 8000 posterior samples. Convergence was established using the CODA package (Plummer et al., 2006). Posterior inference consisted of posterior medians and 95% credible intervals.

4.1 Results

We measured the diameter of 854 hollow-bearing Mountain Ash trees on our 119 field sites. The number of hollow-bearing trees per site ranged from 1 to 23 with a mean of 7.2 per site. The average diameter of all measured hollow-bearing trees was 1.76m with a range of 0.40m to 4.40m. An additional 184 trees that regenerated after the 1939 fires were measured in 2015 in the 10m x 10m vegetation structure plots on 40 of our 119 field sites that remained unburned in the 2009 wildfires. The average diameter of the 1939 trees was 0.57m with a range of 0.45m to 1.2m.

From our stagwatching surveys, we recorded Leadbeater’s Possum emerging from 44 hollow-bearing trees, Greater Glider from 132 trees, Mountain Brushtail Possum from 107 trees, Sugar Glider from 29 trees, Yellow-bellied Glider from 12 trees, Common Ringtail Possum from 11 trees, Feathertail Glider from two trees, and Eastern Pygmy Possum from one tree, with a total of 265 emergences of any species of arboreal marsupial. Table 1 shows the percentage of occupied trees by the age of the forest surrounding those trees.

Table 1. Percentage emergence from a given hollow-bearing tree prior to the 2009 fire, according to the age of the stand surrounding particular trees and species of arboreal marsupial. The total number of hollow-bearing trees assessed in each age group is given in parentheses.

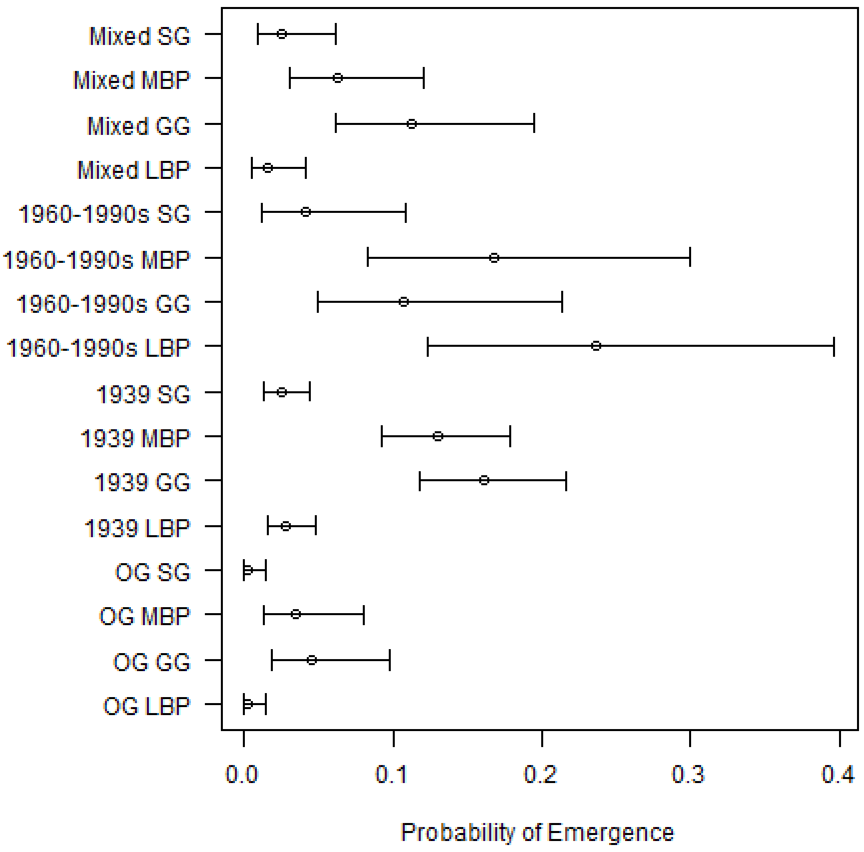
		Stand Age		
Occupancy by:	**Old growth**	**1939**	**1960-1990**	**Mixed age**
	(156)	**(444)**	**(75)**	**(179)**
Leadbeater's Possum	0.6	4.5	22.7	3.4
Greater Glider	8.3	18.7	17.3	12.9
Mountain Brushtail Possum	5.8	15.3	18.7	8.9
Sugar Glider	0.6)	3.6	6.7	3.9
Any species	17.9	34.2	48.0	27.4

4.1.1 Relationship between tree occupancy by any arboreal marsupial, tree diameter and the age of the surrounding forest

We found that the occupancy of a hollow-bearing tree by any species of arboreal marsupial was positively associated with tree diameter (posterior mean slope= 0.43, 95% credible interval [0.15, 0.72] and lowest on sites dominated by old growth) (see Appendix 1; Figure 2).

Figure 2. Probability of occupancy by stand age and species of arboreal marsupial, for a tree of average diameter and a site of average elevation. We present posterior means and 95% credible intervals for each of the 16 combinations of stand age and species. Responses are shown for Sugar Glider (SG), Mountain Brushtail Possum (MTB), Greater Glider (GG) and Leadbeater's Possum (LBP) in relation to mixed aged stands (mixed), stands regenerating

between 1960 and 1990s (1960-1990s), stands regenerating after the 1939 fires (1939) and old growth (OG).

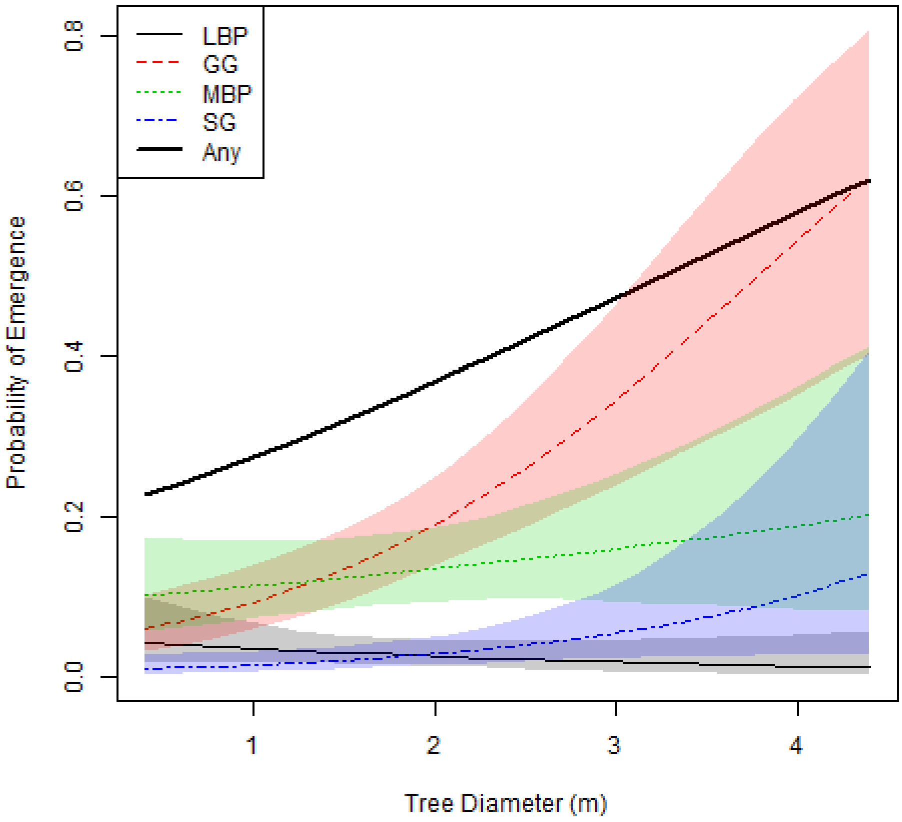


4.1.2 Relationship between tree occupancy by individual species of arboreal marsupials, tree diameter and the age of the surrounding forest

Two species of arboreal marsupial showed positive relationships between the probability of occupancy and diameter of hollow-bearing trees: Greater Glider (posterior mean slope, 0.82, [95% credible interval, 0.49, 116]) and Sugar Glider (posterior mean slope, 0.67, [95% credible interval, 0.09, 1.25]) (Figure 3; Appendix 1). Leadbeater's Possum (posterior mean slope, -0.34, [95% credible interval, -0.89, 0.22]) and Mountain Brushtail Possum (posterior mean slope, 0.20, [95% credible interval, -0.17, 0.56]) showed no relationship between occupancy and hollow-bearing tree diameter. The slope for diameter relationship for Greater Glider was greater than both the slope for the relationship for

Leadbeater's Possum (difference in slope = 1.15, 95% credible interval [0.52, 1.77]) and the Mountain Brushtail Possum (difference in slope = 0.62, [95% credible interval = 0.17, 1.07]). In addition, the slope of the relationship for the Sugar Glider was greater than Leadbeater's Possum slope (difference in slope = 1.01, [95% credible interval = 0.25, 1.80]) (Appendix 1).

Figure 3. Relationships between tree diameter and the probability of occupancy of a hollow-bearing tree by Leadbeater's Possum (LBP), the Greater Glider (GG), the Mountain Brushtail Possum (MBP), the Sugar Glider (SG), and any species of arboreal marsupial (ANY). Estimates were computed for a 1939-aged stand at an average elevation. Pointwise 95% credible intervals are depicted as shaded regions. Note, that the 95% credible intervals are not displayed for the relationship for any species of arboreal marsupial.



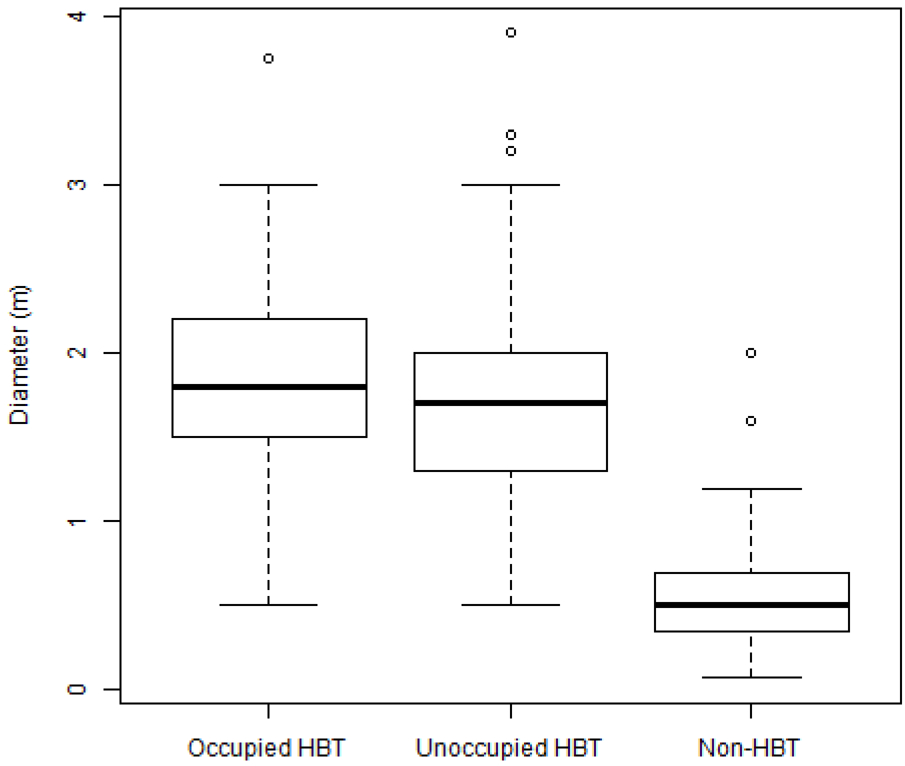
Tree occupancy was influenced by the age of surrounding forest (at an average tree diameter and elevation) for some species (Table 1). In old growth forests, the occupancy of hollow-bearing trees by the Greater Glider was higher than for Leadbeater's Possum (Odds Ratio = 25.98, 95% credible interval [3.21, 638.59]) and the Sugar Glider (Odds Ratio = 25.13, [95% credible interval = 3.31, 585.96]). Similarly, the occupancy of hollow-bearing trees by the Mountain Brushtail Possum was higher than for Leadbeater's Possum (Odds Ratio = 19.84, [95% credible interval = 2.39, 461.60]) and Sugar Glider (Odds Ratio = 19.20, [95% credible interval = 2.36, 424.25]). Such occupancy patterns exhibited by these species in old growth forests also was observed in 1939 and mixed aged forests. However, in 1960-1990s aged stands, occupancy of hollow-bearing trees by Leadbeater's Possum was greater than that for the Greater Glider (Odds Ratio = 2.56, [95% credible interval = 1.04, 6.45]) and the Sugar Glider (Odds Ratio = 7.27, [95% credible interval = 2.32, 26.09]); occupancy of hollow-bearing trees by the Mountain Brushtail Possum were higher than the Sugar Glider in stands dating from 1960-1990 (Odds Ratio = 4.77, [95% credible interval = 1.50, 17.39]) (see Appendix 1 for more details).

Leadbeater's Possum and the Mountain Brushtail Possum were more likely to occupy a given hollow-bearing tree on sites at high elevation (Appendix 2) with the remaining species exhibiting no such elevational responses.

4.1.3 Differences in the diameter of hollow-bearing trees occupied by arboreal marsupials and the diameter of non-hollow-bearing trees

Our analyses revealed that for a site at average elevation, the diameter of occupied hollow-bearing trees (mean diameter 1.87m, 95% credible interval [1.67, 1.91]) was larger than both unoccupied hollow-bearing trees (1.71m, [1.60, 1.80]) and non-hollow-bearing trees that regenerated after the 1939 wildfires (0.57m [0.47, 0.67]) (see Figure 4; Appendix 1). Unoccupied hollow-bearing trees also were larger in diameter than non-hollow-bearing trees that regenerated after the 1939 wildfires (see Figure 4; Appendix 1).

Figure 4. Diameter and occupancy of trees: hollow-bearing trees (HBT) occupied by an arboreal marsupial, hollow-bearing trees that remained unoccupied by an arboreal marsupial, non-hollow-bearing trees for the 40 unburned field sites in our study.



5.1 Discussion

Hollow-bearing trees are keystone structures in many ecosystems worldwide (Lindenmayer and Laurance 2016). Their role in providing denning and/or nesting sites for cavity-dependent fauna has been demonstrated in numerous forest types and other treed environments globally (Rose et al., 2001; Gibbons and Lindenmayer 2002; Remm and Lohmus 2011). Our analyses contained evidence of: **(1)** interspecific differences in the diameter of hollow-bearing trees occupied by arboreal marsupials (Figure 3), and **(2)** the occupancy at the individual hollow-bearing tree level being influenced by the age of the surrounding forest as well as elevation (for two species of arboreal marsupial). Hollow-bearing trees occupied by arboreal marsupials were larger in diameter than unoccupied hollow-bearing trees. In addition, the mean diameter of both occupied and unoccupied hollow-bearing trees was almost three times that of non-hollow-bearing trees that regenerated after the 1939 wildfires (Figure 4). We discuss our key findings in the remainder of Section 5.1 and conclude with a commentary on implications for forest management and biodiversity conservation.

5.1.1 Relationships between tree occupancy and tree diameter

Consistent with our predictions associated with answering Question #1 posed at the outset of this investigation (Are there relationships between tree diameter and tree occupancy by arboreal marsupials?), we found strong positive relationships between the diameter of hollow-bearing trees and the probability of occupancy by any species of arboreal marsupial *per se* and the Greater Glider in particular. Essentially, trees with hollows were larger than trees without hollows, and even among the subset of trees that had hollows, the larger trees had a greater occupancy rate than smaller ones. These positive relationships were expected given that relative to smaller and younger trees, larger (and therefore typically older) trees support greater volumes of dead wood tissue and heartwood that, over time, are subject to attack by termites, fungi and other decay agents (Perry et al., 1985; Gibbons and Lindenmayer 2002). Because this decay process generally takes many decades and is the most common way hollows develop in these forests, cavities are less common in smaller, younger trees. Large old trees also have senescing crowns with large branches. When these branches or even the apical stem of the tree break (often in storms), the resulting stub may form cavities of sufficient size for arboreal marsupials, unlike the branches of younger trees (Mackowski 1987; Lindenmayer et al., 1993; Lindenmayer et al., 2000b).

Among the trees with hollows that we surveyed, tree diameter did not appear to influence the probability of occupancy by either Leadbeater's Possum or the Mountain Brushtail Possum (Figure 3; Appendix 3). We note that this part of our analysis focused on trees that were already large (the mean diameter of hollow-bearing trees *per se* was 1.76 m) and amongst this set of large trees, diameter influenced some species of arboreal marsupials but not others. This indicates interspecific differences in occupancy-tree diameter relationships, congruent with predictions from Question #2 posed at the outset of this investigation (*viz*: Are there inter-specific differences in the diameter of trees selected by different species of arboreal marsupials?). Leadbeater's Possum is a relatively small-bodied species (weighing ~120 grams) whereas the Mountain Brushtail Possum is the largest arboreal marsupial in Mountain Ash forests (weighing ~3+ kg). This suggests that interspecific variation in occupancy-tree diameter relationships is not always clearly linked with cavity size-body size relationships. Other factors, therefore, must have important effects on occupancy patterns. For instance, distinction between live and dead trees, and the stage of decay of trees, may influence their occupancy by the different species of arboreal marsupial (Gibbons et al., 2002). Tree decay stage may influence the size, height, type and entrance shape of hollows. The thermal dynamics of cavities within hollow-bearing trees also may vary between live and dead trees, for example, the amount of water in the xylem providing insulation within living trees and additional heat generated by rotting wood inside dead trees. There also may be inter-relationships between thermal properties of trees and the social organization and thermoregulatory requirements of some species. Leadbeater's Possum, for example, is colonial and builds large nests of interwoven bark streamers whereas the Mountain Brushtail Possum is generally solitary or lives in pairs and does not construct a nest.

5.1.2 Tree occupancy and surrounding stand age

Stands of old growth Mountain Ash forest support significantly more hollow-bearing trees than forests in other age cohorts (Lindenmayer et al., 2000a; Lindenmayer et al., 2016) and arboreal marsupials can be more numerous in old growth forests (Lindenmayer et al., 1990b; Lindenmayer et al., 1999). The third question in this study examined occupancy at the individual tree level and sought to determine if occupancy of hollow-bearing trees was influenced by the age of the surrounding forest. Our analyses revealed that, for all species of arboreal marsupial, the probability of occupancy of an individual hollow-bearing tree was lowest in old growth stands (Figure 2; Appendix 1). Earlier research (Banks et al., 2013) found that the relationship between animal abundance and hollow-bearing tree abundance was positive, but less than 1:1. This was due primarily to a significant increase by all species in the proportional use of hollow-bearing trees where the abundance of this resource was low (Banks et al., 2013). These earlier results also suggest that other resources or social constraints become limiting for arboreal marsupials under conditions of high hollow-bearing tree availability, such as that found in old growth forest. Conversely, low levels of abundance of hollow-bearing trees in younger aged forests mean that cavity-dependent arboreal marsupials have little choice other than to occupy the fewer remaining nest trees in these kinds of forests where alternative nesting resources are depleted (see Banks et al., 2013). That is, the marginal value of a given large hollow-bearing tree for occupancy may be higher in stands dominated by otherwise much younger-aged forest and where such important nesting and denning resources are uncommon or rare (Fischer et al., 2010). However, we note there is likely to be a threshold level for hollow tree abundance (and possibly spatial distribution) below which animals will be unable to persist; a pattern that appears to be reflected in the increasing number of long-term survey sites in our monitoring program that no longer support hollow-bearing trees or arboreal marsupials (Lindenmayer et al., unpublished data).

Critically, the larger diameter trees found in regrowth forest are in fact old growth elements and in the absence of these trees, arboreal marsupials do not occur in regrowth forests.

5.1.3 Contrasts in the diameter of hollow-bearing trees and non-hollow-bearing trees

Answering our fourth question (Are there differences in the diameter of hollow-bearing trees occupied by arboreal marsupials and the diameter of non-hollow-bearing trees?) revealed that the mean diameter of hollow-bearing trees was almost three times that of non-hollow-bearing trees that regenerated after the 1939 wildfires (Figure 4). This result was expected given that earlier work (e.g. Ambrose 1982) suggests that Mountain Ash trees are typically 120 years old before they **first** begin to start developing obvious cavities. This is more than 40 years older that the 77-year old trees in stands that regenerated after the 1939 wildfires and for which we made comparisons in this study. We note, however, that given the large (three-fold) differences in the mean diameter of occupied hollow-bearing trees versus non-hollow-bearing trees, that it may be substantially more than an additional 40 years before existing 1939 regrowth trees become suitable denning and nesting sites for arboreal marsupials. Indeed, based on relationships between tree diameter and tree age (e.g. see Ashton 1976), our data on tree diameter and occupancy suggest that existing 77 year old 1939 regrowth trees will need to reach, on average, approximately 190 years of age (1.87m dbh) before they become suitable nest sites for some of the species of arboreal marsupials targeted in this study.

Some forest managers have suggested that the time until cavity development might be brought forward by strategic thinning of stands to accelerate the diameter increments of unthinned trees. However, we note that cavity development in large trees is as much a function of decay processes (e.g. physiological changes that impair successful lateral branch occlusion; (Gibbons and Lindenmayer 2002)) as it is about overall, tree size. Hence, the likely success (or otherwise) of accelerated tree growth in promoting cavity development remains unclear (Lindenmayer 2016). Moreover, the time elapsed until existing non-hollow-bearing trees eventually develop cavities, especially those suitable for use by arboreal marsupials, is likely to be prolonged, even if the surrounding stands are thinned. A further issue is that thinning operations can damage understory vegetation that provides important foraging resources for some species of arboreal marsupials (Seebeck et al., 1984; Smith 1984).

In summary, our analyses indicate that the occupancy of hollow-bearing trees is influenced by a range of factors. These include those at the tree-level such as tree diameter, but also stand-level attributes like stand age as well as elevation (that is a landscape attribute).

5.1.4 Fire-damaged regrowth trees and their suitability as nest and den sites for arboreal marsupials

Many of the hollow-bearing trees in this study were large trees killed or fire-scarred in fires in 1939 and 1983 and that have remained standing until now. Many of these trees are collapsing and at a rapid rate; 41% of a population of more than 1170 hollow-bearing trees first measured in 1997 had collapsed by 2015 (Lindenmayer et al., 2016). More than 50 000 ha of montane ash forest was burned in wildfires in 2009 (Berry et al., 2015; Lindenmayer et al., 2015). Much of the fire-killed forest was aged 70-years or younger at the time of the 2009 fires and it remains unclear whether these dead trees will become eventually suitable nest sites for arboreal marsupials. However, the diameter-occupancy relationships quantified in this study (Figure 2; Figure 4) suggest that it is unlikely that these trees will be of sufficient diameter to support cavities of sufficient internal volume to be suitable nesting sites for most species of arboreal marsupials.

The future availability of fire-killed trees as potential nest sites for arboreal marsupials is dependent not only on these trees being of sufficient diameter to develop cavities of suitable size for these animals but also remaining standing long enough for cavities to eventually develop. Past research has indicated smaller diameter trees are more likely to collapse than larger ones, not only in Mountain Ash forests (Lindenmayer et al., 1990a) but in a range of other forest types worldwide (e.g. Keen 1955). This also suggests that regrowth trees killed in the 2009 fires are unlikely to eventually become suitable hollow-bearing trees for arboreal marsupials in the future. If this is the case, then it is important that forest managers allow the amount of old growth Mountain Ash forest to increase and thereby ensure that, in the event of future fires, trees that are killed or fire-scarred are of a size that they are likely to remain standing long enough and be able to support cavities of sufficient internal volume that will eventually become suitable hollow-bearing trees for cavity-dependent arboreal marsupials.

5.1.5 Management implications

The findings of our study have some important implications for the management of Mountain Ash forests as large diameter hollow-bearing trees are favoured nesting and denning sites for many species of arboreal marsupials. Other work has indicated that these trees are declining rapidly in both spatial distribution and abundance within Mountain Ash forests (Burns et al., 2015; Lindenmayer et al., 2016). Moreover, the existing areas of old growth forest where these trees are most abundant is extremely limited (< 1.16% of the forest estate) and the protection of regrowth forest to recruit extensive new stands of old growth forest is critical. We argue that forest managers must better protect all existing hollow-bearing trees, this includes in regrowth forest where populations of such trees can often be limited but their marginal value is high (as reflected by high levels of per-tree occupancy). A further critical reason why the protection of existing hollow-bearing trees is important is that the diameter relationships we have quantified here suggest it will be a prolonged period, likely exceeding another 100 years, before trees that currently lack cavities will eventually develop these critical structures suitable for occupancy by arboreal marsupials.

Unfortunately, many hollow-bearing trees are directly or indirectly destroyed by logging operations in Mountain Ash forests and this will threaten the viability of Critically Endangered species like Leadbeater's Possum (Todd et al., 2016) as well as negatively affect populations of other cavity-dependent fauna (Lindenmayer et al., 2015).

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Appendix 1. Emergence model comparing species. The reference category (intercept) corresponds to Leadbeater's Possum on an old growth stand. Note: model parameters are on the logit scale, while the stand age comparisons are given on the odds ratio scale.

Parameter	**Estimate**	**l-95% CI**	**u-95% CI**
Intercept	-9.16	-13.29	-5.68
Species: GG	5.34	1.83	9.49
Species: MBP	3.33	-0.31	7.56
Species: SG	0.56	-4.53	5.67
Diameter (m)	-0.34	-0.89	0.22
Stand Age: 1939	2.77	0.64	5.92
Stand Age: 1960-1990s	5.14	2.89	8.34
Stand Age: Mixed	2.18	-0.11	5.37
Elevation (km)	4.46	1.38	7.60
Species: GG x Diameter (m)	1.15	0.52	1.77
Species: MBP x Diameter (m)	0.54	-0.11	1.17
Species: SG x Diameter (m)	1.01	0.25	1.80
Species: GG x Stand Age 1939	-1.36	-4.53	0.83
Species: MBP x Stand Age 1939	-1.34	-4.51	0.86
Species: SG x Stand Age 1939	-0.16	-3.84	3.63
Species: GG x Stand Age 1960-1990s	-4.20	-7.48	-1.88
Species: MBP x Stand Age 1960-1990s	-3.41	-6.71	-1.08
Species: SG x Stand Age 1960-1990s	-2.02	-5.77	1.92
Species: GG x Stand Age.Mixed	-1.19	-4.42	1.18
Species: MBP x Stand Age.Mixed	-1.55	-4.77	0.77
Species: SG x Stand Age.Mixed	0.46	-3.29	4.34
Species: GG x Elevation (km)	-5.34	-8.58	-2.19
Species: MBP x Elevation (km)	-1.67	-4.97	1.60
Species: SG x Elevation (km)	-2.99	-7.06	1.05
Site RE SD	0.84	0.61	1.09
Tree RE SD	0.45	0.03	0.85
Species Diameter relationships			
Leadbeater's Possum (LBP)	-0.34	-0.89	0.22
Greater Glider (GG)	0.82	0.49	1.16
Mountain Brushtail Possum (MBP)	0.20	-0.17	0.56
Sugar Glider (SG)	0.67	0.09	1.25
Differences in slopes			
GG vs LBP	1.15	0.52	1.77
MBP vs LBP	0.54	-0.11	1.17
SG vs LBP	1.01	0.25	1.80
MBP vs GG	-0.62	-1.07	-0.17
SG vs GG	-0.14	-0.80	0.48
SG vs MBP	0.47	-0.19	1.13
Species Elevation relationships			
Leadbeater's Possum (LBP)	4.46	1.38	7.6
Greater Glider (GG)	-0.88	-2.70	0.93
Mountain Brushtail Possum (MBP)	2.79	0.80	4.80
Sugar Glider (SG)	1.47	-1.59	4.61

Differences in slopes			
GG vs LBP	-5.34	-8.58	-2.19
MBP vs LBP	-1.67	-4.97	1.60
SG vs LBP	-2.99	-7.06	1.05
MBP vs GG	3.67	1.50	5.92
SG vs GG	2.35	-0.82	5.65
SG vs MBP	-1.31	-4.62	2.07
Stand Age comparisons			
Old Growth– Odds Ratios			
GG vs LBP	25.98	3.21	638.59
MBP vs LBP	19.84	2.39	461.60
SG vs LBP	1.03	0.03	37.32
MBP vs GG	0.76	0.29	1.97
SG vs GG	0.04	0.00	0.30
SG vs MBP	0.05	0.00	0.42
1939 – Odds Ratios			
GG vs LBP	6.69	3.86	12.37
MBP vs LBP	5.19	2.96	9.50
SG vs LBP	0.88	0.42	1.86
MBP vs GG	0.78	0.53	1.13
SG vs GG	0.13	0.07	0.24
SG vs MBP	0.17	0.09	0.30
1960-1990s – Odds Ratios			
GG vs LBP	0.39	0.15	0.96
MBP vs LBP	0.66	0.27	1.56
SG vs LBP	0.14	0.04	0.43
MBP vs GG	1.68	0.68	4.21
SG vs GG	0.35	0.10	1.13
SG vs MBP	0.21	0.06	0.67
Mixed Age – Odds Ratios			
GG vs LBP	7.94	2.95	25.35
MBP vs LBP	4.20	1.48	13.64
SG vs LBP	1.64	0.46	5.69
MBP vs GG	0.53	0.25	1.11
SG vs GG	0.21	0.07	0.52
SG vs MBP	0.39	0.13	1.02

Appendix 2. Diameter comparisons between 1939 regrowth (non-hollow-bearing trees), hollow-bearing trees unoccupied by arboreal marsupials and hollow-bearing trees occupied by arboreal marsupials. The reference category (intercept) corresponds to occupied hollow-bearing trees.

	Estimate	**l-95% CI**	**u-95% CI**
Intercept	1.88	1.45	2.29
Hollow-bearing tree: Unoccupied	-0.09	-0.21	0.03
Non-hollow-bearing-trees	-1.22	-1.34	-1.1
Elevation (km)	-0.11	-0.63	0.42
sd(Intercept)	0.23	0.16	0.31
Estimated mean diameter at an average Elevation Site			
Hollow-bearing tree: Occupied	1.79	1.67	1.91
Hollow-bearing tree: Unoccupied	1.70	1.60	1.80
Non-hollow-bearing tree: Occupied	0.57	0.47	0.67
Differences			
Hollow-bearing tree: Occupied – Unoccupied	0.19	0.03	0.21
Hollow-bearing tree: Occupied – Non-hollow-bearing tree	1.22	1.10	1.34
Hollow-bearing tree: Unoccupied – Non-hollow-bearing tree	1.13	1.03	1.23

Appendix 3. Emergence model for tree occupancy by any marsupial. The reference category (intercept) corresponds to an old growth stand age. Note that model parameters are on the logit scale, while the stand age comparisons are given on the odds ratio scale.

Any species of arboreal marsupial

Parameter	**Estimate**	**l-95% CI**	**u-95% CI**
Intercept	-3.31	-4.92	-1.75
Diameter (m)	0.43	0.15	0.72
Stand Age:1939	1.23	0.45	2.03
Stand Age:1960-1990s	1.75	0.77	2.79
Stand Age: Mixed	0.90	-0.03	1.84
Elevation (km)	0.88	-0.75	2.52
Site RE SD	0.90	0.63	1.22
Stand Age Comparisons: Odds Ratios			
1939 vs OG	3.43	1.57	7.62
1960-1990s vs OG	5.76	2.15	16.2
Mixed vs OG	2.46	0.97	6.27
1960-1990s vs 1939	1.68	0.79	3.60
Mixed vs 1939	0.72	0.37	1.37
Mixed vs 1960-1990s	0.43	0.17	1.05