

*Biological Conservation***1 Fire severity and landscape context effects on arboreal marsupials**

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27 **Running Head:** Mammal responses to fire and resource availability

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29

30 **Abstract**

31 Although fire is a major form of natural disturbance worldwide, both fire-derived
32 landscape context effects and the impacts of fire severity are poorly known for many
33 species. To address this knowledge gap, we quantified the response of Australian arboreal
34 marsupials to: **(1)** the spatial effects of fire, **(2)** fire severity, and **(3)** fire impacts on the
35 availability of critical nesting resources – hollow-bearing trees.

36 We identified substantial differences among species in response to fire severity and
37 landscape-scale fire. The Sugar Glider (*Petaurus breviceps*) and the endangered
38 Leadbeater's Possum (*Gymnobelideus leadbeateri*) were extremely rare on burned sites
39 irrespective of fire severity. In addition, these two species declined with the amount of
40 burned forest in the surrounding landscape even when their habitat remained unburnt. The
41 Mountain Brushtail Possum (*Trichosurus cunninghami*) and the Greater Glider
42 (*Petauroides volans*) both occurred on burned and unburned sites. The Greater Glider
43 responded negatively to fire severity at the site level and also negatively to the amount of
44 forest burned in the surrounding landscape. The abundance of the Mountain Brushtail
45 Possum was lowest on sites subject to moderate severity fire.

46 On unburned sites, the presence and abundance of virtually all species was
47 characterised by a common positive response to the availability of nesting resources in
48 hollow-bearing trees.

49 Our findings underscore the importance of management practices to better protect
50 species that decline after fire. These include conserving areas of unburned forest,
51 particularly those with hollow-bearing trees which are critical nest sites for arboreal

52 marsupials. These recommendations are currently the opposite of existing management
53 practices.

54

55 **Highlights**

- 56 • The endangered Leadbeater's Possum was virtually eliminated by fire of any severity.
- 57 • Leadbeater's Possum declined with increasing area of burnt forest in the landscape,
58 even when its immediate habitat remained unburnt.
- 59 • All arboreal marsupial species were positively associated with hollow-bearing trees.
- 60 • Protecting unburnt forest with tree-hollows is now critically important.

61

62 **Key words:** Relative disturbance sensitivity, forest management, fire regime, cavity-
63 dependent arboreal marsupials, south-eastern Australia

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65

66 **1. Introduction**

67 Fire is a major form of natural disturbance influencing the diversity and distribution
68 of biota worldwide (Bowman et al. 2009; Nimmo et al. 2013b; Valentine et al. 2012).

69 Understanding relationships between fire and biodiversity is particularly important given

70 the increasing extent and number of fires in many ecosystems (Bowman et al. 2009).

71 Inappropriate fire regimes (including changes in fire -severity) could produce shifts in

72 ecosystem states (Lindenmayer et al. 2011a; Staver et al. 2011) as well as threaten the

73 persistence of many species (Rush et al. 2012; Taylor et al. 1972; Valentine et al. 2012).

74 A major knowledge gap concerns the quantification of the spatial effects of fire on

75 biota; the vast majority of studies have focused on time since fire and not spatial effects

76 (Clarke 2008). There is some literature on the spatial mosaics created by fire, including

77 studies of the concept of invisible (historical) mosaics (Bradstock et al. 2005) and the

78 “pyrodiversity begets biodiversity” hypothesis (Parr and Andersen 2006; Nimmo et al.

79 2013a; Taylor et al. 2012). However, there are comparatively few landscape context studies

80 in fire-modified landscapes (Bradstock et al. 2012; Clarke 2008; McKenzie et al. 2011) that

81 document the occurrence of species on unburned sites where the surrounding landscape has

82 been burned. In contrast, the landscape fragmentation literature includes numerous studies

83 of landscape context effects (reviewed by Collinge 2009; Lindenmayer and Fischer 2006)

84 showing that patch biota is influenced by the amount and condition of vegetation

85 surrounding those patches (Viveiros de Castro and Fernandez 2004). The widespread

86 evidence for landscape context effects in fragmented systems suggests that similar effects

87 may occur where variation in fire extent and severity create a heterogeneous landscape.

88 Quantifying fire-derived landscape context effects is critical for informing the conservation
89 and management of fire-prone areas, such as developing policies and practices to protect
90 unburned refugia (Mackey et al. 2012) and protect burnt areas from additional disturbances
91 like post-fire salvage logging (Lindenmayer et al. 2008).

92 Another key knowledge gap concerns the effects of fire severity on fauna. Fire
93 severity refers to the extent of loss or consumption of the vegetation and other biomass as a
94 result of fire (Keeley 2009). While many studies have compared the post-fire recovery of
95 biota on burned sites and unburned sites, few have quantified the effects of variation in fire
96 severity on biodiversity (although see Rush et al. 2012; Smucker et al. 2005). Fire severity
97 is a fundamental component of fire regimes (Gill 1975) and therefore without a good
98 understanding of its effects, accurate predictions of the response of fauna to fire will remain
99 elusive (Driscoll et al. 2010). It is imperative to remedy this deficiency quickly because
100 fires are predicted to become larger, more frequent and more severe as a result of climate
101 change (Driscoll et al. 2012; Westerling et al. 2006; Cary et al. 2012).

102 In this study, we aimed to help close knowledge gaps about landscape context and
103 fire severity effects on biota. We report new findings from a detailed study of arboreal
104 marsupials in the montane ash forests of Victoria, south-eastern Australia. Work on
105 arboreal marsupials in this system over the past three decades has indicated that these
106 animals are highly sensitive to human-generated disturbances, particularly clearcut logging
107 at both site and landscape scales (Lindenmayer et al. 1991a, 1999). Indeed, among the eight
108 species of arboreal marsupials in montane ash forests, Leadbeater's Possum
109 (*Gymnobelideus leadbeateri*) is listed as nationally endangered (Department of
110 Sustainability, Environment, Water, Population and Communities 2012). Montane ash

111 forests are fire-regime dependent ecosystems, with the regeneration of key overstorey tree
112 species dictated by infrequent, high severity conflagrations (Ashton 1981; Lindenmayer
113 2009; McCarthy et al. 1999). However, the impacts of fire on arboreal marsupials remain
114 virtually unknown.

115 In late-summer 2009, widespread fires burned over 72 000 ha of montane ash
116 forests. These were the most damaging fires in Australian history in terms of loss of human
117 life and property (Gibbons et al. 2012). The severity of these fires varied substantially, with
118 some areas remaining unburned, others subject to moderate severity fire, and some fire-
119 affected areas reputed to have experienced among the most intense fires ever recorded
120 reaching 88 000 kW/m (Cruz et al. 2012). In addition, the effects of the fires varied
121 spatially, with some landscapes almost completely burned, whereas others experienced
122 either patchy fire or no fire (Price and Bradstock 2012). The 2009 fires therefore provided a
123 unique opportunity to explicitly test hypotheses about the impacts of fire severity and
124 landscape context on arboreal marsupials. The array of 108 field sites used in our
125 investigation also varied in vegetation structure, topographic position and stand age
126 allowing us to construct novel composite models that integrated data on site- and
127 landscape-level disturbance, stand structure, and environmental conditions.

128 We posed three key questions in our investigation:

- 129 • Are there landscape context effects of fire on the occurrence of arboreal
130 marsupials? Some species of arboreal marsupials are sensitive to changes in
131 landscape-level forest cover resulting from clearcutting of the landscape
132 surrounding otherwise intact sites (Lindenmayer et al. 1993, 1999). Given these
133 earlier findings and with the extensive evidence for landscape context effects

134 from the habitat fragmentation literature (Collinge 2009), we postulated that
135 unburned sites surrounded by extensive areas of burned forest would be less
136 likely to support animals than sites where the surrounding forest remained
137 unburned. Under this hypothesis, even if species can survive in unburned
138 refuges during wildfire, they may still be sensitive to fire in the surrounding
139 landscape.

140 • What are the impacts of fire severity on the occurrence of arboreal marsupials?

141 We predicted that animals would be negatively affected by high-severity fire
142 more than by moderate severity fire. This was because of the increased effects
143 of high severity fire on: (i) animal mortality (Hewish 1983; Keith et al. 2002),
144 and, (ii) indirect impacts of severe fire on habitat suitability – particularly the
145 increased levels of destruction of severe fire of large old trees (Banks et al.
146 2011b; Lindenmayer et al. 2012) which arboreal marsupials use as nest and den
147 sites (Lindenmayer et al. 1991a).

148 • Will an abrupt change in the abundance of key nesting resources influence the

149 presence/abundance of arboreal marsupials? Repeated past statistical modeling
150 has demonstrated that a key habitat attribute for arboreal marsupials is the
151 occurrence of hollow-bearing trees which are denning sites for these animals.
152 All species are significantly more likely to occur on sites where such trees are
153 abundant and do not occur in the absence of hollow-bearing trees (Lindenmayer
154 et al. 1991b, 1994). However, the condition and abundance of key vegetation
155 attributes can change over time (Swanson et al. 2011) and this can in turn

156 influence the temporal suitability of a site as habitat for a particular species
157 (Haila et al. 1996; Monamy and Fox 2000). Recent work in montane ash forests
158 has shown that fire has marked negative effects on populations of hollow-
159 bearing trees, with their numbers significantly reduced in burned areas
160 (Lindenmayer et al. 2012). Given that virtually all species of arboreal
161 marsupials are obligate hollow-users in montane ash forests (Lindenmayer et al.
162 1991a), we postulated that previously established hollow-tree/animal
163 occurrence relationships would persist over time on sites that continue to
164 support hollow-bearing trees, including on sites that had been burned.

165 The insights from our empirical study are critical for understanding the impacts of
166 fire (including very high fire severity) on biodiversity at both a site level and a landscape
167 level. They are also valuable for highlighting which kinds of species within an assemblage
168 may be sensitive to fire severity. Our work provides a valuable model for illustrating the
169 conservation management and ecological learning that can arise from the early initiation of
170 studies that follow major natural disturbances such as unplanned fires.

171 **2. Methods**

172 **2.1 Study area**

173 Our study took place in the montane ash forests of the Central Highlands of
174 Victoria, south-eastern Australia. The dominant tree species in these forests were Mountain
175 Ash (*Eucalyptus regnans*), and Alpine Ash (*Eucalyptus delegatensis*). These two tree
176 species are obligate seeders and intensive stand-replacing fire is a common natural
177 disturbance pathway (Ashton 1981; Lindenmayer 2009).

178 The Central Highlands region lies about 120 km north-east of the city of Melbourne
179 and covers approximately $\frac{1}{2}$ degree of latitude and one degree of longitude ($37^{\circ}20'-37^{\circ}55'S$
180 and $145^{\circ}30'-146^{\circ}20'E$) (Fig. 1). Further information on the study area including climate,
181 land use and other features are given in Lindenmayer et al. (2011a).

182 **2.2 *The arboreal marsupial fauna of montane ash forests***

183 In addition to Leadbeater's Possum, three other species of arboreal marsupials are
184 relatively common in montane ash forests – the Greater Glider (*Petauroides volans*), the
185 Mountain Brushtail Possum (*Trichosurus cunninghami*), and the Sugar Glider. These
186 species vary widely in life history attributes such as body size, group size, home range,
187 mating system and social organization (Lindenmayer 1997) (see Online Appendix Table
188 A1). The different species also: **(1)** swap regularly between dens in different hollow-
189 bearing trees (Lindenmayer et al. 1996), **(2)** select different morphological forms of trees
190 with hollows as den sites, ranging from intact, living trees through to highly decayed dead
191 trees in the late stages of senescence (Lindenmayer et al. 1991b), and **(3)** rarely co-occur in
192 the same tree (Lindenmayer et al. 1990). Thus, sites with numerous hollow-bearing trees
193 will meet the behavioural and resource requirements of arboreal marsupials. These three
194 behavioural effects explain why arboreal marsupials are significantly more likely to occur
195 on sites with numerous hollow-bearing trees (Lindenmayer et al. 1991a).

196 Leadbeater's Possum is largely confined to montane ash forests. Within these
197 forests, the species has specialised habitat requirements for large decayed den trees and a
198 dense understory of *Acacia* spp. food trees (Lindenmayer 2009). The other species of
199 arboreal marsupials have broader resource and habitat requirements and occur in a wide

200 range of environments throughout large parts of eastern Australia (Goldingay and Jackson
201 2004).

202 **2.3 *Field monitoring sites***

203 In 1997 we established 162 permanent research and monitoring sites each
204 measuring 1 ha in size throughout the montane ash forests of the Central Highlands of
205 Victoria (Lindenmayer et al. 2003). These sites were targeted in a major study of the decay
206 and collapse of hollow-bearing trees in montane ash forests (Lindenmayer et al. 2012). The
207 minimum distance between field sites is 1.5 km. In this study, we surveyed 108 of the 162
208 sites for arboreal marsupials after the 2009 fire.

209 Our 108 field sites are well distributed throughout the study region and cover a wide
210 range of variation in environmental conditions. The number of hollow-bearing trees on a
211 site ranged from 1-31. Our sites varied in slope (inclination: 2-38°), elevation (220-1040m),
212 topographic position (gully, midslope, ridge) and aspect (assigned to one of two categories:
213 northerly and westerly vs. southerly and easterly). At the outset of this investigation (1997),
214 our 108 field sites encompassed a variety of stand ages including those dating from the
215 mid-1700s, mid-1850s, the early 1900s (1905, 1919, 1926 and 1932), 1939 and 1983-1990
216 (see Tables A2, A3, A4 and Fig. A1).

217 **2.4 *The 2009 wildfire***

218 Within four weeks of the 2009 fires, we completed on-ground surveys to quantify
219 fire severity and assigned each of our 108 field sites to one of three categories: **(1)** no fire
220 (63 sites), **(2)** moderate severity fire where the ground and understory layer had the
221 majority of their above-ground biomass scorched or consumed but the overstorey remained
222 green (32 sites), and **(3)** high fire severity in which plants in the ground, shrub, understory

223 and eucalypt tree layers had the majority of their above-ground biomass scorched or
224 consumed (13 sites).

225 We obtained spatial data on fire extent within a 500 m and a 1 km radius circle
226 surrounding each survey site from the Government of Victoria and calculated the area of
227 forest (ha) that had been burned in the 2009 fire.

228 **2.5 *Surveys of arboreal marsupials***

229 We counted arboreal marsupials on our 108 field sites over three successive summer
230 field seasons - 2009/2010 (N = 41 sites), 2010/2011 (N = 34 sites) and 2011/2012 (N= 33
231 sites) using the stagwatching method. Any given site was surveyed in one of these three
232 field sampling periods. Stagwatching involves counting the number of individuals of each
233 species of arboreal marsupial emerging from every tree with a hollow on a given survey
234 site (Lindenmayer et al. 1991a) and is the most reliable survey method for arboreal
235 marsupials (Smith et al. 1989). All hollow-bearing trees on a given site are observed
236 simultaneously by multiple, trained observers. Stag-watching surveys commenced an hour
237 before dusk and continued until an hour after dusk to ensure the detection of both small-
238 and large-bodied species which have different emergence times.

239 **2.6 *Statistical analysis***

240 We completed our statistical analyses of arboreal marsupials in two stages. First, we
241 examined the relationship between the abundance of each species with high severity fire,
242 moderate severity fire, and no fire at the site level, ignoring other potential explanatory
243 variables. Second, we fitted hurdle models (presence/absence and then abundance on
244 occupied sites) using all covariates. We employed hurdle models because past work has
245 shown that some species of arboreal marsupials are absent from many areas but, because of

246 their social organization, where they are present, there may be a number of individuals
 247 (Welsh et al. 1996). We completed two sets of hurdle models – one for unburned sites only
 248 for those taxa virtually absent from burned sites (Leadbeater’s Possum and the Sugar
 249 Glider) and a second set for the remaining two species (the Mountain Brushtail Possum and
 250 the Greater Glider) which occurred on both burned and unburned sites as well as for species
 251 richness.

252 To assess the effect of fire severity on the probability of the presence of a species or
 253 presence of any species after fire at the site level, we compared the rates of non-zero
 254 detections on each site using Bayesian logistic regression (Dey et al. 2000) as follows: Let
 255 D_i indicate whether or not the i th site was observed to have an animal present after fire and
 256 let π_i be the probability of this event, that is, $P(D_i > 0) = \pi_i$. The logistic regression
 257 model is given by:

$$258 \quad \text{logit}(\pi_i) = \eta + \delta f_i$$

259 where f_i has a value of one if the i th site experienced fire and zero otherwise and

260 $\text{logit}(\pi) = \log \frac{\pi}{1-\pi}$. The probability of an animal being present on an unburned site is

$$261 \quad \pi = \frac{e^\eta}{1+e^\eta} \text{ and the probability of an animal being present on a burned site is } \pi = \frac{e^{\eta+\delta}}{1+e^{\eta+\delta}},$$

262 which correspond to odds of e^η and $e^{\eta+\delta}$ respectively and the odds ratio is e^δ . To complete
 263 the Bayesian logistic regression specification, we assigned non-informative independent
 264 prior distributions to η and δ . Furthermore, each parameter was assigned a normal
 265 distribution with a zero mean and variance 1000 (Gelman et al. 2003; Kéry 2010). This
 266 approach was applied to our data on Leadbeater’s Possum, Mountain Brushtail Possum,

267 Greater Glider, Sugar Glider and the presence of any possum or glider. For the Mountain
 268 Brushtail Possum, Greater Glider and the presence of any possum or glider, we generalized
 269 the above model to include moderate and high fire severity.

270 The conditional Poisson or hurdle model was first used in ecology by Welsh et al.
 271 (1996) to account for excess zeros in Poisson regression situations. We implemented a
 272 Bayesian approach to the hurdle model described in Neelon et al. (2010). The hurdle model
 273 can be written as follows:

$$274 \quad P(Y_i > 0) = p, \quad 0 \leq p \leq 1$$

$$275 \quad P(Y_i = k) = p \frac{\mu^k e^{-\mu}}{k! (1 - e^{-\mu})}, \quad k = 1, \dots, \infty, 0 < \mu < \infty$$

276 where Y_i denotes the response for site $i = 1, \dots, n$ and μ is the mean of the truncated
 277 Poisson distribution. We extended the basic hurdle model to allow for covariates to affect
 278 the zero process and the truncated Poisson process:

$$279 \quad \text{logit}(p_i) = \mathbf{z}_i^T \boldsymbol{\beta}$$

$$280 \quad \text{log}(\mu_i) = \mathbf{x}_i^T \boldsymbol{\alpha}$$

281 where \mathbf{z}_i is a vector of covariates that influence the zero process and \mathbf{x}_i is a vector of
 282 covariates that influence the truncated Poisson or abundance process. We set independent
 283 multivariate normal priors for the unknown regression parameters $\boldsymbol{\beta}$ and $\boldsymbol{\alpha}$ with zero means
 284 and covariance matrices proportional to the identity matrix with large variance to indicate
 285 lack of prior knowledge about these parameters (Gelman et al. 2003; Kéry 2010). The
 286 model was fitted using OpenBUGS (Lunn et al. 2009) called from R (R Development Core
 287 Team 2011) using the R2OpenBUGS package (Sturtz et al. 2005). The code used was

288 adapted from Neelon et al. (2010). We also implemented the model assessment procedures
289 described in Neelon et al. (2010). Specifically, we computed the three test statistics
290 recommended: the proportion of observations equal to zero, the overdispersion index and
291 the sample skewness.

292 We fitted hurdle models to data on Leadbeater's Possum and the Sugar Glider on
293 unburned sites only (as there were too few records on burned sites). For the Mountain
294 Brushtail Possum, Greater Glider and the species richness of any arboreal marsupial we
295 fitted hurdle models to data from all sites. We quantified the effects of the following
296 covariates for each species: log (number of hollow-bearing trees on a site), elevation, pre-
297 fire forest age, site-level fire severity (only for the Mountain Brushtail Possum, Greater
298 Glider and the species richness of any arboreal marsupial), the fraction of the landscape
299 burned in a 500 m and 1 km radius of a site, and northerly and westerly facing aspects.

300 **3. Results**

301 Extensive details of the models generated from our analyses are contained in Table
302 A5. We present only those results for the analysis of the 1 km landscape context effects as
303 our findings were very similar to those for the 500 m landscape context analysis.

304 Leadbeater's Possum was recorded on ~1.3% of burned sites versus ~27.3% of unburned
305 sites while the Sugar Glider was recorded on 3% of burned sites but 17.1% of unburned
306 sites (Table 1).

307 **3.1 *Hurdle models of the presence and abundance of arboreal marsupials***

308 On unburned sites, Leadbeater's Possum was more likely to occur on sites where
309 there were numerous hollow-bearing trees (Fig. 2a), at high elevation and on sites that
310 regenerated after the 1939 fires. Given the species' presence, more individuals were

311 recorded on sites with numerous hollow-bearing trees (Fig. 3a), at higher elevation, with a
312 southerly or easterly aspect, and that were either old growth (> 100 years) or young
313 regrowth (stands ~25 years old) (but not stands of intermediate aged forest that are 73 years
314 old and date from the 1939 fires). The abundance of Leadbeater's Possum on unburned
315 sites declined with increasing amounts of burned forest in the surrounding landscape (Fig.
316 4a), with a similar responses observed for both the 500 m and the 1 km radius around
317 unburned sites.

318 On unburned sites, the abundance of the Sugar Glider was lowest on sites
319 dominated by young forest (Table A5). The abundance of this species also declined with an
320 increasing fraction of the surrounding landscape burned. This relationship was strong for
321 the amount of forest burned in a 1 km radius around unburned sites (Fig. 4b), but less so for
322 the 500 m radius. We also found more animals on sites with a north and westerly aspect
323 than a south and easterly aspect (Table A5).

324 The presence of the Mountain Brushtail Possum was highest on sites characterised
325 by a large number of hollow-bearing trees (Fig. 2b) and sites at high elevation (Table A5).
326 The abundance of the species was lowest on sites subject to moderate severity wildfire
327 (Table A5).

328 The probability of occurrence of the Greater Glider was highest on sites with a large
329 number of hollow-bearing trees (Fig. 2c). The abundance of the Greater Glider declined
330 with: **(a)** increasing amounts of burned forest in the surrounding landscape (Fig. 4c), with a
331 similar response observed in both a 500 m and 1 km radius a site, **(b)** increasing fire
332 severity at the site level (Table A5), and **(c)** increasing elevation (Table A5). We also found

333 more animals on sites with a north and westerly aspect than south and easterly aspect
334 (Table A5).

335 The presence of any arboreal marsupial (irrespective of species) and overall species
336 richness of arboreal marsupials was highest on sites that supported numerous hollow-
337 bearing trees (Fig. 2d) and lowest on sites subject to high severity fire (Fig. 3b). We also
338 identified a positive relationship between the presence of any arboreal marsupial and
339 elevation (Table A5). Finally, the overall species richness of arboreal marsupials was
340 greatest in areas of young (~20-30 year old) forest (Table A5).

341 The five hurdle models we constructed were all adequate for the logistic portion of
342 the model (Neelon et al. 2010). That is, the Bayesian p-values as described in Neelon et al.
343 (2010), were all in the acceptable range. However, all of the models were under-dispersed
344 in that the over-dispersion index and the sample skewness were all on the lower end of the
345 reference distribution. As a further check of model adequacy, we added site level random
346 effects to the truncated Poisson portion of the hurdle models for Leadbeater's Possum, the
347 Mountain Brushtail Possum, and species richness. This did not change the results in any
348 substantive way, indicating that the under-dispersion was a minor issue and our models
349 were adequate.

350 **4. Discussion**

351 Understanding the responses of biota to disturbances such as fire is a fundamentally
352 important part of both ecology (Johnson and Miyanishi 2008) and informed conservation
353 management (Nimmo et al. 2013b). Our analyses produced new insights into disturbance
354 ecology by uncovering inter-specific differences in responses to fire severity and novel fire-
355 driven "landscape context" effects. These have only rarely been studied in other ecosystems

356 (Bradstock et al. 2012; McKenzie et al. 2011), despite being potentially important in
357 predicting the consequences of large disturbances on species. We discuss our new findings
358 below and conclude with an overview of some of the major conservation implications of
359 our work.

360 *4.1 Are there landscape context effects of fire and fire severity effects on arboreal* 361 *marsupials?*

362 We uncovered marked inter-specific differences in responses to fire-derived
363 landscape context and fire severity. Our results showed that Leadbeater's Possum, the
364 Sugar Glider and the Greater Glider were less abundant on sites where the surrounding
365 landscape had been burned, even if a site remained unburned. Notably, the fire-mediated
366 landscape context effects we identified for Leadbeater's Possum were similar to those
367 resulting from logging-derived changes in forest landscapes in which the abundance of the
368 species was significantly depressed in narrow strips of retained forest surrounded by
369 recently clearfelled areas (see Lindenmayer et al. 1993).

370 Negative fire-derived landscape context effects may have occurred for several
371 reasons, but particularly the loss of den sites across large parts of the landscape as a result
372 of wildfire (Lindenmayer et al. 2012). An additional source of risk for animals such as
373 Leadbeater's Possum is the species' complex social organization and the need to gather
374 food resources over a comparatively large area to support a functional group (Lindenmayer
375 2009). Indeed, colonies of Leadbeater's Possum may be particularly at risk to the landscape
376 context effects of fire if they use resources on a spatial scale larger than the size of an
377 unburnt patch. Alternatively, surrounding burned areas may act as sinks (Howe et al. 1991),
378 with higher mortality in recently burned forest. Irrespective of the mechanism/s underlying

379 these landscape context effects, they nevertheless suggest a greater level of decline after
380 fire than previously recognized.

381 Our results indicate that landscape context effects extend beyond the habitat
382 fragmentation domain (where they have typically been documented; reviewed by Collinge
383 2009; Lindenmayer and Fischer 2006) and also must be considered as part of investigations
384 of fire effects on biodiversity (Gill et al. 2003). However, as burned areas regenerate
385 rapidly following fire in montane ash forests (Ashton 1976), landscape context effects
386 might be expected to be transitory, with the rate of transition likely to be dependent upon
387 scale (i.e. fire size), the rate of recovery of limiting resources, and the proximity of source
388 populations for recolonisation. Rigorous longitudinal studies will be required to determine
389 if this is indeed the case. However, as part of our analyses (data not shown), we found no
390 effects of time since the 2009 fire with Leadbeater's Possum and Sugar Glider remaining
391 largely absent on burned sites throughout the duration of this study.

392 In addition to novel landscape context effects of fire, we also identified important,
393 site-level fire severity impacts. Leadbeater's Possum and the Sugar Glider were largely
394 absent on burned sites, the abundance of the Mountain Brushtail Possum was lowest on
395 sites subject to moderate severity fire, and the abundance of the Greater Glider was lowest
396 on high burn severity sites. The reasons for the sensitivity of arboreal marsupials to fire
397 remain unclear but we suggest several factors may be important. The strong negative
398 response of Leadbeater's Possum to fire (of any severity) at the site level may be associated
399 with: (1) Direct mortality resulting from fire among animals on burned sites, and, (2) The
400 loss of a major food resource (*Acacia* spp. sap; Hume 1999) with the incineration of the
401 understorey (Banks et al. 2011a). A paucity of food also may explain the Greater Glider's

402 decline from sites burnt at high-severity. The Greater Glider has a diet comprised
403 exclusively of eucalypt leaves (Hume 1999) but few trees survived on our sites subject to
404 high-severity fire. In addition, the Greater Glider is a temperature-sensitive organism
405 (Rubsamen et al. 1984) and high temperatures may have led to substantial levels of
406 mortality on sites subject to high-severity fire.

407 The negative relationship between the abundance of the Mountain Brushtail Possum
408 and moderate severity fire may be associated with the dynamics of understorey vegetation.
409 Earlier work in montane ash forests found limited vegetation regeneration on sites subject
410 to moderate fire (Ashton and Martin 1996). We observed the same pattern in our study and
411 this may occur, in part, because of suppression of germinants by living overstorey trees
412 through shading effects and possibly allelopathic processes (Ashton and Martin 1996).
413 Limited regeneration of ground layer and understorey plants on moderately burned sites
414 may deprive the Mountain Brushtail Possum of key sources of food (Seebeck et al. 1984)
415 leading to a reduced abundance of animals in these areas. By contrast, the regeneration and
416 growth of understorey vegetation has been dense and rapid on sites subject to high-severity
417 and this may explain why the Mountain Brushtail Possum is more abundant than in forest
418 burned at moderate severity.

419 In summary, our analyses suggest that examinations of the response of biota to fire
420 events require not only determining whether a site has or has not been burned, but also
421 quantification of fire severity, and quantification of the extent of fire in the surrounding
422 landscape – even if a given site remains unburned. As examples – two species –
423 Leadbeater’s Possum and the Sugar Glider were virtually absent from burned sites
424 (irrespective of fire severity), and extremely rare on unburned sites where the surrounding

425 landscape had been burned. Our results therefore suggest these species are highly
426 susceptible to the impacts of fire at both the site and landscape levels.

427 **4.2 *How stable are resource-animal occurrence relationships following fire?***

428 The abundance of hollow-bearing trees was a key explanatory variable in models
429 developed for virtually all species of arboreal marsupials on unburned sites. It also was
430 important for the Greater Glider and the Mountain Brushtail Possum on all (both burned
431 and unburned) sites – despite fire heavily altering the abundance of this key resource
432 (Banks et al. 2011b; Lindenmayer et al. 2012). Leadbeater’s Possum and the Sugar Glider
433 were virtually absent from burned sites, even those with some hollow-bearing trees.
434 Although fire significantly reduced the abundance of hollow-bearing trees (Lindenmayer et
435 al. 2012), there were nevertheless some remaining hollow-bearing trees on burned sites (see
436 Table A2) where Leadbeater’s Possum and the Sugar Glider previously occurred. The
437 paucity of these species on burned sites may have occurred because of mortality of animals
438 arising directly from the 2009 fires, the fire-derived loss of the particular kinds of large
439 diameter, decayed hollow-bearing trees used by Leadbeater’s Possum (see Lindenmayer et
440 al. 2012), and/or the temporary loss of understory vegetation dominated by *Acacia* spp.
441 trees that provide foraging substrates for Leadbeater’s Possum and the Sugar Glider.

442 **4.3 *Forest age and environmental effects***

443 We found evidence of factors in addition to landscape context, fire severity and the
444 availability of hollow-bearing trees that influenced the occurrence of arboreal marsupials.
445 These included stand age, aspect and elevation (Tables A2, A3, A4 and Fig. A1). Some of
446 these effects were congruent with current understanding of species’ ecology such as the
447 link between increasing elevation and the cooler and wetter bioclimatic conditions within

448 montane ash forests where Leadbeater's Possum was most abundant (Lindenmayer et al.
449 1991c). Similarly, the occurrence of Leadbeater's Possum on sites with a south and easterly
450 aspect was consistent with the results of earlier studies on the occupancy patterns of
451 hollow-bearing trees on such cooler and more protected aspects (Lindenmayer et al. 1990).

452 **4.4 *Ecological and conservation implications***

453 Our results are important in an applied conservation context for two reasons. First,
454 the paucity of Leadbeater's Possum on burned sites is of conservation concern. This is a
455 globally endangered species and Victorian Government agencies have estimated ~42% of
456 its habitat was burned in 2009 (S. Smith, Department of Sustainability and Environment,
457 personal communication). Our data show that the abundance of the species also was
458 reduced on unburned sites where the surrounding landscape had been burned. These
459 findings, combined with previous research showing similarly negative effects of logging on
460 Leadbeater's Possum in these forests (Lindenmayer et al. 1993), highlight the critical value
461 of large, intact, long-unburned old-growth areas (supporting trees 150-400 years of age) for
462 the conservation of the species. After the 2009 fires, the imperative to retain the remaining
463 unburnt forest areas is even stronger than it had been before the fires. However, over the
464 current five year harvesting period, the Government of Victoria has scheduled logging of
465 17 400 ha of montane ash forest where clearfelling will significantly reduce the remaining
466 stands of unlogged and unburned forest. We suggest the Government of Victoria needs to
467 significantly reduce its present commitments to harvest pulpwood and timber to maintain
468 more intact montane ash forest and better conserve endangered species such as
469 Leadbeater's Possum.

470 Second, our findings have underscored the importance of abundant hollow-bearing
471 trees as a key resource for arboreal marsupials in montane ash forests. Large old trees have
472 declined precipitously in these forests, particularly following the 2009 fires where almost
473 50% of living and dead hollow-bearing trees were consumed (Lindenmayer et al. 2012). In
474 particular, the large, dead and highly decayed hollow-bearing trees typically used by
475 Leadbeater's Possum have been found to be especially vulnerable to being destroyed by
476 fire (Lindenmayer et al. 2012). This does not bode well for the future persistence of viable
477 populations of arboreal marsupials, and particularly Leadbeater's Possum whose
478 distribution is virtually restricted to long-unburned areas of montane ash forest. Not only is
479 there a need to reduce the amount of clearcut logging which reduces the abundance of
480 existing hollow-bearing trees and impairs their recruitment (Lindenmayer et al. 2012), but
481 there is an urgent need to implement new kinds of retention harvest cutting methods (*sensu*
482 Gustafsson et al. 2012) which can better protect these key resources in montane ash forests
483 (Lindenmayer et al. 2010).

484 Our study of arboreal marsupials has been conducted in montane ash forest in which
485 the canopy trees are obligate seeders that are often killed by fire and regenerate primarily
486 from seed shed from the canopy at the time of a conflagration (Ashton 1981; Lindenmayer
487 2009). This is in marked contrast to the vast majority of other eucalypt forest trees in
488 Australia which are capable of resprouting following fire. The extent to which our findings
489 for arboreal marsupials in montane ash forests apply to this group of animals in other forest
490 types remain unclear. The responses of arboreal marsupials to fire, including fire severity
491 and landscape context effects of fire have not been well studied in other Australian forest
492 landscapes. Studies of animals in fire-damaged forests in New South Wales have revealed

493 that animals like the Greater Glider can be relatively sensitive to fire, even when dominant
494 canopy trees are capable of surviving moderate-high severity fire (Lindenmayer et al.
495 2011b). However, studies of other species of arboreal marsupials such as those inhabiting
496 Booderee National Park in coastal New South Wales, have indicated that taxa like the
497 Common Brushtail Possum (*Trichosurus vulpecula*) appear to exhibit no negative
498 relationships with fire in the medium to long-term. Rather, populations are more strongly
499 influenced by other factors like the prevalence (and conversely the control) of feral
500 predators (Dexter et al. 2012).

501 Forests support a significant proportion of the world's biodiversity, including large
502 numbers of threatened and endangered species (FAO 2010). Fire is a major form of natural
503 disturbance in forests (Bowman et al. 2009) and its impacts on biodiversity must be better
504 understood, particularly as increasingly extreme fire weather is expected to develop in
505 some forested areas in the coming decades with climate change (Clarke et al. 2013). Our
506 study demonstrated that some forest-dependent taxa decline dramatically after fire. New
507 management strategies aimed at protecting large areas of intact and unburned forests are
508 critical for the conservation of such species.

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- 724
- 725

726

727 Table 1. Posterior medians and 90% credible intervals (given in parentheses) for the
 728 response to fire of Leadbeater's Possum and Sugar Glider. The odds ratio is the ratio of the
 729 odds of occurrence on burned sites to the odds of occurrence on the unburned sites.
 730 Credible intervals for the odds ratio that do not include one provide evidence of an effect
 731 (highlighted in bold). Note that, due to MCMC sampling variability and the influence of the
 732 prior, posterior medians do not necessarily equal their sample counterparts.

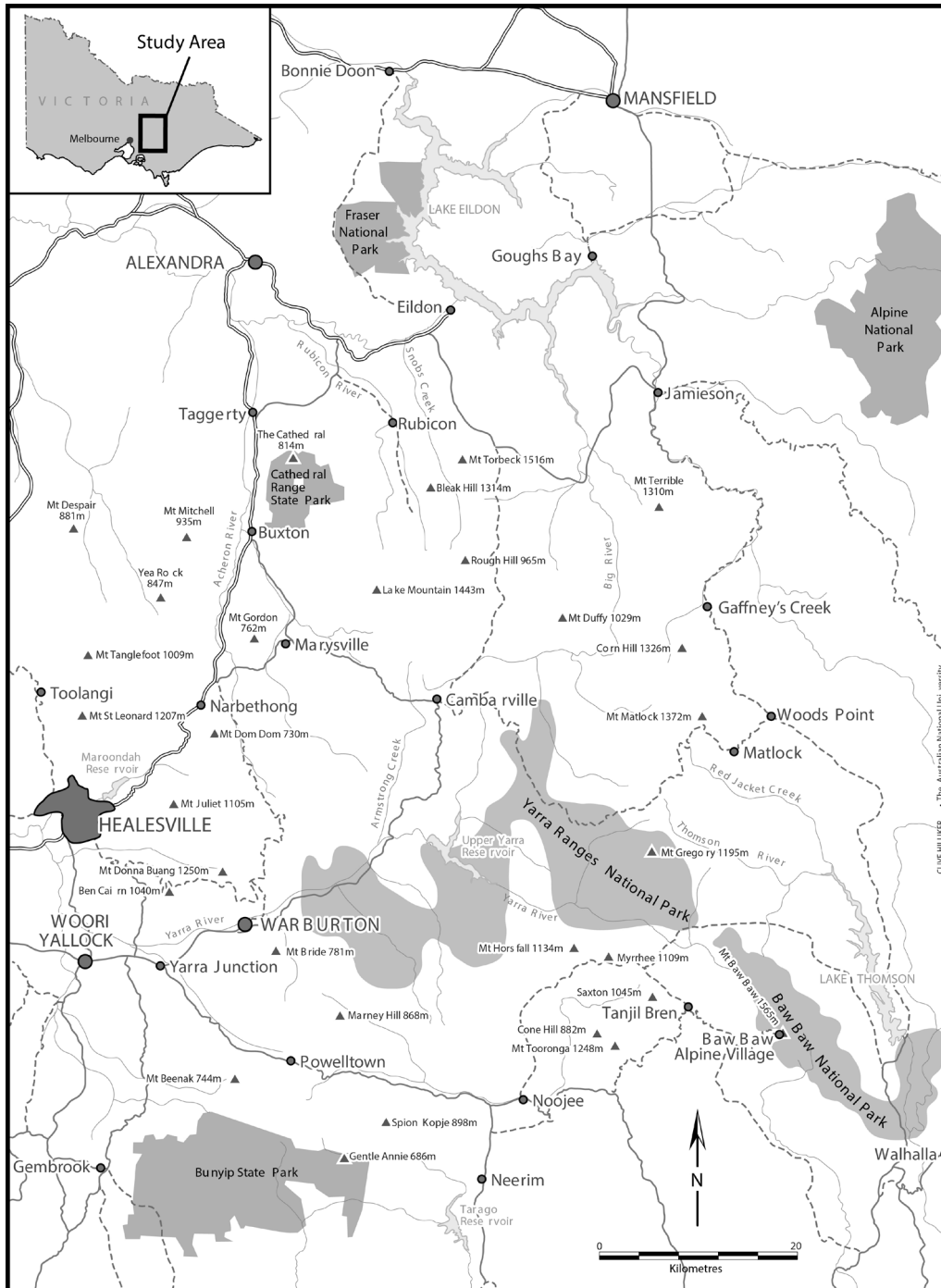
Species	% Occurrence on Unburned Sites (n=63)	% Occurrence on Burned Sites (n=45)	Odds Ratio
Leadbeater's Possum	27.3 (19.11,36.68)	1.26 (0.10,5.31)	0.034 (0.003,0.162)
Sugar Glider	17.08 (10.51,25.31)	3.03 (0.65,8.36)	0.151 (0.029,0.510)

733

734

735 **Figure legends**

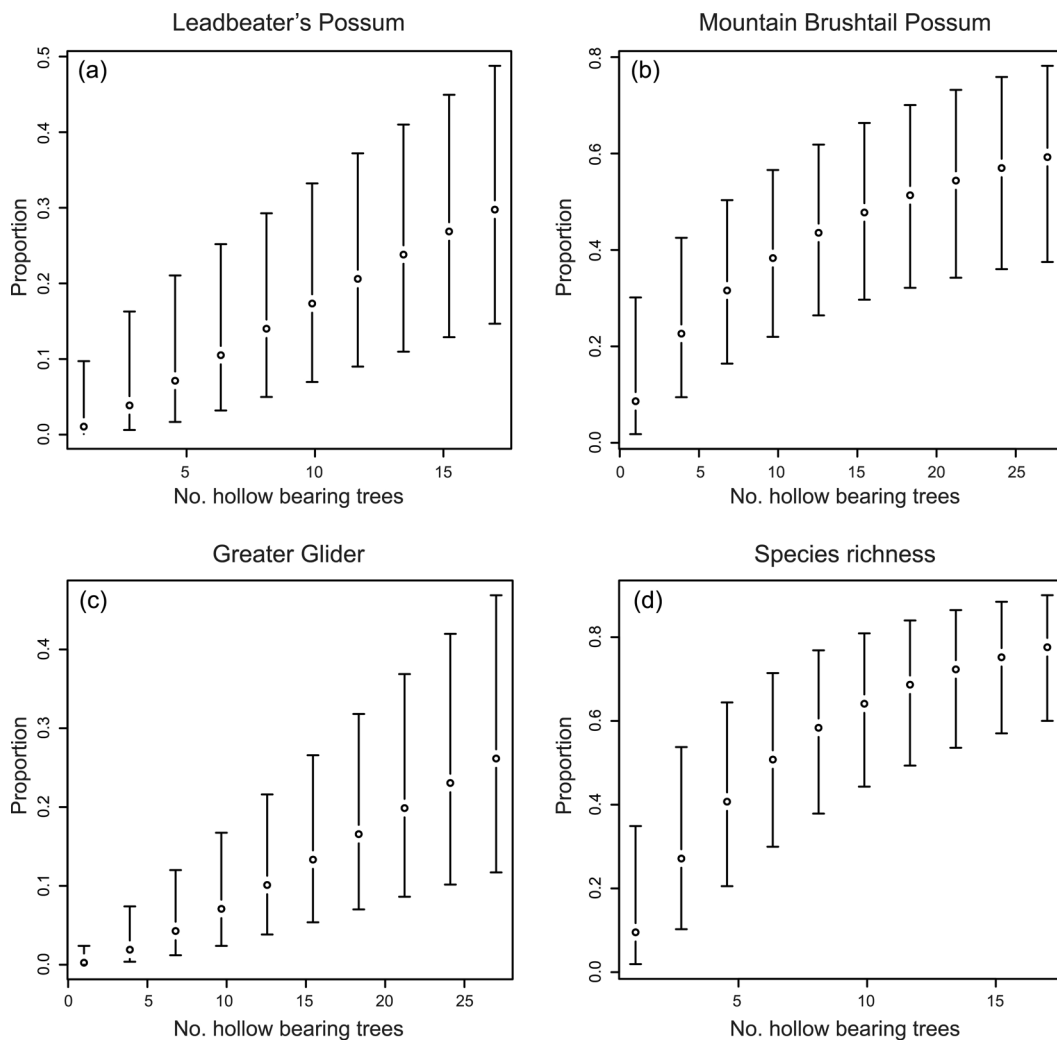
736 **Fig. 1. The location of the study region in the Central Highlands of Victoria, south-**
 737 **eastern Australia.**



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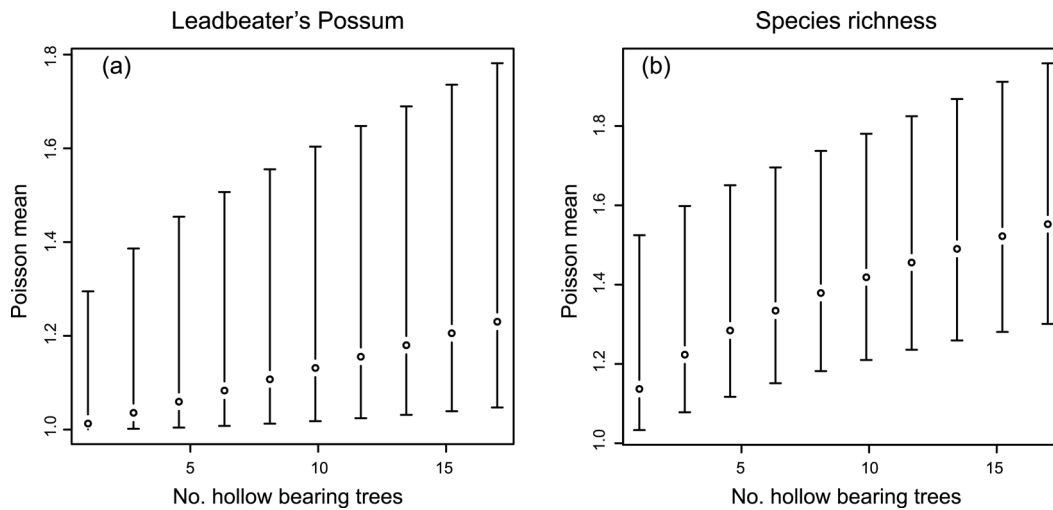
740 **Fig. 2. Relationships between presence of arboreal marsupials and abundance of**
 741 **hollow-bearing trees.** The panels show relationships for the proportion of presences (p)
 742 (the logistic component of the hurdle model) of different species of arboreal marsupials and
 743 the abundance of hollow-bearing trees per ha. Note that the model for Leadbeater's Possum
 744 is for unburned sites only as this species is virtually absent from burned areas. The
 745 probabilities were computed by holding the other terms in the model at the reference level
 746 for categorical variables and zero for the continuous variables. The error bars correspond to
 747 90% credible intervals.



748

749

750 **Fig. 3. Relationships between abundance of arboreal marsupials and abundance of**
 751 **hollow-bearing trees.** The panels show relationships between the abundance (μ) (the
 752 truncated Poisson portion of the hurdle model) of difference species of arboreal marsupials
 753 and the abundance of hollow-bearing trees per ha. Note that the models for Leadbeater's
 754 Possum is for unburned sites only as this species is virtually absent from burned areas. The
 755 truncated Poisson means were computed by holding the other terms in the model at the
 756 reference level for categorical variables and zero for the continuous variables. The error
 757 bars correspond to 90% credible intervals.

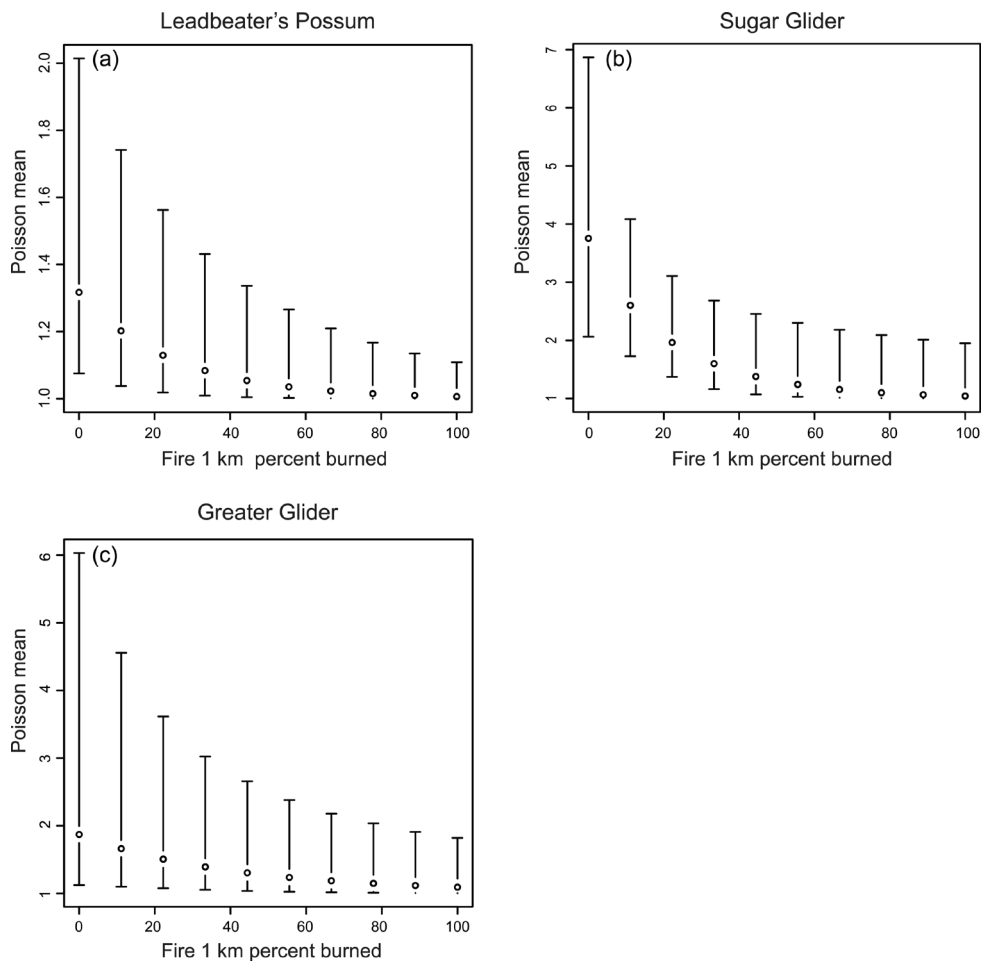


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761 **Fig. 4. Relationships between abundance of arboreal marsupials and fire in the**
 762 **surrounding landscape.** The panels show relationships between the abundance (μ) (the
 763 truncated Poisson portion of the hurdle model) of difference species of arboreal marsupials
 764 and the proportion of moderate and severe fire in the surrounding 1km radius of the site.
 765 Note that the models for Leadbeater's Possum and Sugar Glider are for unburned sites only
 766 as these species are virtually absent from burned areas. The truncated Poisson means were
 767 computed by holding the other terms in the model at the reference level for categorical
 768 variables and zero for the continuous variables. The error bars correspond to 90% credible
 769 intervals.



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