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Microhabitat selection by small mammals in response to fire

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ABSTRACT

Understanding how fire influences animal behaviour, such as movement and resource selection, is important for ecosystem management because it can improve our capacity to predict how species will respond. We assessed microhabitat selection by two small mammals, the bush rat (*Rattus fuscipes*) and agile antechinus (*Antechinus agilis*), in response to a low intensity prescribed fire. We used spool and line tracking and touch pole vegetation surveys to quantify microhabitat selection along 21 trails for bush rats and 22 for antechinuses before and after fire. In unburnt areas, bush rats showed positive selection for sedges, logs, and habitat complexity, with selection further increasing in burnt areas for sedges, ferns, shrubs, habitat complexity and unburnt patches. Agile antechinuses showed no significant microhabitat selection in unburnt or burnt areas and no change in response to fire. Their lack of response to ground fires may be due, partially, to their scansorial behaviour and use of tree hollows as refuge sites. Strong selection by bush rats for small unburnt patches suggests that even low intensity, patchy fires such as planned burns can impact bush rats and that high burn patchiness may help bush rats persist in recently burnt areas. Future fire planning should consider both behavioural and population responses of animals to fire.

Keywords: bushfire, dasyurid, disturbance, fire ecology, habitat use, megafire, planned burn, prescribed burn, resource selection, rodent, wildfire.

Introduction

Fire plays a major role in shaping ecosystems across the world, especially so as fire regimes are disrupted by human influences (He *et al.* 2019). With human-induced climate change and land-use practices (e.g. Lindenmayer *et al.* 2020) leading to a heightened risk of wildfire globally (Pastro *et al.* 2011; Jolly *et al.* 2015), prescribed burning is increasingly used as a hazard reduction tool to protect ecological values, human lives, and infrastructure (Moritz *et al.* 2014). Whilst prescribed burning is now a common management tool across the globe (Fernandes and Botelho 2003; Attiwill and Adams 2013; Clarke *et al.* 2019), the practice may contribute to inappropriate local fire regimes (Driscoll *et al.* 2010) and increase the potential for negative impacts on animal species. Immediate and short-term effects of fire may include increased mortality, altered habitat suitability, reduced resource availability, increased predation or competition, or disruption of demographic processes often leading to reduced fitness and survival (Sutherland and Dickman 1999; Whelan *et al.* 2002; Conlisk *et al.* 2015; Nimmo *et al.* 2019).

Fire impacts vegetation composition and microhabitat availability by reducing cover and structural complexity, which in turn can alter the habitat available for animals, leading to changes in abundance and species richness (Griffiths and Brook 2014; Nimmo *et al.* 2019). Such effects have been recorded for a range of different taxa, including birds, reptiles and small mammals, amongst others (Woinarski *et al.* 2004; Smucker *et al.* 2005; Green and Sanecki 2006; Fontaine *et al.* 2009; Nimmo *et al.* 2014). For example, in Australia, lizards were found to alter their movement patterns in search of shelter after fire (Driscoll *et al.* 2012), and the occurrence of feral cats (*Felis catus*) and foxes (*Vulpes vulpes*) increased after a prescribed burn as they took advantage of more favourable hunting conditions (Hradsky *et al.* 2017). A related study also found

decreased body condition of bush rats (*Rattus fuscipes*) in burnt compared to unburnt areas, possibly related to reduced access to resources after fire (Fordyce *et al.* 2016).

Small mammals and their responses to fire have been the subject of extensive research, but the mechanisms driving changes in behaviour in burnt and unburnt habitat (e.g. predation, immigration and competition) are still relatively poorly understood (Sutherland and Dickman 1999; Griffiths and Brook 2014). Depending on their life histories and habitat requirements, small mammals exhibit a range of behavioural strategies to persist in fire-prone landscapes. Several species change their habitat use and movements to avoid or survive fires. For example, the short-snouted elephant shrew in South Africa (*Elephantulus brachyrhynchus*) shifted its habitat use from grasslands pre-fire to shrub thickets post-fire (Yarnell *et al.* 2008). In Australia, the brown antechinus (*Antechinus stuartii*) and yellow-footed antechinus (*Antechinus flavipes*) increased periods of torpor and decreased foraging times in recently burnt areas (Stawski *et al.* 2015; Matthews *et al.* 2017), while bush rats exhibited sharper turning angles in small unburnt patches, suggesting they prefer to avoid burnt areas (Fordyce *et al.* 2016). For some species though, fire is important for ongoing persistence. The eastern chestnut mouse (*Pseudomys gracilicaudatus*) is a post-fire specialist and disperses willingly through burned vegetation (Pereoglou *et al.* 2013). These examples highlight the value of understanding species' habitat use for fire management and wildlife conservation by, for example, highlighting when patchy burns or habitat-specific burns may aid persistence.

Fire is common in south-eastern Australia and this region recently experienced its worst bushfire season on record (Boer *et al.* 2020), with fire regimes expected to continue intensifying under both a warming and drying climate (King *et al.* 2013; Bradstock *et al.* 2014) and increased rates of prescribed burning (Gazzard *et al.* 2020; Russell-Smith *et al.* 2020). Our study aimed to assess how a low intensity, prescribed fire affected microhabitat selection by two small mammal species in south-eastern Australia: the agile antechinus (*Antechinus agilis*) and the bush rat. While microhabitat use by these two species is relatively well studied (see below paragraph), little attention has been paid to the effects of fire on microhabitat use (but see Fordyce *et al.* 2016; Banks *et al.* 2017). We measured microhabitat use before and after a prescribed burn in the eastern Otway Ranges of Victoria to address three key questions:

- (1) Does each species exhibit microhabitat selection in unburnt areas?
- (2) Does each species exhibit microhabitat selection in burnt areas?
- (3) Does microhabitat selection by the agile antechinus change in response to fire?

The third question was restricted to the antechinus due to sample size limitations for the bush rat (see Methods). Based

on previous research, we hypothesised that the bush rat would preferentially select for habitat attributes associated with dense understorey cover in unburnt areas, and that the preference for these attributes would increase at recently burnt sites (Catling 1991; Fordyce *et al.* 2016). We also hypothesised that the agile antechinus would display positive selection for certain microhabitat attributes (e.g. logs, complex vegetation) in both pre- and post-fire environments (Sutherland and Predavec 1999; Johnstone *et al.* 2011; Swan *et al.* 2016).

Materials and methods

Study area

This study was carried out between February and August 2019 in the Great Otway National Park, Vic., south-eastern Australia, approximately 5 km north of Aireys Inlet (38.415°S, 144.094°E; Fig. 1). The area has a temperate climate with a mean maximum temperature of 18.4°C and mean annual rainfall of 628 mm (Bureau of Meteorology 2019). The vegetation in the study area is primarily comprised of heathy woodland and open forest. The dominant plant species include messmate (*Eucalyptus obliqua*) and brown stringybark (*Eucalyptus baxteri*) in the canopy, with the mid-storey and ground cover dominated by prickly tea tree (*Leptospermum continentale*), twisted bearded heath (*Leucopogon glacialis*), myrtle wattle (*Acacia myrtifolia*), thatch saw sedge (*Gahnia radula*), austral grass tree (*Xanthorrhoea australis*), bracken fern (*Pteridium esculentum*), and grey tussock-grass (*Poa sieberiana hirtella*). The study area is subjected to prescribed burning for both hazard reduction and ecological values by creating a mosaic of different fire classes, and the last major bushfire in the area was the 1983 Ash Wednesday fire (Gazzard *et al.* 2020).

Study species

The bush rat is a small (40–225 g) nocturnal species, with an omnivorous diet of seeds, fungi and invertebrates (Carron *et al.* 1990). It is primarily found in coastal and temperate areas of southern and eastern Australia and prefers dense understorey vegetation (Dickman and Woodside 1983). The agile antechinus is a small (16–40 g) cathemeral dasyurid marsupial, with a diet of invertebrates, small vertebrates, and sometimes plant material (Goldingay 2000; Parrott *et al.* 2007). It is primarily found in wet forest ecosystems of south-eastern Australia (Van Dyck *et al.* 2013). It is semi-arboreal, with a semelparous breeding strategy whereby most males die shortly after breeding (Parrott *et al.* 2007; Swan *et al.* 2016).

Experimental design

The prescribed burn took place in mid-May 2019 to varying degrees of severity, resulting in a mosaic of unburnt and

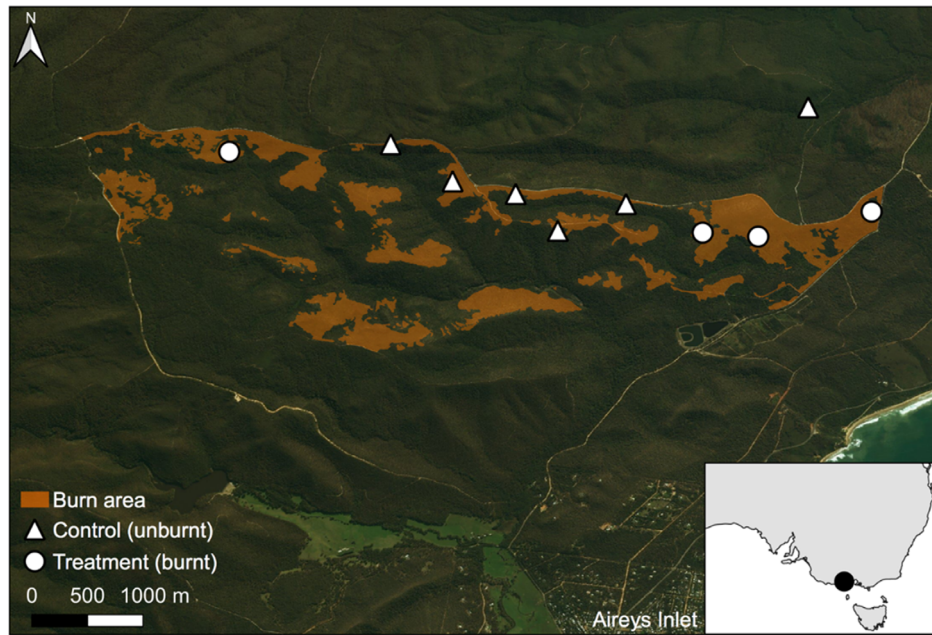


Fig. 1. Map of the study area depicting sites that remained unburnt (triangles) and sites that were burnt (circles) in the prescribed burn (orange shading). Inset map shows study area location (black dot) in south-eastern Australia.



Fig. 2. Photos of an unburnt site before the fire with typically dense understorey (left), and a burnt site displaying a characteristic mosaic of burnt and unburnt patches (right).

burnt patches throughout the study site (Figs 1 and 2). We collected pre-fire data at five sites between February and April 2019 and post-fire data at seven sites (four burnt, three unburnt) between June and August 2019. We initially intended to implement a full before–after, control–impact

design, but due to the patchy nature of the fire, only two of the five sites surveyed pre-fire were adequately burnt, so an additional two burnt sites were added post-fire. Sites were 1 ha in size and each separated by 0.5–1.3 km. To maximise our chances of catching sufficient numbers of the

target species, sites with a moderate slope and densely vegetated gullies were chosen (Bennett 1993; Sutherland and Predavec 1999; Claridge *et al.* 2008).

Animal trapping and handling

All procedures involving animals were approved by the Deakin University Animal Ethics Committee (project B26-2018). Animals were caught using Type A Elliott traps (9 × 10 × 33 cm, Elliott Scientific, Upwey, Australia). Each site comprised 30 trap stations positioned in three parallel lines running downslope into the gully, with each line separated by 30 m and traps within lines separated by 15 m. Traps were baited with a mixture of rolled oats, peanut butter and honey. Two to four sites were operated on any given night, each with 20–30 traps active. We operated control and impact sites concurrently to reduce any bias in data collection. Traps were opened each afternoon before 1700 hours and subsequently checked between 2200 and 0300 hours each night. We captured and tracked animals within this period since this is when they are most active (Van Dyck *et al.* 2013). We recorded the sex, weight and pes length of all animals and marked antechinus with a unique ear punch and bush rats with a metal ear tag.

Spool-and-line tracking

The spools used to track the animals consisted of ~5 g of nylon thread sourced from Danfield Ltd in Lancashire, UK (thread size number metric 120/2, size 10 cocoon bobbin). To ensure that spools weighed less than 5% of animal body weight, we reduced spool lengths by removing excess thread. We enclosed spools in heat shrink and final package weights were 1–1.5 g for antechinus and 2.5–4.5 g for bush rats. We attached spools to the lower back of animals using a small amount of cyanoacrylate glue, holding it in place for approximately 30 s. We then tied the loose end of the thread to the base of a shrub at the point of capture. Spools were attached to the animals' fur and spool packages were expected to detach upon reaching the end of the thread or naturally shed soon thereafter. We then released the animal, allowing it to resume normal activities while leaving a trail indicating the microhabitat it used. We followed each spool line the next day and recorded microhabitat attributes along the lines. We recorded data from 43 animal trails (Table 1), with three individuals being spooled twice post-fire, but in different sessions (two antechinus and one bush rat). Some glue and minor fur loss was visible on animals we retrapped in the same session. No animals were spooled more than once in the same session, with a 'session' indicating a 1-to-2-week period of trapping with approximately 3–4 weeks between each session.

Table 1. The number of bush rats (*Rattus fuscipes*) and agile antechinus (*Antechinus agilis*) tracked at control and impact sites pre- and post-prescribed fire.

Treatment	Bush rat	Agile antechinus
Impact sites (burnt)		
Pre-fire	6	2
Post-fire	6	11
Control sites (unburnt)		
Pre-fire	7	4
Post-fire	2	5
Total	21	22

Measuring used and available habitat

We followed each spool line to its end. The length of the lines varied between 20 and 100 m, with bush rat trails typically longer than those of agile antechinus. Similar to previous studies (e.g. Molyneux *et al.* 2017), we established one random straight line of the same length for each corresponding animal trail. The random lines began at the same starting point, but the direction was randomised using a mobile phone app (Spinner App). Habitat was quantified along both used and available (random) lines every 4 m for bush rats and 2 m for antechinus. We chose a shorter interval for antechinus because their spools were shorter than those of bush rats. The initial 10 m of each line for both species was excluded from measurement to avoid any potential bias from unnatural movements due to a flight response (Kearney *et al.* 2007; Fordyce *et al.* 2016). On several occasions, the spool detached within the first 10 m, therefore precluding any measurements. All lines longer than 10 m and long enough for the above-mentioned sampling distances irrespective of distance were recorded.

Vegetation density was measured vertically at each point along the line using the touch pole method (Elzinga *et al.* 2007), with a 2 m high pole segregated into six height brackets (0–25, 26–50, 51–75, 76–100, 101–150, and 151–200 cm). We recorded the following functional plant groups as present at each height category if they were touching the pole: dead material (e.g. dead branches, shrubs), sedge, fern, spreading grass, tussock grass, grass tree, tree, log, forb, and creeper. At the impact sites post-fire, we also recorded the presence of burnt plant material at each height category, which refers to any plant with only burnt stems and branches remaining. Care was taken to avoid trampling vegetation directly along the lines so as not to affect measurements on the touch pole.

We used the quadrant cover method (Glen *et al.* 2010) to measure the presence or absence of log cover at each point, with a score of 1 applied to each of the four quadrants within a radius of either 1 m (bush rat) or 50 cm (agile antechinus) providing a score of between 0 (no logs) and

4 (present in all quadrants) (Fordyce *et al.* 2016). We used a different radius for each species to reflect their differing sizes. As per Fordyce *et al.* (2016), the minimum measurements for defining a log were 50 cm in length and 10 cm in diameter. To assess litter cover, the same circular radius measurements were used and a scale of 0–4 applied corresponding to percentage cover (0 = 0%, 1 = 1–25%, 2 = 26–50%, 3 = 51–75%, 4 = 76–100%; Fordyce *et al.* 2016).

Statistical analysis

The final list of habitat attributes was narrowed down to nine variables most appropriate for determining microhabitat selection of the focal species, while those that were rejected contained insufficient data to provide any meaningful additional insight. Seven of the included variables were calculated as the proportion of sampling points on a line where a plant functional group was present within a specific height category. The variables were: dead material 0–50 cm, sedge 0–100 cm, fern 0–100 cm, shrub 0–200 cm, grass tree 0–100 cm, spreading grass 0–50 cm, and log 0–50 cm. These categories encompassed multiple height brackets, as outlined above, in order to best represent the heights that each variable was present at. We also generated a habitat complexity score by taking the average number of functional plant groups at each height category at individual sampling points and then calculating the mean across all points along each line (Fordyce *et al.* 2016). Finally, because the impact sites contained a mosaic of burnt and unburnt vegetation post-fire, we calculated the proportion of points along each line that were located in unburnt vegetation ('unburnt patches'). The chosen variables had low auto-correlation (Pearson's $r < \pm 0.5$), except for the habitat complexity score, which had moderate correlation ($r = 0.56$ – 0.73) with dead material, sedge and unburnt patches; and unburnt patches with sedge and shrub ($r = 0.56$ – 0.59). We take these correlations into consideration when interpreting the results.

We used logistic regression models (logit link function) with Firth's bias reduction method to assess microhabitat selection, implemented in the `logistf` R package (Heinze *et al.* 2018). The response variable indicated whether the microhabitat variables were from used (1) or available (0) trails. We used Firth's bias reduction to counter the effects of complete or quasi-complete separation which can result in infinite or very large parameter estimates and confidence intervals that are not informative (Albert and Anderson 1984; Firth 1993). It was not possible to include random effects in the bias-corrected models, which in this case may have been appropriate given the paired nature of the data (i.e. paired used and available trails). However, we initially fitted generalised linear mixed models that included a random effect of trail identity, and the variance component was 0 in every case, which indicates that the inclusion of a random effect is not necessary. We did not consider it necessary or feasible to include a random effect

representing individual animals because only three individuals were tracked more than once.

Ideally the data would have been analysed using two crossed factors of time and treatment. However, this was not possible due to low numbers of animals tracked for some treatment combinations (Table 1). We instead analysed the pre-fire and post-fire data separately for both species. We first analysed the pre-fire data (pooled for impact and control sites) to answer Question 1: *Does each species exhibit microhabitat selection in unburnt areas?* We then analysed the data from only the burnt sites post-fire to answer Question 2: *Does each species exhibit microhabitat selection in burnt areas?* The predictor variables in each case were the nine microhabitat variables described above. We only included one variable per model because the small dataset precluded fitting more complex models. In the context of this study, positive parameter estimates from the logistic regression models indicate that average values of a microhabitat variable were higher on used compared to available trails, and the opposite for negative estimates. When 95% confidence intervals did not overlap zero, we inferred selection for or against individual variables and present plots of the modelled relationships.

For the agile antechinus, we were also able to pool the pre-fire data for the control and impact sites (to create an adequate sample size), such that there were three treatments: unburnt pre-fire, burnt post-fire and unburnt post-fire. This allowed us to answer Question 3: *Does agile antechinus microhabitat selection change in response to fire?* By including unburnt post-fire sites, we control for any possible temporal changes independent of fire. This was not possible for the bush rat (due to there only being two unburnt trails sampled post-fire), however, we are confident that our results accurately reflect the effects of fire because they strongly align with previous research (e.g. Banks *et al.* 2011; Fordyce *et al.* 2016). The models for question 3 were fitted in the same way as for questions 1 and 2 (see above), except that an interaction between the microhabitat variable and treatment was included. We specified 'burnt post-fire' as the reference level in the model, which allows us to determine whether selection/avoidance of a microhabitat variable at unburnt sites pre- and post-fire differs from that at burnt sites. We present parameter estimates and 95% confidence intervals to make these inferences.

Results

Across all sites and treatments, we measured 21 trails for the bush rat and 22 for the agile antechinus, with average trail length being 57.81 m (5.32 s.e.) and 43.36 m (3.32 s.e.), respectively. Both pre- and post-fire, bush rats predominantly passed through dense understory vegetation and along and under logs within a well-established network of

tunnels created by a thick matting of sedges, ferns, and to a lesser extent, grass trees. The tunnels and pathways appeared to be used by more than one individual both within and between species. Agile antechinuses, on the other hand, frequented areas where the understory was more open and quite often spool lines traversed logs or scaled trees.

Question 1: Microhabitat selection in unburnt areas

Bush rats exhibited significant selection for three of the eight microhabitat variables analysed: sedges, logs, and habitat complexity (Table 2, Fig. 3). Positive trends were also observed for spreading grass, dead material, ferns and negative trends for shrubs and grass trees, although the confidence intervals overlapped zero (Table 2, Fig. 3). Agile antechinuses displayed no significant preferential selection for any of the habitat attributes, although there were non-significant positive trends for logs and habitat complexity (Table 2, Fig. 3).

Question 2: Post-fire microhabitat selection in burnt areas

Bush rats exhibited selection for a higher number of variables post-fire. There was a significant positive selection for sedges, ferns, shrubs, habitat complexity, and unburnt patches

(Table 2, Fig. 4). Although there was no evidence of significant preferential selection by agile antechinuses in burnt areas, dead material, sedges, and unburnt patches had confidence intervals that only marginally included zero (−0.85, 8.63; −0.96, 5.41; −0.74, 7.50, respectively), thus suggesting a possible weak positive association with those variables (Table 2, Fig. 4).

Question 3: Changes in antechinus habitat selection in response to fire

Similar to the separate pre- and post-fire analyses for the agile antechinus, there were no significant relationships when comparing microhabitat selection in burnt areas to either unburnt areas pre-fire or unburnt areas post-fire (Table 3). All variables had wide confidence intervals that included zero (Table 3).

Discussion

Fire can have strong impacts on vegetation structure by reducing understorey and ground cover, but not all mammal species find this change disadvantageous (Monamy and Fox 2000; Letnic 2003; Torre and Díaz 2004; Lindenmayer *et al.* 2008;

Table 2. Modelling results regarding microhabitat selection in response to fire.

Species	Microhabitat variable	Coefficient (95% CI)	
		Pre-fire	Post-fire
Bush rat	Dead material	1.31 (−1.98, 4.88)	3.09 (−0.71, 8.18)
	Sedge	7.36 (2.39, 14.48)	6.51 (1.82, 23.08)
	Fern	1.40 (−1.62, 5.01)	6.55 (0.46, 16.37)
	Shrub	−0.23 (−3.43, 2.90)	11.02 (2.13, 42.81)
	Grass tree	−2.13 (−6.01, 0.98)	4.50 (−0.29, 17.60)
	Spreading grass	1.90 (−0.59, 4.97)	NA ^A
	Logs	13.71 (2.83, 32.30)	NA ^A
	Habitat complexity	19.18 (7.77, 47.17)	10.76 (3.15, 37.16)
	Unburnt patches	NA	6.75 (2.29, 17.22)
Agile antechinus	Dead material	0.14 (−2.74, 3.08)	3.27 (−0.85, 8.63)
	Sedge	−0.18 (−6.34, 5.92)	1.99 (−0.96, 5.41)
	Fern	0.03 (−3.56, 3.64)	3.60 (−2.37, 10.96)
	Shrub	1.58 (−2.90, 6.70)	0.02 (−2.76, 2.80)
	Grass tree	0.37 (−5.87, 6.81)	1.13 (−2.45, 6.44)
	Spreading grass	0.24 (−3.65, 4.21)	5.18 (−5.98, 25.52)
	Logs	7.81 (−0.41, 23.59)	17.32 (−2.73, 150.73)
	Habitat complexity	3.33 (−1.83, 10.53)	4.11 (−1.10, 10.78)
	Unburnt patches	NA	2.43 (−0.74, 7.50)

Coefficient values along with their 95% confidence intervals are shown for each treatment site pre- and post-fire. Bold values indicate variables where the confidence intervals do not include zero.

^ASpreading grass and logs were omitted due to there being insufficient data for analysis.

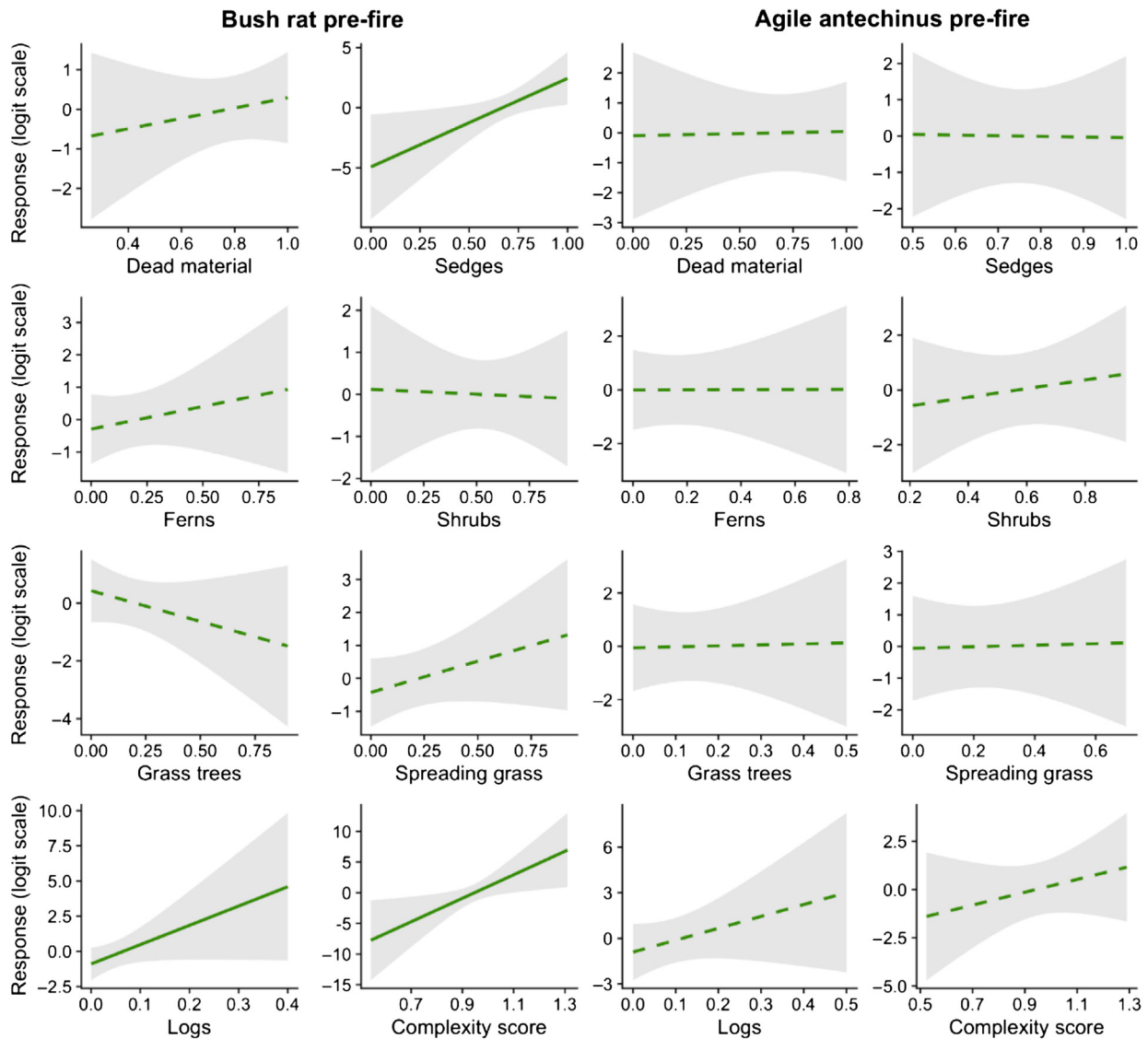


Fig. 3. Modelled relationships between microhabitat use and availability for the bush rat (left) and agile antechinus (right) pre-fire. Positive values on the y-axis represent selection for an attribute and negative values represent avoidance. Green lines are mean relationships and grey bands are 95% confidence intervals, with statistically significant relationships represented by a solid line and all others a dashed line.

Kelly *et al.* 2010; Zwolak *et al.* 2012; Doherty *et al.* 2015; Sharp Bowman *et al.* 2017). We found that bush rats, as predicted, demonstrated clear selection for dense understorey vegetation, with stronger habitat selection exhibited after fire. We found no evidence for selection of specific microhabitat features by agile antechinuses, nor changes in habitat use in response to fire.

Pre-fire microhabitat use

In unburnt areas pre-fire, bush rats displayed non-random movement, with preferences for sedges, habitat complexity and logs (acknowledging that the first two were moderately correlated with each other). This is consistent with an

earlier study that found positive selection for logs, rushes and complex habitat (Fordyce *et al.* 2016). Other studies have also made similar findings, with Spencer *et al.* (2005) highlighting the importance of complex and dense vegetation, and Strauß *et al.* (2008) and Maitz and Dickman (2001) identifying logs and rushes as important habitat components, respectively. These have been suggested as key habitat features used by the bush rat for foraging, nesting, and predator avoidance (Strauß *et al.* 2008; Fordyce *et al.* 2016). Many other small mammals depend on similar features, including the swamp rat (*Rattus lutreolus*; Kearney *et al.* 2007), common vole (*Microtus arvalis*; Jacob and Brown 2000) and oldfield mouse (*Peromyscus polionotus*; Orrock *et al.* 2004).

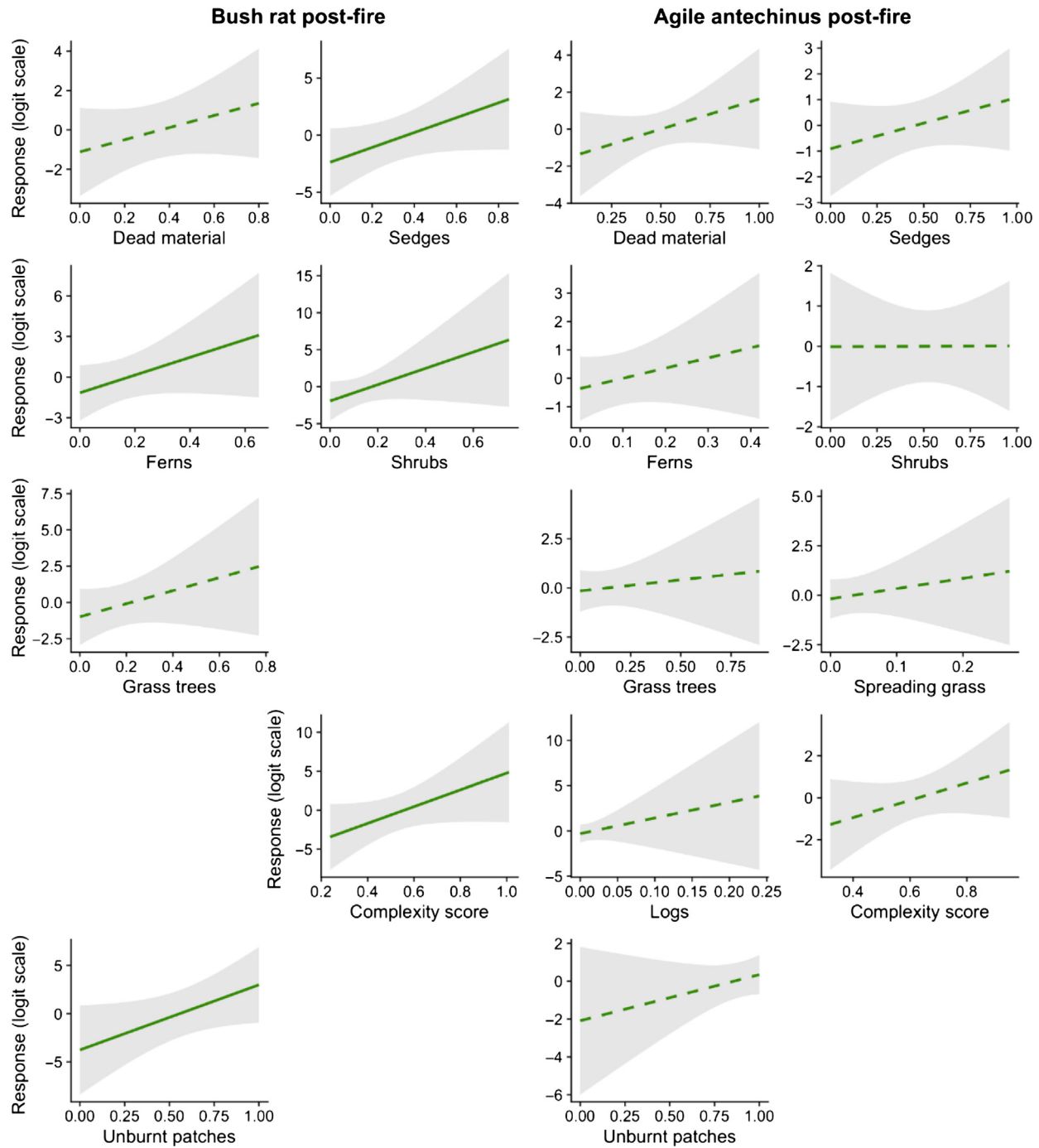


Fig. 4. Modelled relationships between microhabitat use and availability for the bush rat (left) and agile antechinus (right) post-fire. Positive values on the y-axis represent selection for an attribute and negative values represent avoidance. Green lines are mean relationships and grey bands are 95% confidence intervals, with statistically significant relationships represented by a solid line and all others a dashed line.

In contrast to the bush rat, there was no evidence of selection for specific habitat features by the agile antechinus in unburnt areas, although there were positive trends for logs and complex habitat. Previous studies on agile antechinus microhabitat have revealed conflicting results, in particular regarding vegetation density. Some

have pointed to positive selection for dense low cover (Bennett 1993; Sutherland and Predavec 1999), or association with sparse but structurally complex vegetation (Moro 1991), whilst others found that microhabitat use was proportional to availability (Wilson *et al.* 1986). These differing results across studies may be attributable to site

Table 3. Modelling results regarding changes in microhabitat selection by agile antechinus in response to fire.

Microhabitat variable	Coefficient (95% CI)	
	Burnt vs unburnt pre-fire	Burnt vs unburnt post-fire
Dead material	-3.13 (-9.09, 1.91)	12.20 (-3.23, 44.16)
Sedge	-2.17 (-9.08, 4.60)	0.66 (-6.05, 8.43)
Fern	-3.56 (-11.56, 3.32)	-3.60 (-32.85, 25.62)
Shrub	1.57 (-3.67, 7.29)	-0.78 (-9.26, 7.27)
Spreading grass	-4.94 (-22.57, 6.85)	-4.23 (-22.31, 8.47)
Logs	-9.51 (-143.24, 16.83)	-2.55 (-137.07, 59.32)
Complexity	-0.79 (-9.12, 7.94)	2.11 (-7.63, 15.22)

Coefficient values along with their confidence intervals are shown for the interaction between fire treatment and microhabitat use.

specific differences in vegetation composition and structure, variable behaviour by the agile antechinus across its range, or differences in methodology. Previous studies were based on trapping data (Moro 1991; Bennett 1993; Wilson *et al.* 1986), or both trapping data and fluorescent pigment tracking (Sutherland and Predavec 1999). We may not have detected selection for specific microhabitat components by the agile antechinus if the trails were too short to adequately capture foraging and sheltering behaviour, with mean trail length being 43 m. However, fluorescent pigment tracking does not seem to be a suitable alternative given that pigment trails are of a similar length or shorter than the average spool length in our study. For example, the average pigment trail length was 26 m for *Sminthopsis youngsoni* (Haythornthwaite 2005), 32 m for *A. flavipes* and 46 m for *S. murina* (Stokes *et al.* 2004), which are of broadly similar size to *A. agilis*. Automated high frequency radio-tracking (e.g. Wallace *et al.* 2021) may be the only suitable alternative for high resolution tracking of this species over longer periods until miniature GPS tags (~1 g) become widely available and more affordable.

Post-fire microhabitat use

Following the prescribed burn, bush rats exhibited significant selection for an additional three microhabitat features compared to pre-fire: ferns, shrubs and unburnt patches (the latter being moderately correlated with sedges and shrubs). Fordyce *et al.* (2016) also noted a strengthening of bush rat microhabitat selection in post-fire environments, although they also observed increased selection for spreading grass, which was not common at our study sites. Reasons for these observed increases could include loss of food and shelter due to a reduction in understory vegetation from the burn and a resultant increase in perceived or actual predation risk. Indeed, it has been noted that small mammals succumb primarily to predation or starvation rather than fire itself

(Thompson *et al.* 1989; Hale *et al.* 2021), as evidenced in studies on hispid cotton rats (*Sigmodon hispidus*) in North America (Conner *et al.* 2011; Morris *et al.* 2011). In northern Australia, predation rates on rodents were greater in burnt compared to unburnt habitat (Leahy *et al.* 2016) and feral cats were attracted to recently burnt areas (McGregor *et al.* 2016), likely due to the increased hunting success they experience in simplified vegetation (McGregor *et al.* 2014). However, the relative importance of changes in food availability, shelter and predation post-fire is poorly resolved and ideally would be assessed using further manipulative experiments in a range of environments.

Of particular note in this study was the strong selection for unburnt patches post-fire, coupled with an increase in the number of attributes compared to pre-fire. As a result, we suggest that the additional microhabitat features used by bush rats post-fire in our study may be a method of seeking refuge to decrease the risk of predation. No bush rats were recorded moving in burnt patches, despite their ready availability at impact sites. Other studies have noted this preferential selection for unburnt patches in other small mammals, including the yellow-footed antechinus *A. flavipes* in the jarrah forest of Western Australia, which preferentially used unburnt grass trees (Swinburn *et al.* 2007), the eastern chestnut mouse in New South Wales, which selected for tall and dense vegetation (Pereoglou *et al.* 2011), and populations of small mammals more generally (e.g. Lunney *et al.* 2008). In this regard, unburnt patches can allow bush rat populations to persist within a burnt landscape and re-establish over time (Lunney *et al.* 2008; Robinson *et al.* 2013; Banks *et al.* 2017).

In a similar trend to its pre-fire microhabitat use, agile antechinuses showed no significant preference for any of the habitat attributes analysed. There were, however, positive increases across all variables tested, except for shrubs. This could indicate a weak preference for unburnt patches within burnt locations, similar to that found for the yellow-footed antechinus (Swinburn *et al.* 2007). In terms of changes in response to fire, selection for dead material and sedges increased, although the confidence intervals included zero. Overall, these findings are consistent with previous studies suggesting the agile antechinus is more resilient to low intensity fires than bush rats, which they may achieve by seeking refuge in tree hollows (Banks *et al.* 2011; Swan *et al.* 2016). Additionally, studies on the brown antechinus, *A. stuartii*, reported increased periods of torpor and reduced foraging activity for those in burnt patches compared to unburnt habitat (Stawski *et al.* 2016). This further suggests that the agile antechinus is able to employ alternative strategies to cope with fire and hence be less reliant on specific microhabitat features after fire, in contrast to the bush rat (although bush rats may occasionally go into torpor, Nowack *et al.* 2020).

Our results are consistent with previous studies suggesting bush rats have more specific microhabitat requirements than

agile antechinuses and therefore could be more susceptible to the immediate and short-term effects of low-severity fire including planned burns. For example, Banks *et al.* (2011) reported a higher occurrence of agile antechinuses compared to bush rats in very recently burnt areas, most likely due to higher rates of *in situ* survival by antechinuses. Similarly, Swan *et al.* (2016), found that the ability of agile antechinuses to disperse and their flexibility in the use of available habitat better equipped them to survive the immediate impacts of a low intensity prescribed burn, compared to the bush rat's greater reliance on dense understorey vegetation.

Additionally, body size could be an influential factor. A systematic review by Griffiths and Brook (2014) reported increased sensitivity to fire for mammals between 101 and 1000 g and with higher affinity with dense ground cover. This is pertinent since bush rats weigh up to 225 g and prefer dense ground vegetation, where agile antechinuses reach up to 45 g, prefer more open vegetation and are semi-arboreal. The agile antechinus also primarily feeds on invertebrates (Moro 1991; Lunney *et al.* 2001), which may be less limited after fire compared to plant matter and fungi, which are important to bush rats (Cheal 1987; Carron *et al.* 1990). Agile antechinuses also shelter in tree hollows, which could further mitigate predation risk in the short-term following fire, although high intensity burns may destroy some hollows. Loyn *et al.* (1986) found that sooty owls (*Tyto tenebricosa*) preyed solely on bush rats post-fire, even when arboreal mammals were available, presumably due to reduced cover and increased exposure of bush rats, whereas arboreal mammals likely sought shelter in tree hollows and benefitted from persistent canopy cover.

Conservation implications and future research

This study has provided further understanding of multi-species microhabitat use in response to fire. Future research could look to build on this by increasing sample sizes, potentially using more sophisticated tracking methods, and importantly, by considering a wider range of fire conditions. Although logistically challenging, this would further add to the body of knowledge regarding the effects of varying fire regimes on animal movement and behaviour, particularly higher severity fires. Furthermore, this study only took into account animal responses immediately following the fire (0–3 months). Examining successional changes over a longer period would enable the duration of impacts to be defined more precisely. For example, bush rat abundance would be expected to increase along with time-since-fire as understorey vegetation gradually recovers (Lunney and Ashby 1987), and this may also be reflected in changes in their microhabitat use.

Improved knowledge of small mammal responses to fire is particularly important as fire frequency and intensity is forecasted to increase in warming and drying climates (King *et al.* 2013; Bradstock *et al.* 2014). Small mammals

respond to fire in varying ways as evidenced in this study, and in other ecosystems worldwide (Torre and Díaz 2004; Horn *et al.* 2012; Doherty *et al.* 2015; Sharp Bowman *et al.* 2017). Strong selection by bush rats for small unburnt patches within burnt areas shows that even low intensity, patchy fires such as planned burns, can substantially constrain their use of the landscape, and suggests that more complete or severe fires would be extremely detrimental. In contrast, low intensity planned burns apparently have comparatively little impact on the habitat use of the small, semi-arboreal agile antechinus, though higher severity fires are more likely to impact on the availability of tree hollows where they seek shelter. Unburnt refuges will therefore become increasingly important for many small mammal species to persist in fire-prone landscapes (Robinson *et al.* 2013). Future work should take into account multi-species responses and identify key habitat features for at-risk species to avoid implementing inappropriate fire regimes.

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Data availability. The data that support this study will be shared upon reasonable request to the corresponding author.

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