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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

24 Abstract

25 Hollow-bearing trees are keystone structures in many ecosystems worldwide and they play
26 critical habitat roles for a vast array of fauna through providing denning and/or nesting sites.
27 We quantified empirical relationships between the diameter of hollow-bearing trees and
28 probability of occupancy of these trees by cavity-dependent arboreal marsupials in the
29 Mountain Ash (*Eucalyptus regnans*) forests of the Central Highlands of Victoria, south-
30 eastern Australia. We also quantified the effects of other variables such as stand age and
31 elevation on tree occupancy. Finally, we compared the diameter of occupied and unoccupied
32 hollow-bearing trees with non-hollow-bearing trees in 77-year old forest that regenerated
33 after fires in 1939 and form the dominant age cohort of trees in our study region.
34 Hollow-bearing trees occupied by arboreal marsupials had a larger diameter than unoccupied
35 hollow-bearing trees. The mean diameter of both occupied and unoccupied hollow-bearing
36 trees was almost three times that of 1939-aged trees that did not contain hollows. Our
37 analyses contained evidence of inter-specific differences in the diameter of hollow-bearing
38 trees occupied by different species of arboreal marsupials. Beyond the influence on
39 occupancy of tree-level factors such as diameter, we also found that the probability of
40 occupancy of a hollow-bearing tree was affected by the age of the surrounding forest and
41 landscape attributes such as elevation. The probability of occupancy of an individual hollow-
42 bearing tree was highest when that tree was located in regrowth forest, most likely because of
43 the scarcity of these critical nesting and denning resources in such stands.
44 Populations of large hollow-bearing trees, including those typically selected for occupancy by
45 arboreal marsupials, are in rapid decline in Mountain Ash forests. This decline, coupled with
46 the prolonged period until current cohorts of existing younger trees eventually reach an age
47 (and therefore diameter) that are suitable for occupancy by arboreal marsupials, underscores
48 the critical need to protect all existing hollow-bearing trees from practices that can otherwise

49 destroy them, including industrial clearfelling operations. Better protection is important not
50 only in the small remaining areas of old growth Mountain Ash forest but also in regrowth
51 forest where such trees are scarce and have high marginal value as nesting sites, as reflected
52 by high rates of per tree occupancy rates in stands of this age.

53

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

56

57 **1.1 Introduction**

58 Large old trees are a critical structural feature of many ecosystems worldwide and
59 they have several key characteristics not found in small young trees or small old trees
60 (Lindenmayer and Laurance 2016). One of these characteristics is the presence of cavities
61 that provide nesting and denning sites for a wide range of fauna globally (Fischer and
62 McClelland 1983; Rose et al., 2001; Gibbons and Lindenmayer 2002; Remm and Lohmus
63 2011). Australia lacks primary cavity-excavating vertebrates such as woodpeckers, and trees
64 on the continent develop cavities in several ways, for example through the activities of
65 organisms such as fungi and termites (Perry et al., 1985; Remm and Lohmus 2011),
66 disturbances such as fires (Inions et al., 1989), and age-related changes in tree physiology
67 such as incomplete occlusion of wound tissue following damage such as stem wounding
68 and/or branch breakage (Gibbons and Lindenmayer 2002). The effects of these processes can
69 be both time and tree-size mediated, meaning that hollow-bearing trees should be the largest
70 and longest-living individuals in most ecosystems. Those trees with large cavities suitable for
71 occupancy by cavity-dependent species should be larger than unoccupied trees. We tested
72 these simple premises in an investigation from the wet Mountain Ash (*Eucalyptus regnans*)
73 forests of the Central Highlands of Victoria, south-eastern Australia.

74 Hollow-bearing trees in wet ash-type eucalypt forests can be recruited over prolonged
75 periods of ontological development meaning that such trees are typically most abundant in
76 old growth forests (Lindenmayer et al., 2000a). Hollow-bearing trees also may develop in
77 pulses or cohorts as a result of major disturbance events such as wildfires (Gibbons and
78 Lindenmayer 2002). For example, large numbers of hollow-bearing trees in Mountain Ash
79 forests were created when old growth trees and stands were burned in high-severity, stand-
80 replacing wildfires in 1939 (Lindenmayer et al., 1991b). In contrast, stands subject to
81 clearfell logging commonly retain few or no live or dead large old trees, and new hollow-

82 bearing trees will typically take over 120 years to form (Ambrose 1982). Importantly,
83 hollow-bearing trees in Mountain Ash forests are critical nesting and denning sites for an
84 array of species of cavity-dependent vertebrates including eight species of arboreal
85 marsupials such as the Critically Endangered Leadbeater's Possum (*Gymnobelideus*
86 *leadbeateri*) (Lindenmayer et al., 2015) and the nationally vulnerable Greater Glider
87 (*Petauroides volans*) and regionally vulnerable Yellow-bellied Glider (*Petaurus australis*).
88 Specifically, we posed four key questions in this study:

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

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

100 **Q2: *Is the occupancy of hollow-bearing trees by arboreal marsupials influenced the age of***
101 ***the surrounding forest?*** At the outset of this study, we were agnostic about the kinds of
102 relationships that might occur between tree occupancy and the age of the surrounding forest.
103 Potentially, the proportion of hollow trees used per animal may vary with hollow tree
104 availability (for instance, due to changes in resource sharing; (Banks et al., 2011) or due to
105 resources other than the availability of hollow trees limiting animal occurrence (Banks et al.,
106 2013). For example, the probability of occupancy of individual hollow-bearing trees may be

107 reduced in old growth forests where animals have access to many alternative trees; that is, the
108 marginal value of a given tree will be lower where there are already many hollow-bearing
109 trees (Fischer et al., 2010). Conversely, the probability of occupancy of trees in old growth
110 forest may be greater because of the suitability of surrounding areas as a food source for
111 particular species (Lindenmayer et al., 1990b). In addition to test for the effects of stand age,
112 we also sought to determine tree occupancy was influenced by factors such as the elevation
113 of the site in which trees were located.

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

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

126 **Q4: *Are there differences in the diameter of hollow-bearing trees occupied by arboreal***
127 ***marsupials and the diameter of non-hollow-bearing trees?*** For this analysis, we focused on
128 stands of trees that regenerated following the 1939 wildfires. We targeted this age class
129 because it is the dominant age cohort in Mountain Ash forests and given the current lack of
130 old growth forest in this ecosystem (< 1.16% of the estate (Lindenmayer et al., 2012a)), trees
131 in these stands will be the next ones to develop into old growth if they are able to reach

132 ecological maturity (Lindenmayer et al., 2015). Cavities in 77-year-old trees are very rare and
133 typically lack the depth required for use by arboreal marsupials. As cavities typically develop
134 in older and therefore larger Mountain Ash trees (Lindenmayer and Laurance 2016), we
135 postulated that hollow trees would be significantly larger than other Mountain Ash trees that
136 lacked cavities in the surrounding stand.

137 Populations of large old hollow-bearing trees are declining in many (although not all)
138 ecosystems globally (Lindenmayer et al., 2012b; Lindenmayer and Laurance 2016). Such
139 declines characterise Mountain Ash forests in the Central Highlands of Victoria (Burns et al.,
140 2015). The loss of these trees will likely have corresponding negative conservation outcomes
141 for an array of cavity-dependent species, including arboreal marsupials. Therefore, better
142 understanding of the patterns of occupancy of trees of different sizes and contexts (i.e.
143 relative to surrounding stand conditions) will have important implications for how to best
144 manage ecosystems where hollow-bearing trees are keystone structures (sensu Tews et al.,
145 2004).

146 **2.1 Methods**

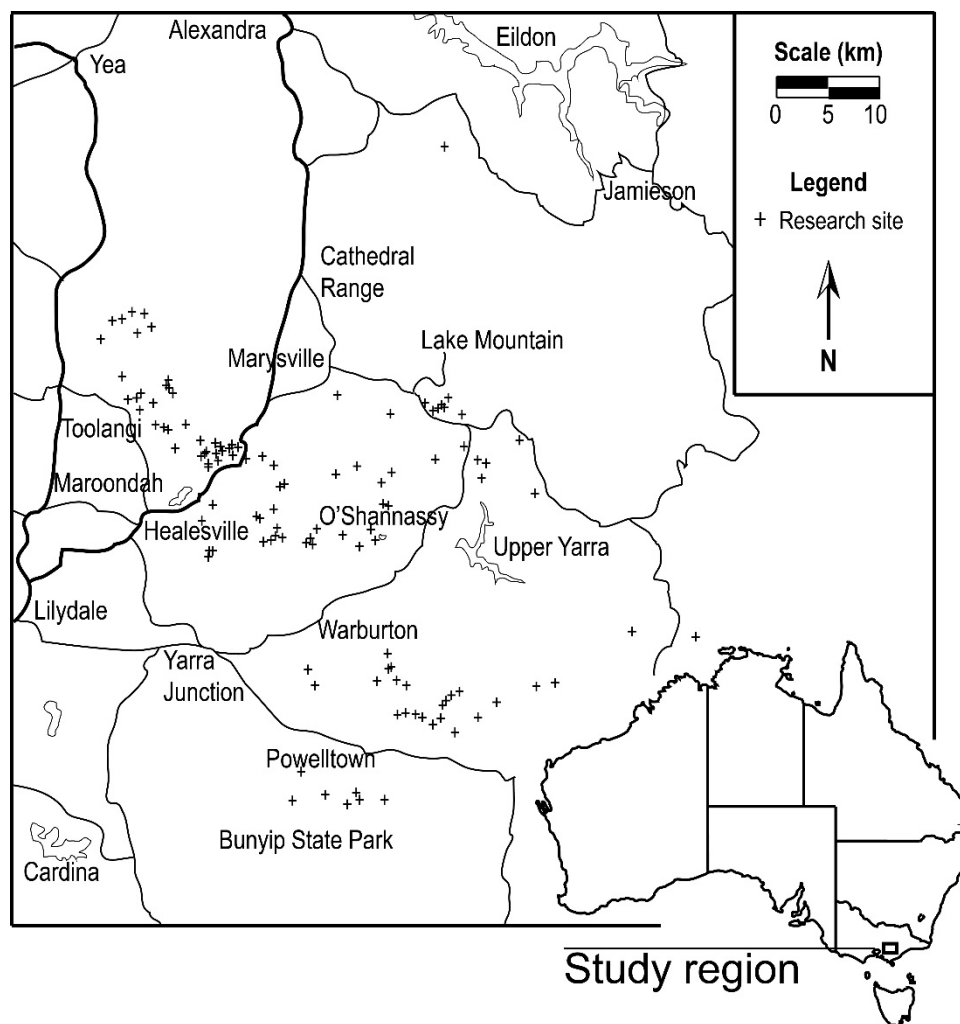
147 **2.1.1 Study area**

148 We completed this study in the Mountain Ash forests of the Central Highlands of
149 Victoria, south-eastern Australia (Figure 1). We established 119 long-term ecological
150 research sites in the study region (Lindenmayer et al., 2003). Each of these sites measured 1
151 ha in size and were well distributed throughout the study region, covering a wide range of
152 variation in environmental conditions. Our sites varied in slope (inclination: 2-38°), elevation
153 (220-1040 m), topographic position (gully, midslope, ridge) and aspect (assigned to one of
154 the following categories: north, east, south, west). At the outset of this investigation (1997),
155 we assigned our 119 field sites to one of four stand age classes: old growth (stands where the
156 dominant age class of the overstorey had established pre-1900), stands that regenerated after

157 the major wildfires in 1939, stands that regenerated after logging conducted between 1960-
 158 1990, and stands of overstorey trees of mixed age.

159

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



162

163

164 We completed three kinds of repeated surveys on our 119 field sites: **(1)** surveys of
 165 arboreal marsupials, **(2)** measurements of hollow-bearing trees, and **(3)** measurements of
 166 vegetation structure, primarily stand age. We briefly describe these surveys and associated
 167 measurements in Section 2.1.2. Notably, more than 50 000 ha of Mountain Ash forest was

168 burned in wildfires in 2009 (Berry et al., 2015; Lindenmayer et al., 2015) and this demanded
169 subsetting of some datasets for subsequent statistical analyses (see below).

170 **2.1.2 Surveys of hollow-bearing trees**

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

176 **2.1.3 Occupancy of hollow-bearing trees by arboreal marsupials**

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

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

193 small- and large-bodied species that have different emergence times (Lindenmayer et al.,
194 1991c).

195 **2.1.4 Surveys of stand structure**

196 We completed surveys of vegetation structure at each of our 1 ha sites. At each site,
197 we established a central 100m long transect running perpendicular from the middle of the
198 site's front edge. We established three 10m x 10m plots straddling the transect at 10-20m, 50-
199 60m and 90-100m. The first plot (10-20m) was set back from the site's edge to reduce edge
200 effects. On these plots, we recorded the height and diameter of each individual live and dead
201 woody plant over 2m tall, of all species, including dominant overstorey eucalypt trees.

202 **3.1 Statistical analysis**

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

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

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

214 We extended the model constructed to answer questions 1 and 2 to allow for potential
215 differences in the relationships between tree occupancy and diameter and forest age in the
216 following manner. We modelled data for the most commonly occurring species: Leadbeater's
217 Possum, Greater Glider, Mountain Brushtail Possum, and Sugar Glider. The remaining four

218 species did not occur frequently enough to facilitate further analysis. The response variable
219 was the occupancy of a tree by an arboreal marsupial and the linear predictor contained the
220 following terms: species (a four level factor), diameter, forest age, elevation, and the
221 following interactions: species x diameter, species x forest age and species by elevation. We
222 included two random effects in the analysis: site and tree. Site, as before, accounted for the
223 dependence among the trees at a given site and the tree-level random effect accounted for the
224 dependence among the species at a given tree.

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

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

231 We modelled the diameter of three different types of trees: **(1)** living and dead
232 hollow-bearing trees with evidence of occupancy by arboreal marsupials emerging (i.e.
233 occupancy), **(2)** hollow-bearing trees with no evidence of occupancy by arboreal marsupials
234 prior to the 2009 wildfire, and **(3)** living 1939 regrowth trees that we measured in the three
235 10m x 10m plots (these trees showed no visible evidence of hollow development). We
236 selected stands dominated by 1939 regrowth forest because the age class distribution in
237 Mountain Ash forests means that these trees are now the next nearest cohort of large old trees
238 in these ecosystems given the scarcity of the old growth estate (< 1.16% of forest cover in the
239 Central Highlands region; (Lindenmayer et al., 2012a)). We restricted our analyses to 40 sites
240 that remained unburned in the 2009 wildfires because measurements on burned sites would
241 have included substantial regrowth and including these trees would have biased the results.

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

244 We employed Bayesian inference methods for all models and they were implemented
245 in R (R Core Team 2015) using the brm function from brms package (Buerkner 2016). We
246 employed non-informative priors on all model parameters and ran four parallel chains for 10
247 000 iterations, discarding the initial burn in of 2 000 iterations with a thinning factor of four,
248 yielding 8000 posterior samples. Convergence was established using the CODA package
249 (Plummer et al., 2006). Posterior inference consisted of posterior medians and 95% credible
250 intervals.

251 **4.1 Results**

252 We measured the diameter of 854 hollow-bearing Mountain Ash trees on our 119
253 field sites. The number of hollow-bearing trees per site ranged from 1 to 23 with a mean of
254 7.2 per site. The average diameter of all measured hollow-bearing trees was 1.76m with a
255 range of 0.40m to 4.40m. An additional 184 trees that regenerated after the 1939 fires were
256 measured in 2015 in the 10m x 10m vegetation structure plots on 40 of our 119 field sites that
257 remained unburned in the 2009 wildfires. The average diameter of the 1939 trees was 0.57m
258 with a range of 0.45m to 1.2m.

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

265

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

Occupancy by:	Stand Age			
	Old growth (156)	1939 (444)	1960-1990 (75)	Mixed age (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

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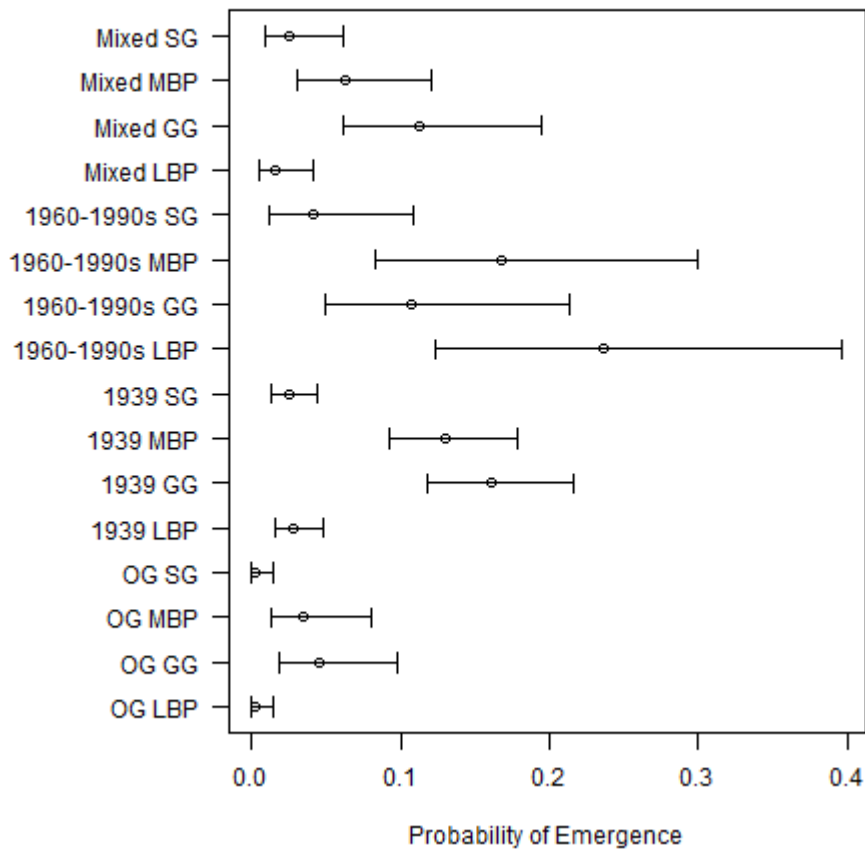
271 **4.1.1 Relationship between tree occupancy by any arboreal marsupial, tree diameter** 272 **and the age of the surrounding forest**

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

277

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

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



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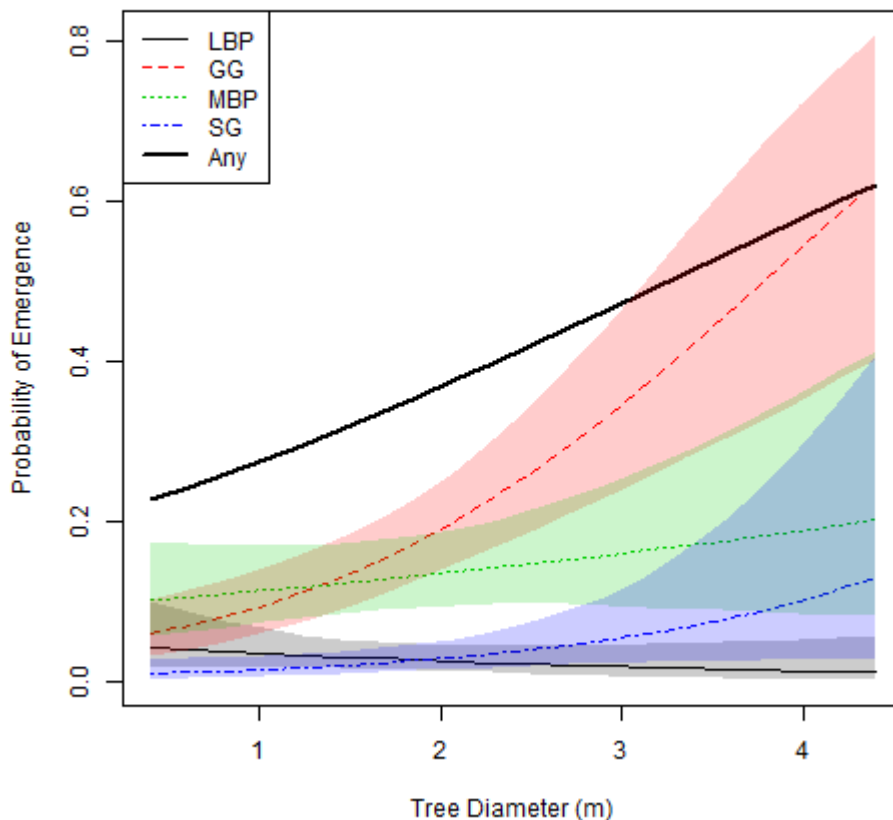
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287 4.1.2 Relationship between tree occupancy by individual species of arboreal 288 marsupials, tree diameter and the age of the surrounding forest

289 Two species of arboreal marsupial showed positive relationships between the
 290 probability of occupancy and diameter of hollow-bearing trees: Greater Glider (posterior
 291 mean slope, 0.82, [95% credible interval, 0.49, 1.16]) and Sugar Glider (posterior mean slope,
 292 0.67, [95% credible interval, 0.09, 1.25]) (Figure 3; Appendix 1). Leadbeater's Possum
 293 (posterior mean slope, -0.34, [95% credible interval, -0.89, 0.22]) and Mountain Brushtail
 294 Possum (posterior mean slope, 0.20, [95% credible interval, -0.17, 0.56]) showed no
 295 relationship between occupancy and hollow-bearing tree diameter. The slope for diameter
 296 relationship for Greater Glider was greater than both the slope for the relationship for

297 Leadbeater's Possum (difference in slope = 1.15, 95% credible interval [0.52, 1.77]) and the
 298 Mountain Brushtail Possum (difference in slope = 0.62, [95% credible interval = 0.17, 1.07]).
 299 In addition, the slope of the relationship for the Sugar Glider was greater than Leadbeater's
 300 Possum slope (difference in slope = 1.01, [95% credible interval = 0.25, 1.80]) (Appendix 1).
 301

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



308

309 Tree occupancy was influenced by the age of surrounding forest (at an average tree

310 diameter and elevation) for some species (Table 1). In old growth forests, the occupancy of

311 hollow-bearing trees by the Greater Glider was higher than for Leadbeater's Possum (Odds
312 Ratio = 25.98, 95% credible interval [3.21, 638.59]) and the Sugar Glider (Odds Ratio =
313 25.13, [95% credible interval = 3.31, 585.96]). Similarly, the occupancy of hollow-bearing
314 trees by the Mountain Brushtail Possum was higher than for Leadbeater's Possum (Odds
315 Ratio = 19.84, [95% credible interval = 2.39, 461.60]) and Sugar Glider (Odds Ratio = 19.20,
316 [95% credible interval = 2.36, 424.25]). Such occupancy patterns exhibited by these species
317 in old growth forests also was observed in 1939 and mixed aged forests. However, in 1960-
318 1990s aged stands, occupancy of hollow-bearing trees by Leadbeater's Possum was greater
319 than that for the Greater Glider (Odds Ratio = 2.56, [95% credible interval = 1.04, 6.45]) and
320 the Sugar Glider (Odds Ratio = 7.27, [95% credible interval = 2.32, 26.09]); occupancy of
321 hollow-bearing trees by the Mountain Brushtail Possum were higher than the Sugar Glider in
322 stands dating from 1960-1990 (Odds Ratio = 4.77, [95% credible interval = 1.50, 17.39]) (see
323 Appendix 1 for more details).

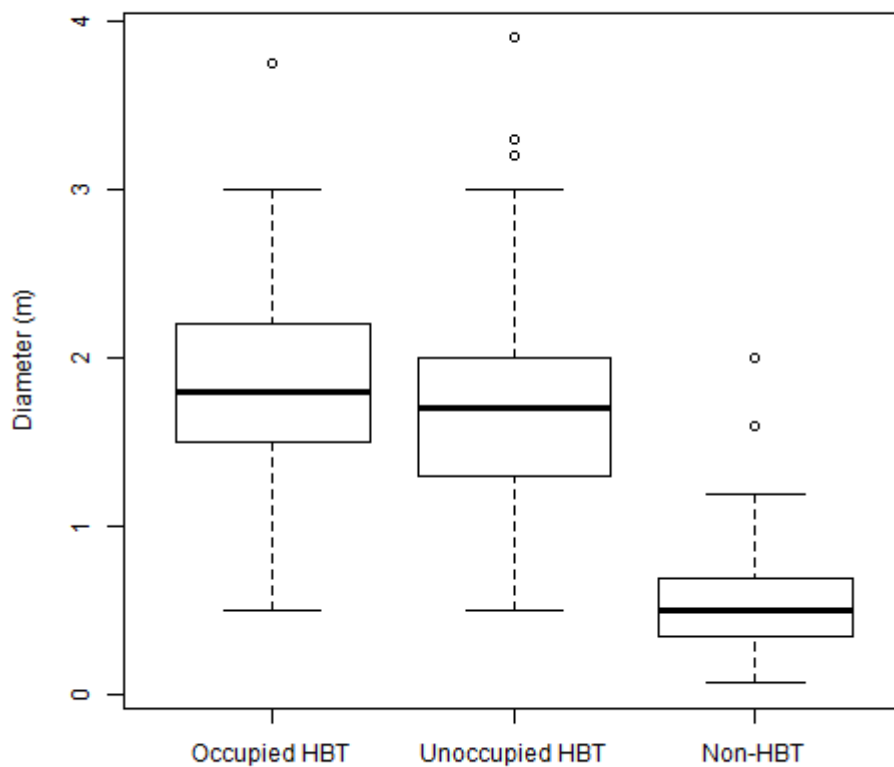
324 Leadbeater's Possum and the Mountain Brushtail Possum were more likely to occupy
325 a given hollow-bearing tree on sites at high elevation (Appendix 2) with the remaining
326 species exhibiting no such elevational responses.

327 **4.1.3 Differences in the diameter of hollow-bearing trees occupied by arboreal** 328 **marsupials and the diameter of non-hollow-bearing trees**

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

335

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



339

340

341 5.1 Discussion

342 Hollow-bearing trees are keystone structures in many ecosystems worldwide
 343 (Lindenmayer and Laurance 2016). Their role in providing denning and/or nesting sites for
 344 cavity-dependent fauna has been demonstrated in numerous forest types and other treed
 345 environments globally (Rose et al., 2001; Gibbons and Lindenmayer 2002; Remm and
 346 Lohmus 2011). Our analyses contained evidence of: **(1)** interspecific differences in the
 347 diameter of hollow-bearing trees occupied by arboreal marsupials (Figure 3), and **(2)** the
 348 occupancy at the individual hollow-bearing tree level being influenced by the age of the

349 surrounding forest as well as elevation (for two species of arboreal marsupial). Hollow-
350 bearing trees occupied by arboreal marsupials were larger in diameter than unoccupied
351 hollow-bearing trees. In addition, the mean diameter of both occupied and unoccupied
352 hollow-bearing trees was almost three times that of non-hollow-bearing trees that regenerated
353 after the 1939 wildfires (Figure 4). We discuss our key findings in the remainder of Section
354 5.1 and conclude with a commentary on implications for forest management and biodiversity
355 conservation.

356 **5.1.1 Relationships between tree occupancy and tree diameter**

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

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

397 **5.1.2 Tree occupancy and surrounding stand age**

398 Stands of old growth Mountain Ash forest support significantly more hollow-bearing
399 trees than forests in other age cohorts (Lindenmayer et al., 2000a; Lindenmayer et al., 2016)
400 and arboreal marsupials can be more numerous in old growth forests (Lindenmayer et al.,
401 1990b; Lindenmayer et al., 1999). The third question in this study examined occupancy at the
402 individual tree level and sought to determine if occupancy of hollow-bearing trees was
403 influenced by the age of the surrounding forest. Our analyses revealed that, for all species of
404 arboreal marsupial, the probability of occupancy of an individual hollow-bearing tree was
405 lowest in old growth stands (Figure 2; Appendix 1). Earlier research (Banks et al., 2013)
406 found that the relationship between animal abundance and hollow-bearing tree abundance
407 was positive, but less than 1:1. This was due primarily to a significant increase by all species
408 in the proportional use of hollow-bearing trees where the abundance of this resource was low
409 (Banks et al., 2013). These earlier results also suggest that other resources or social
410 constraints become limiting for arboreal marsupials under conditions of high hollow-bearing
411 tree availability, such as that found in old growth forest. Conversely, low levels of abundance
412 of hollow-bearing trees in younger aged forests mean that cavity-dependent arboreal
413 marsupials have little choice other than to occupy the fewer remaining nest trees in these
414 kinds of forests where alternative nesting resources are depleted (see Banks et al., 2013). That
415 is, the marginal value of a given large hollow-bearing tree for occupancy may be higher in
416 stands dominated by otherwise much younger-aged forest and where such important nesting
417 and denning resources are uncommon or rare (Fischer et al., 2010). However, we note there is
418 likely to be a threshold level for hollow tree abundance (and possibly spatial distribution)
419 below which animals will be unable to persist; a pattern that appears to be reflected in the
420 increasing number of long-term survey sites in our monitoring program that no longer
421 support hollow-bearing trees or arboreal marsupials (Lindenmayer et al., unpublished data).

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

424 **5.1.3 Contrasts in the diameter of hollow-bearing trees and non-hollow-bearing trees**

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

441 Some forest managers have suggested that the time until cavity development might be
442 brought forward by strategic thinning of stands to accelerate the diameter increments of
443 unthinned trees. However, we note that cavity development in large trees is as much a
444 function of decay processes (e.g. physiological changes that impair successful lateral branch
445 occlusion; (Gibbons and Lindenmayer 2002)) as it is about overall, tree size. Hence, the
446 likely success (or otherwise) of accelerated tree growth in promoting cavity development

447 remains unclear (Lindenmayer 2016). Moreover, the time elapsed until existing non-hollow-
448 bearing trees eventually develop cavities, especially those suitable for use by arboreal
449 marsupials, is likely to be prolonged, even if the surrounding stands are thinned. A further
450 issue is that thinning operations can damage understory vegetation that provides important
451 foraging resources for some species of arboreal marsupials (Seebeck et al., 1984; Smith
452 1984).

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

456 **5.1.4 Fire-damaged regrowth trees and their suitability as nest and den sites for** 457 **arboreal marsupials**

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

469 The future availability of fire-killed trees as potential nest sites for arboreal marsupials
470 is dependent not only on these trees being of sufficient diameter to develop cavities of
471 suitable size for these animals but also remaining standing long enough for cavities to

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

482 **5.1.5 Management implications**

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

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

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508

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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