



Fire affects microhabitat selection, movement patterns, and body condition of an Australian rodent (*Rattus fuscipes*)

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Resource selection by animals influences individual fitness, the abundance of local populations, and the distribution of species. Further, the degree to which individuals select particular resources can be altered by numerous factors including competition, predation, and both natural- and human-induced environmental change. Understanding the influence of such factors on the way animals use resources can guide species conservation and management in changing environments. In this study, we investigated the effects of a prescribed fire on small-scale (microhabitat) resource selection, abundance, body condition, and movement pathways of a native Australian rodent, the bush rat (*Rattus fuscipes*). Using a before-after, control-impact design, we gathered data from 60 individuals fitted with spool and line tracking devices. In unburnt forest, selection of resources by bush rats was positively related to rushes, logs and complex habitat, and negatively related to ferns and litter. Fire caused selection for spreading grass, rushes, and complex habitat to increase relative to an unburnt control location. At the burnt location after the fire, rats selected patches of unburnt vegetation, and no rats were caught at a trapping site where most of the understory had been burnt. The fire also reduced bush rat abundance and body condition and caused movement pathways to become more convoluted. After the fire, some individuals moved through burnt areas but the majority of movements occurred within unburnt patches. The effects of fire on bush rat resource selection, movement, body condition, and abundance were likely driven by several linked factors including limited access to shelter and food due to the loss of understory vegetation and heightened levels of perceived predation risk. Our findings suggest the influence of prescribed fire on small mammals will depend on the resulting mosaic of burnt and unburnt patches and how well this corresponds to the resource requirements of particular species.

Key words: animal movement, distribution and abundance, ecological refuge, habitat fragmentation, niche, predation risk, prescribed fire, pyrodiversity, resource selection, small mammal

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Animals use resources selectively based on their requirements for growth, survival, and reproduction (Johnson 1980). Numerous factors can influence resource use, including environmental change, conspecific density, and intraspecific competition (Johnson 1980; Strauss et al. 2008; Swan et al. 2008). A central task in ecology is to quantify the relative importance of different resources for fauna and determine the factors that influence their access and use (Wiens 2002). Such information underpins ecological theories such as the niche concept and has direct application to biodiversity conservation and management, allowing us to identify and prioritize the preservation of species' key habitat components (e.g., hollow-bearing trees—Martin and Martin 2007).

A greater understanding of resource use can be achieved by analyzing resource selection, i.e., the proportion of resource units used relative to their availability (Boyce et al. 2002;

Manly et al. 2002). Resource selection occurs along an inter-linked hierarchy of spatial and temporal scales (Johnson 1980; Wiens et al. 1987; Boyce 2006). For example, at large spatial scales, resource selection relates to the physical or geographical range of a species, while at fine scales it may involve the procurement of food items. Selection at one scale can impact selection elsewhere in the hierarchy: selection for feeding sites, for example, is conditional upon selection of home ranges within the wider landscape (Johnson 1980). In this study, we considered the selection of resources within an individual's home range. Analysis of resource selection at this scale is often referred to as microhabitat selection and is relatively poorly studied because it is difficult and time-consuming to collect data at an appropriate resolution (Jorgensen 2004).

Resource selection by animals is influenced by several interacting factors including the distribution and abundance of

important resources, internal processes such as perception and movement, and external processes such as predation. Drivers of animal movement are particularly important, as resource selection is strongly influenced by movement decisions. For example, the presence or absence of shelter, and associated changes in perceived predation risk, may influence where and when individuals choose to forage (Lima and Dill 1990; Jacob and Brown 2000; Kotler et al. 2002). Further, movement patterns can be used to infer habitat quality: short distance movements and frequent turns are generally associated with high-quality foraging habitat, while longer, straighter movements are expected to be associated with poor-quality or riskier habitat (Reiners 2005). Movement patterns can influence rates of predation, competition, reproduction, and dispersal capacity and so affect both individuals and the structure and dynamics of populations, communities, and ecosystems (Nathan et al. 2008).

Fire is a common agent of change in many ecosystems (Bond and Keeley 2005) and is increasingly used as a tool for ecosystem management (Castellnou et al. 2010; Stephens et al. 2012; Attiwill and Adams 2013). Fire consumes biomass, alters structural complexity, and influences the distribution and abundance of fauna (e.g., Fox 1982; Catling et al. 2001; Smucker et al. 2005; Plavsic 2014; Roberts et al. 2015, and see reviews by Fontaine and Kennedy 2012; Griffiths and Brook 2014). Despite this, the mechanisms underlying faunal responses to fire are poorly understood (Driscoll et al. 2010; Robinson et al. 2013; Griffiths and Brook 2014), including how spatial changes in resource availability affect important behavioral processes such as movement and resource selection. A better understanding of the links between habitat change and animal behavior will increase our capacity to predict species' responses to landscape change, such as those caused by fire (Knowlton and Graham 2010).

In this study, we used a before-after, control-impact design to quantify the influence of a prescribed fire on microhabitat selection, movement patterns, abundance, and body condition of the bush rat (*Rattus fuscipes*), a native Australian rodent. In the absence of fire, we predicted that: 1) Bush rats would select some microhabitat attributes disproportionately to their availability. Further, because the fire was expected to reduce the availability of important habitat attributes, we predicted the following fire effects: 2) Increased selection of habitat attributes, due to expected reductions in availability in the post-fire environment. 3) Decreased bush rat abundance and body condition. 4) Straighter movement paths and longer step lengths, reflecting an increase in perceived predation risk post fire.

MATERIALS AND METHODS

Study area.—We conducted our study within the Great Otway National Park, south-east Australia (38°24' S, 144°1' E). The eucalypt forests of this region are prone to wildfire and prescribed fire is frequently used as a land management tool, providing the opportunity to study fire-fauna relationships experimentally. The region has a temperate climate, with mean daily maximum temperatures varying between 13.3 °C in July

and 22.7 °C in January and a mean annual rainfall of 635 mm (Bureau of Meteorology 2014).

Within the National Park, we selected 2 study locations. The impact location was a 1,190 ha block designated for prescribed burning, while the control location was an equivalent area approximately 10 km away with broadly similar topography and vegetation. At both locations, the overstorey was dominated by messmate stringybark (*Eucalyptus obliqua*), narrow-leaved peppermint (*E. radiata*), and broad-leaved peppermint (*E. dives*). Midstorey species included prickly leaved wattle (*Acacia verticillata*), variable sword-sedge (*Lepidosperma laterale* var. *majus*), and hop goodenia (*Goodenia ovata*), while ground covers include austral bracken (*Pteridium esculentum*) and forest wire-grass (*Tetrarrhena juncea*).

Sampling design.—Within each location, we established 3 sites, each centered on a gully. Sites were deliberately chosen to a) be suitable habitat for bush rats, b) have a high probability of a patchy burn outcome, and c) be accessible at night. We caught bush rats and quantified habitat attributes (see below) concurrently at the impact and control locations before (January–March) and after (May–June) the fire. As such, our study corresponded to a before-after, control-impact design, enabling us to distinguish the effects of the prescribed fire from natural variability (Downes et al. 2002). Due to logistical constraints and lack of other appropriate blocks on the burning schedule, we were unable to replicate our study at the scale of the fire. However, ours is one of very few studies of its kind to include both spatial and temporal controls.

Animal capture and spool attachment.—All activities associated with capture and spool attachment were approved by the University of Melbourne Animal Ethics Committee (ID 1011632.6) and were consistent with the American Society of Mammalogists' guidelines outlined in Sikes et al. (2011). We caught bush rats using Type A Elliot traps (9×10×33 cm—Elliott Scientific, Upwey, Australia) deployed along a transect following the bottom of each gully site. Traps were baited with a mixture of rolled oats, golden syrup, pistachio essence, and peanut butter and were positioned about 5 m apart, with 20 to 60 traps deployed per night/per site. We opened traps between 1500 and 1600h, and checked them between 2200 and 0400h. All captured bush rats were weighed, had their tail lengths and sex recorded, and were given a unique ear clip using surgical scissors. Nontarget species were identified and released.

We only used individuals weighing > 90 g for spool and line tracking, as this ensured that the spool (total weight = 4.5 g) was < 5% of the minimum body weight. A 120 m nylon spool (120/2 Nymo cocoon bobbin—Danfield Limited, Lancashire, England) encased in heat shrink rubber was attached externally just below the shoulder blades using cyanoacrylate (Selleys Supa Glue—Selleys Pty. Ltd., Padstow, Australia). Once attached, the thread was tied off at the point of release and the spool unwound as the rat moved around the landscape, marking the use of habitat attributes. Individuals were released between 2200 and 0400h, the period during which this species is generally active. In total, we collected data from 60 rats, and spooled

5 individuals twice, once before and once after the fire. Sample sizes per location are given in Table 1.

Our primary aim was to quantify the effect of fire on rat behavior. Given that there was a distinct possibility that some impact sites would remain unburnt, we relocated approximately 30% of individuals from each site in each survey period a maximum of 50 m from the site of capture, reasoning that burnt patches were likely to occur within this distance. The fire ultimately burnt all impact sites to some degree but we retained this aspect of the design for consistency. At the impact location after the fire, individuals were relocated into burnt patches. Individuals relocated before the fire served as a control for any behavioral changes associated with the relocation process.

Defining used and available habitat.—Habitat used by bush rats was quantified along spool lines within 24 h of spool attachment. We discarded the first 10 m of each spool to avoid bias from a possible flight response and thereafter measured habitat attributes at 10 sampling points spaced 4 m apart (total distance assessed = 40 m). In 4 cases, the spool line snapped, so data were only collected for the available length of the spool. Two spools detached before any habitat measurements could be taken.

Vertical vegetation structure was quantified using the point-intercept method (Elzinga et al. 2007). A wooden pole was held vertically at each sampling point and vegetation was recorded as present or absent in each of 5 height categories (0–20 cm; 21–50 cm; 51–100 cm; 101–200 cm; 201–400 cm) for 12 functional groups: spreading grass, tussock grass, rush or sedge, forb, stalked fern, clumped fern, tree fern, shrub, tree, small tree, creeper, and dead material.

The cover of logs and litter was estimated in 1-m-radius circular plots centered on each sampling point along the spool. We applied the quadrant cover method (Glen et al. 2010) to estimate log cover, which we defined as dead wood at least 50 cm long and 10 cm in diameter. Plots were split into 4 equal quadrants, and the presence of a log in each quadrant scored as 1, resulting in a score between 0 and 4. We defined litter as any ground-based dead material other than logs and estimated its cover using a 5-point scale, where 0 = no litter cover, 1 = 1–25%, 2 = 26–50%, 3 = 51–75%, and 4 = 76–100%.

We used ArcMap 10.1 (ESRI 2012) to define the area available to individuals at each site by establishing a circle of 50 m radius around each individual’s release point, and then enclosing all circles in the smallest possible polygon. We used circles of this size as they approximated a bush rat’s home range area (Sanecki et al. 2006). Within the enclosing polygon, we used

the methods described above to quantify habitat attributes along 30 randomly located 40 m transects. The start-point location and transect direction were both randomly assigned.

We used 6 habitat attributes in our final analyses: the cover of logs, litter, spreading grass, rushes, and ferns, and a habitat complexity index. For each spool or random transect, values for log and litter cover were calculated as the mean of values from the 10 sampling points. Cover of spreading grass (principally *T. juncea*) was calculated as the proportion of sampling points where it was present between 0 and 50 cm. Values for fern and rush cover (principally *P. esculentum* and *L. laterale* var. *majus* respectively) were derived in the same way except that presences between 0 and 200 cm were included. A habitat complexity index was derived by calculating the mean number of functional groups per vertical stratum at each sampling point and then averaging across sampling points. The final set of attributes was principally uncorrelated ($r^2 \leq 0.36$) and had a good spread of values (Table 2). Several additional habitat variables were initially investigated but rejected due to strong correlations with at least 1 in the final set or insufficient variance for useful modeling.

Movement pathways.—Movement pathways were defined using turning angles and step length. Turning angles were recorded at every point along the spool where it changed direction $\geq 5^\circ$. For analyses, the raw data were converted into values between 0° and 180° , where 0° represents movement straight ahead and 180° a U-turn. Step lengths were calculated as the distance between each turning point.

Data analysis.—Analyses of habitat selection were conducted using logistic regression with the binary response variable defined as used (1) or available (0—Manly et al. 2002). We used a mixed effects version of this model, enabling the inclusion of random factors to account for repeated temporal measurements and spatial nestedness in our design (Gillies et al. 2006). Predictions from logistic regression are usually interpreted as probability of use, but because points designated as available may be used by some individuals, predictions from use-availability models do not reflect true probabilities. Rather, predictions are correlated with the true values and can be interpreted as an index of resource selection (Manly et al. 2002).

First, we applied this model to quantify rat selection of habitat attributes (Table 2) in unburnt forest using data from the impact location pre-fire and the control location during both survey periods. Models were built using each habitat attribute as a separate predictor variable, specifying site nested within location as the random effect. Second, we assessed the effect of fire on the selection of each attribute by modeling time (before, after) and location (control, impact) as 2 categorical predictors and the attribute as a continuous predictor. We interpreted the fire effect by considering the magnitude, uncertainty and statistical significance associated with the 3-way time \times location \times attribute interaction. We initially ran these analyses using a mixed effects model with site specified as the random factor. However, as the associated variance component was zero in all cases, we excluded the random factor from the final analyses (Zuur et al. 2009). In both analyses, relocation (relocated or

Table 1.—The number of bush rats (*Rattus fuscipes*) spooled at the control and impact locations before and after a prescribed fire, Great Otway National Park, Australia. In total, we sampled 60 individuals but numbers sum to 65 as 5 rats were spooled twice (see text).

Location	Time	
	Before	After
Control	12 (6m, 6f)	19 (7m, 12f)
Impact	19 (5m, 14f)	15 (2m, 13f)

Table 2.—Habitat attributes used in the final analyses. Mean values and their standard errors are shown for the control and impact locations before and after the fire.

Attribute	Units	Range	$\bar{X}(SE)$			
			Control before	Control after	Impact before	Impact after
Logs	1–4 rating	0.0–3.8	0.96 (0.06)	1.17 (0.06)	0.65 (0.04)	0.85 (0.07)
Litter	1–4 rating	1.0–4.0	3.77 (0.03)	3.68 (0.04)	3.45 (0.05)	1.89 (0.06)
Spreading grass	Proportion	0.0–1.0	0.66 (0.03)	0.60 (0.02)	0.73 (0.02)	0.17 (0.03)
Rush	Proportion	0.0–1.0	0.14 (0.02)	0.12 (0.01)	0.27 (0.02)	0.05 (0.01)
Fern	Proportion	0.0–0.9	0.24 (0.02)	0.32 (0.02)	0.37 (0.03)	0.09 (0.02)
Habitat complexity	Unitless index	0.1–4.0	2.73 (0.05)	2.72 (0.05)	2.68 (0.06)	1.14 (0.10)

not) was not included as a factor, as preliminary analysis indicated that it had little effect.

At the impact location following fire, we used the forage ratio (proportional use/proportional availability) to quantify selection of unburnt vegetation patches. A ratio value of 1 represents selection in proportion to availability, while values greater and less than 1 indicate selection for and against the focal resource, respectively. Use and availability of unburnt vegetation were assessed by classifying each sampling point along spool lines and randomly located transects respectively as either burnt or unburnt. A simulation procedure using routines in PopTools 3.2.5 (Hood 2011) was used to calculate 95% confidence intervals (CIs) around the forage ratio.

An index of bush rat abundance was calculated by dividing the number of unique individuals caught at each site by the number of deployed traps. In addition, we evaluated body condition by calculating a scaled mass index (SMI—Peig and Green 2009) using body weight and tail length as inputs. We used tail length rather than body length in the calculation as we found the measurement of tails both simpler and more precise. The effects of fire on abundance and body condition were quantified using a linear model, with the abundance and body condition indices as response variables. We ran a model including time, treatment, and their interaction and used the interaction term to interpret the fire effect. We were unable to consider sex as a factor because only 2 males were caught at the impact location after the fire. Site was initially included as a random factor in a linear mixed model but removed as its associated variance component was zero.

The effect of fire on bush rat movements was analyzed using a linear mixed model, with turning angle and step length as response variables. Initially, we ran a model including time, treatment, and their interaction but then ran a 2nd model that also included relocation (relocated or not) as an additional predictor to examine whether the fire effects depended on this factor. In all analyses focusing on movement, we included a variable that identified individual rats as a random factor.

All statistical modeling was conducted in the R statistical environment (R Core Team 2014). Mixed effects logistic regression and linear mixed models were run using lme4 (Bates et al. 2014) and nlme (Pinheiro et al. 2013). All other analyses were conducted using the R base package. For Gaussian models, assumptions of normality and equal variances were assessed using graphical methods and no major violations were detected.

RESULTS

The prescribed fire burnt the impact location between the 6th and 10th of May 2013 creating a mosaic of burnt and unburnt patches. Unburnt areas tended to be centered around gullies and drainage lines, while ridges were more severely burnt. A fire severity map generated by the local land management agency identified fire severity to be high, moderate, and low in 21%, 20%, and 14% of the treated area, respectively, while 45% of the block remained unburnt. One of the rat capture sites at the impact location was burnt severely, with most of the understory vegetation removed. No bush rats were caught at this site after the fire. The other 2 sites were partially burnt, with much of the vegetation in the gullies remaining intact and the most severely burnt sections on adjacent northern (drier) slopes.

Microhabitat selection.—Individuals spooled in the unburnt forest (i.e., at the impact location prior to the fire and at the control location during both survey periods) commonly moved through dense vegetation and under logs. We observed well-defined tunnels in the understory, particularly through wire-grass mats and the base of rush clumps. These tunnels were used communally, with spool lines from several individuals often present.

With the exception of spreading grass, bush rats used habitat attributes selectively in unburnt forest ($P < 0.001$ for logs, ferns, and habitat complexity; $P < 0.01$ for rushes and litter; Fig. 1). Selection was positively related to rushes, logs, and the habitat complexity index and negatively related to ferns and litter. Patterns of selection for habitat attributes were generally similar at the control location during both survey periods but in some cases differed from those observed at the impact location prior to the fire (Fig. 1), reflecting pre-existing structural differences between the 2 areas.

Fire reduced the availability of all habitat attributes except log cover, which remained fairly constant (Table 2). Relative to pre-fire trends, selection for spreading grass, rushes, complex habitat, ferns, and litter increased at the impact location post-fire, while little change occurred at the control location (Fig. 1). Although the effect of fire on selection for each of these attributes was moderate or large (for example, fire reversed the negative relationship between selection and litter cover; Fig. 1i and j), the uncertainty associated with the effects was also substantial in some cases. There was strong evidence that fire increased selection for spreading grass ($P = 0.02$; Figs. 1a and b)

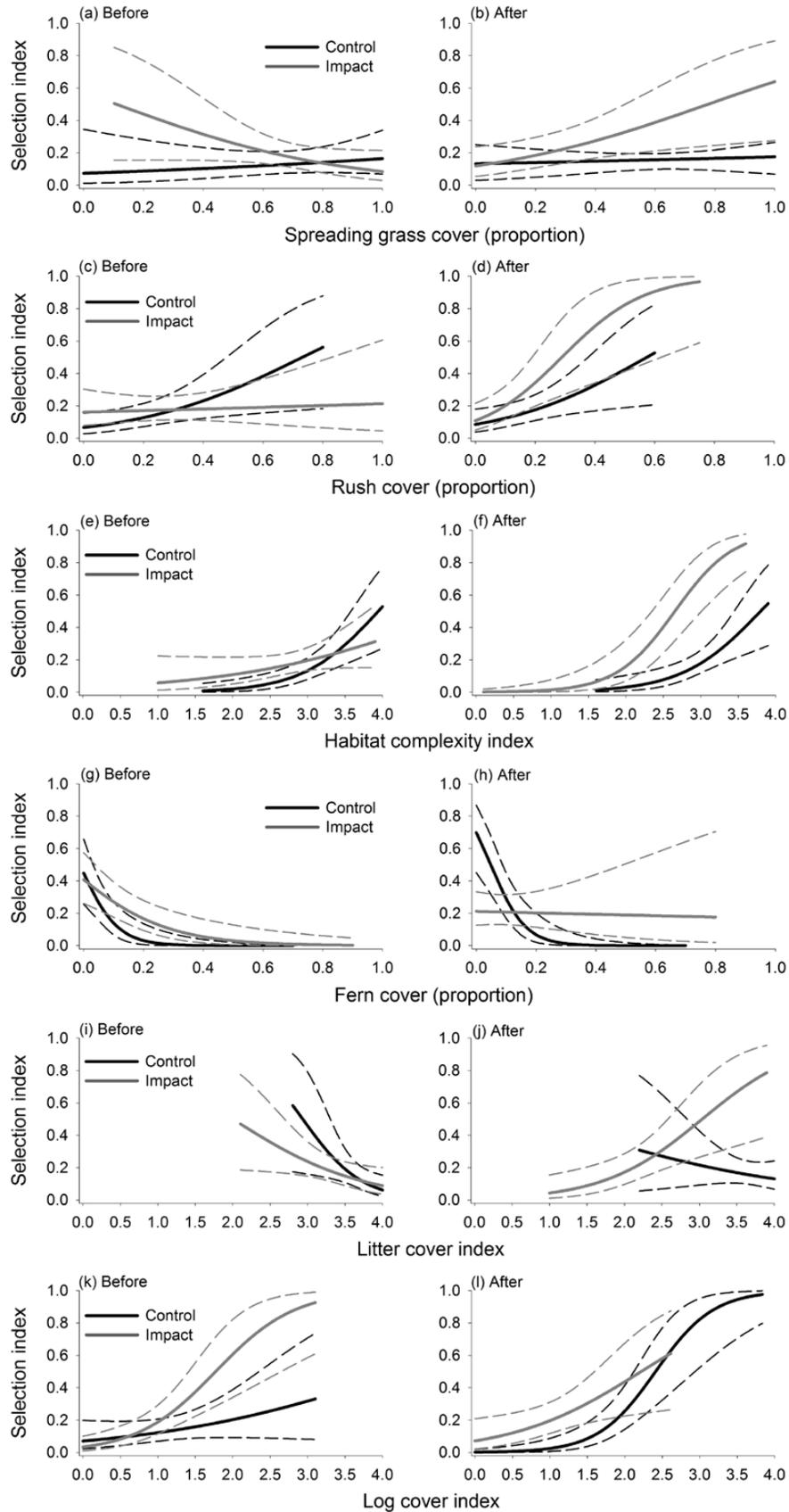


Fig. 1.—Predicted relationships between an index of bush rat (*Rattus fuscipes*) resource selection and a–b) spreading grass, c–d) rush, e–f) habitat complexity, g–h) fern, i–j) litter, and k–l) logs, before and after a prescribed fire at control and impact locations, Great Otway National Park, Australia. Dashed lines represent 95% confidence limits.

and rushes ($P = 0.06$; Figs. 1c and d). For habitat complexity, there was moderate evidence of a positive effect ($P = 0.11$; Figs. 1e and f), while for ferns and litter positive effects were observed but confidence limits were wide ($P = 0.32$ and 0.62 , respectively; Figs. 1g–j). For logs, the time \times location \times attribute interaction rendered a P -value of 0.01, but as the major change in selection occurred at the control location (Figs. 1k and l) we do not consider evidence for a fire effect to be strong.

At the impact location after the fire, 41.0% of the area remained unburnt, while rats used unburnt vegetation 73.3% of the time. The forage ratio for unburnt vegetation was 1.79 (lower 95% confidence limit 1.56, upper 95% confidence limit 2.05), indicating that bush rats selected unburnt patches more than expected based on their availability.

Abundance and body condition.—The fire reduced bush rat abundance (interaction effect \pm 95% CI: 0.040 ± 0.039 ; $P = 0.04$; Fig. 2) and body condition (30.82 ± 22.44 ; $P < 0.01$; Fig. 3).

Movement patterns.—Of the 15 individuals spooled at the impact location post-fire, 7 moved through burnt vegetation. One individual moved from a patch of unburnt vegetation into a burnt area and remained in burnt vegetation for the length of the spool. Several other individuals used burnt areas to move between isolated patches of unburnt vegetation.

Ignoring any relocation effect, fire resulted in more convoluted movements (increased turning angles) at the impact location relative to the control; the estimate associated with the time \times treatment interaction \pm 95% CI was 20.09 ± 12.88 , $P < 0.01$. Inclusion of relocation in the model demonstrated this effect was largely driven by individuals released at the site of capture at the impact location after fire ($P = 0.09$ for the time \times treatment \times relocation interaction; Figs. 4a and b). There was no detectable effect of the fire on step length, either with the inclusion (interaction estimate \pm 95% CI: 0.12 ± 0.92 , $P = 0.79$) or exclusion (0.19 ± 0.43 , $P = 0.38$) of relocation as a factor in the model.

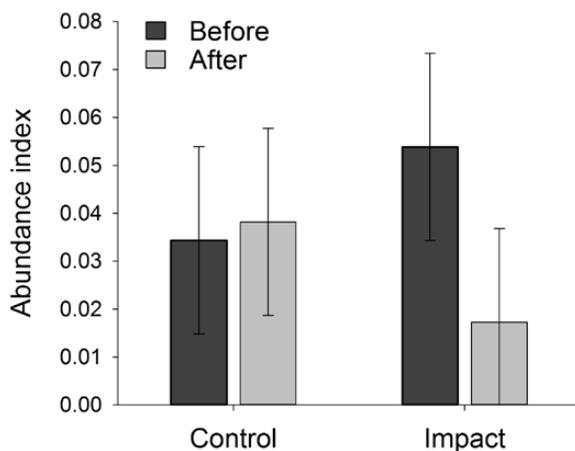


Fig. 2.—Mean values of the bush rat (*Rattus fuscipes*) abundance index at control and impact locations before and after a prescribed fire, Great Otway National Park, Australia. Error bars are 95% confidence intervals.

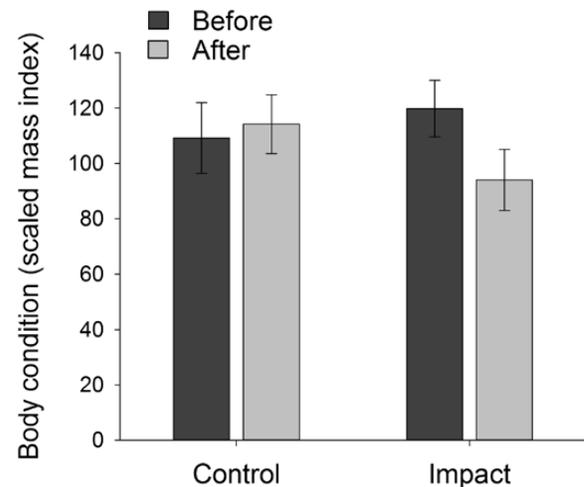


Fig. 3.—Mean values of the bush rat (*Rattus fuscipes*) body condition index at control and impact locations before and after a prescribed fire, Great Otway National Park, Australia. Error bars are 95% confidence intervals.

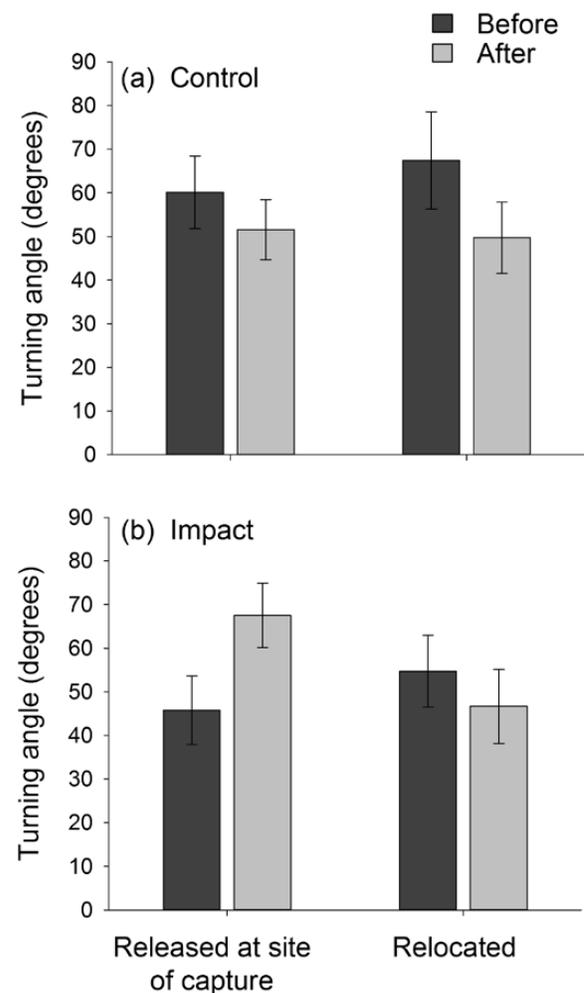


Fig. 4.—Mean turning angle of bush rats (*Rattus fuscipes*) at a) control and b) impact locations before and after a prescribed fire for relocated individuals and those released at the site of capture, Great Otway National Park, Australia. Higher turning angles represent more convoluted movement pathways. Error bars are 95% confidence intervals.

DISCUSSION

Prescribed fires are used to manage flammable ecosystems in Australia and around the world (Castellnou et al. 2010; Stephens et al. 2012; Attiwill and Adams 2013). They often greatly reduce the biomass of plants and dead material within a few meters of the ground and thus are expected to influence the behavior of species that depend on these resources, such as small- and medium-sized mammals. Nevertheless, general predictions regarding the effects of fire events on animal populations are difficult to derive (Lindenmayer et al. 2008; Nimmo et al. 2014), as exemplified by the contrasting responses of swamp rats (*Rattus lutreolus*) to different fire events at the same south-eastern Australian site (Monamy and Fox 2000). This highlights the need to better understand the mechanisms underlying faunal responses to fire (Driscoll et al. 2010), including the effects of fire-related changes in resource availability on key behavioral processes such as movement and resource selection.

As predicted, bush rats behaved selectively in unburnt forest. Habitat selection was positively associated with the cover of logs, rushes, and complex habitats and negatively associated with fern and litter cover. This is largely consistent with previous work quantifying important resources for bush rats (e.g., selection for logs [Strauss et al. 2008], rushes [Maitz and Dickman 2001], and dense understory vegetation [Spencer et al. 2005; Kearney et al. 2007; Strauss et al. 2008]). Selection for logs and complex vegetation may be related to predator avoidance, as noted previously for other rodent species such as the common vole (*Microtus arvalis*—Jacob and Brown 2000). Selection against areas of high fern cover was most likely driven by the typically sparse understory vegetation associated with these areas.

There was strong to moderate evidence that fire increased rat selection for spreading grass, rushes, and complex habitat. Increased selection for these attributes may have been influenced by several linked factors including limited access to shelter and food resulting from the loss of understory vegetation in burnt areas and heightened levels of perceived predation risk.

Attributes for which selection increased after the fire were all strongly associated with patches of unburnt vegetation, and individuals were clearly selecting these areas in the post-fire environment. Bush rats are known to use structurally complex habitat (Spencer et al. 2005; Kearney et al. 2007; Strauss et al. 2008), but our study is the first to show experimentally that fire can increase selection for habitat attributes associated with unburnt patches. Use of unburnt vegetation in recently burnt areas also occurs in other small mammal species such as the eastern chestnut mouse (*Pseudomys gracilicaudatus*—Pereoglou et al. 2011), mardo (*Antechinus flavipes leucogaster*—Swinburn et al. 2007), and short-snouted elephant shrew (*Elephantulus brachyrhynchus*—Yarnell et al. 2008), although these studies did not use both spatial and temporal controls. More generally, unburnt vegetation is likely to provide small mammals with refuge from fire and act as sources for the recolonization of surrounding burnt areas, thus promoting the persistence of small mammals in flammable ecosystems (Robinson et al. 2013).

Selection for attributes present in unburnt vegetation may have been influenced by increased predation pressure. Although experimental evidence for increased predation after fire is scarce (Griffiths and Brook 2014), it is generally assumed to be an important influence on small mammal populations (Sutherland and Dickman 1999; Letnic et al. 2005; Yarnell et al. 2008; Derrick et al. 2010; Woinarski et al. 2010). Open areas created by fire may increase prey vulnerability (Conner et al. 2011) and predators can be attracted to recently burnt areas (McGregor et al. 2014). Bush rats are known to reduce their use of key shelter structures (i.e., feel safer) when predators are removed or excluded from the system (Strauss et al. 2008), indicating that behavior is driven by perceived predation risk to at least some extent. However, bush rat responses to predation have not been studied in relation to fire, and the potentially interacting effects of fire and predation on this species remain unknown.

In line with previous work (Thompson et al. 1989; Banks et al. 2011), we found that the fire reduced bush rat abundance, probably due to the species' requirement for dense vegetation discussed above. This is consistent with results for other small mammal species with similar dependencies on dense vegetation (Morris et al. 2011a; Horn et al. 2012; Plavsic 2014). An important finding was that no bush rats were caught at the most severely burnt site that had little remaining understory vegetation. Further, consistent with a previously detected wild-fire effect (Banks et al. 2011), we found the fire resulted in reduced body condition, perhaps indicating that food, in addition to shelter, was an important driver of post-fire resource selection. Bush rats are generalist feeders with spatially and temporally variable diets consisting of fibrous plant material, fleshy fruits and seeds, fungi and invertebrates (e.g., Watts and Braithwaite 1978; Cheal 1987). Cheal (1987) found that fibrous plant matter consumed at forested sites was composed largely of grasses, including *Poa* spp. and wire-grass. As the latter species dominated the habitat attribute we called spreading grass and was greatly reduced by the fire, it is possible that the fire reduced the availability of an important component of bush rat diet. Nevertheless, the influence of food resources on small mammals following fire remains unclear. For example, supplemental feeding experiments demonstrated relatively subtle and inconsistent effects of post-fire food availability on the response of cotton rats (*Sigmodon hispidus*—Morris et al. 2011a), and cotton mice (*Peromyscus gossypinus*) and oldfield mice (*P. polionotus*—Morris et al. 2011b). In future studies, it will be instructive to determine the length of time needed to regain lost body condition and examine whether other response parameters such as survival and reproductive output are also reduced.

We expected fire to reduce habitat suitability and thus result in straighter movement paths with longer step lengths. However, our data did not support this prediction as rats released at the site of capture followed more convoluted movement paths. Convoluted movements typically reflect passage through high-quality habitat and are often associated with foraging (Vernes and Haydon 2001; Reiners 2005). In our case, the increase in movement path complexity may have been due to the way

rats used the fine-grained mosaic of burnt and unburnt patches generated by the fire. As discussed above, bush rats selected complex vegetation and used remnant unburnt vegetation patches intensely after fire. We suggest that rats using unburnt patches in the post-fire environment tended to remain within them, turning sharply when encountering patch edges, and so had more convoluted movement pathways with larger turning angles. This idea is supported by data on fine-scale habitat transitions: at the impact location after fire, 73% of bush rat movement steps started and ended in unburnt vegetation, while only 6% started in unburnt vegetation and ended in burnt patches.

We detected no effect of fire on either turning angle or step length for relocated bush rats. Our decision to relocate some individuals was a bet-hedging strategy designed to account for the possibility that some trapping sites at the impact block would remain unburnt. However, relocation can be a powerful stressor, potentially eliciting a fight or flight response and affecting subsequent behavior (Dickens et al. 2010). In relation to movement pathways, we suspect that relocation effects overshadowed any fire effects for the relocated group.

We have demonstrated that bush rats responded to a prescribed fire by altering both resource selection and movement pathways. Understanding how fire affects these processes is important as they underlie faunal responses to environmental change and influence a species' capacity to maintain viable populations in a changing landscape (Nathan et al. 2008; Knowlton and Graham 2010). Further, the fire reduced rat abundance and body condition, and no rats were caught at a site where most of the understory was removed by the fire. However, at the less severely burnt sites, many individuals survived the fire and continued to use the fine-grained mosaic of burnt and unburnt patches. These individuals increased selection for spreading grass, rushes, and complex habitat; increased the complexity of their movement pathways; and selected patches of unburnt vegetation. Unburnt patches may provide refuge from predation and support individuals that can recolonize surrounding burnt areas over time, thus facilitating population recovery after fire. Overall, our findings suggest that the impacts of prescribed fire events on small mammals will depend on the resulting mosaic of burnt and unburnt patches and how well this corresponds to the resource requirements of particular species. At a broader spatial and temporal extent, small mammal persistence in flammable ecosystems will be influenced by interactions between each fire's realized mosaic and other factors such as the rate of post-fire regeneration, fire frequency, and the spatial extent of fire in the landscape.

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