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We investigated the influence of vegetation structure and fire history on the foraging behavior of small rodents (Notomys mitchellii, Pseudomys hermannsburgensis, and Mus musculus) by conducting giving-up density (GUD) experiments in recently burnt (9-13 years since last fire) and long unburnt shrublands (> 40 years), and open and sheltered microhabitats, in a semiarid region of Western Australia. We predicted that rodents would spend less time foraging in recently burnt shrublands and open microhabitat and that the influence of microhabitat would be weaker in long unburnt compared to more recently burnt vegetation. Our findings show that fire history and microhabitat structure influence the foraging behavior of the study species and that the influence of microhabitat varies between fire histories. GUDs were higher in long unburnt vegetation and in open microhabitats. There was a microhabitat effect in recently burnt vegetation, but not in long unburnt. Rodents foraged more in sheltered microhabitats probably because predator encounters are less likely to occur there and it provides them with greater refuge from predation. The presence of a microhabitat effect in recently burnt, but not long unburnt vegetation suggests that understory vegetation density is more important in mediating predation risk than canopy density. Future studies of small mammal responses to land management actions should include behavioral, as well as population-level responses to differing fire regimes.

Key words: Australia, feral cat, fire, foraging behavior, giving-up density, Notomys, predation risk, Pseudomys, rodent

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Vegetation cover provides small mammals with food, shelter, nesting sites, and refuge from predators (Sutherland and Dickman 1999; Monamy and Fox 2000). Small mammals assess predation risk using indirect cues and minimize predator encounters by modifying their activity (Rosenzweig 1981; Lima and Dill 1990). Habitat structure is a well-studied cue and can indicate relative predation risk if prey vulnerability depends upon vegetation structure (Verdolin 2006). Encounters with predators are more likely to occur in open areas (Kotler et al. 1988; Dickman et al. 1991; Janssen et al. 2007) and vegetation cover plays an important role in mediating the lethal and nonlethal effects of predation on small mammals (Arthur et al. 2005; Conner et al. 2011). Structurally complex habitats can reduce predation rates by providing refuges for prey (Kotler et al. 1991). For example, in high refuge areas the survival rates and population density of house mice Mus musculus were higher than in low refuge areas (Arthur et al. 2005) and preferential use of complex microhabitats during times of high predator activity has been demonstrated for house mice (Dickman 1992), gerbils Gerbillus spp. (Abramsky et al. 1996), and Australian desert rodents (Dickman et al. 2010). In addition to changes in predator activity, temporal changes in cover availability can influence predation risk and subsequently alter the behavior, demographics, and growth rates of prey populations (Arthur et al. 2004; Spencer et al. 2005).

Small mammals are also affected by wildfire and prescribed burning because fire alters vegetation structure and reduces cover availability (Capitanio and Carcaillet 2008; Craig et al. 2010), which can lead to changes in small mammal community composition, particularly in fire-prone regions (Friend 1993; Fontaine and Kennedy 2012; Doherty et al. 2015). Torre and Díaz (2004) found that small mammal abundance and richness decreased with time since fire in Mediterranean forests, whereas Horn et al. (2012) found that recently burnt areas had lower small mammal abundance and richness when compared to unburnt areas in the Mojave Desert, United States. Fire can also affect the dynamics and behavior of small mammal populations, leading to reduced population size, resource availability, and individual fitness, along with increased competition (Sutherland and Dickman 1999).

The influence of vegetation cover and fire on small mammals may have a synergistic influence on predation pressure (Arthur et al. 2010; Conner et al. 2011) because reduced cover caused by fire results in less shelter for prey species and allows

predators increased access to structurally complex habitats and thus better hunting opportunities (Dees et al. 2001; Birtsas et al. 2012; McGregor et al. 2014). Conner et al. (2011) found that prescribed fire resulted in higher predation rates on cotton rats *Sigmodon hispidus* because it created suboptimal habitat for the rats. Although the combined effects of fire and predation on fauna are not well understood (Sutherland and Dickman 1999), the interaction between these 2 processes is considered to be a contributing factor to recent declines in Australia's mammal fauna (Woinarski et al. 2010; Fisher et al. 2014). Altered fire regimes and predation by introduced predators, such as red foxes *Vulpes vulpes* and feral cats *Felis catus*, present land managers with a formidable challenge; knowledge of how fire alters the habitat and foraging behavior of small mammals is needed if these communities are to be conserved.

In this study, we investigated how fire history and microhabitat structure influence risk-sensitive foraging behavior of small rodents (Notomys mitchellii, Pseudomys hermannsburgensis, and M. musculus) in semiarid shrublands in southwestern Australia. These shrublands are a fire-prone environment where canopy cover and continuity increase with time since fire (Parsons and Gosper 2011; Dalgleish et al. 2015). We expected that rodents would prefer to forage in more structurally complex habitats (i.e., sheltered microhabitat and long unburnt vegetation). We used giving-up densities (GUDs-Brown 1988) to indirectly measure the influence of predation risk on foraging activity. This method, commonly used in field experiments (e.g., Dickman et al. 2011; Hinkelman et al. 2011), predicts that an optimally foraging animal ceases foraging in an area when the benefits no longer exceed the costs (Brown 1988). In an experimental setting where other factors are controlled for, a decrease in the GUD corresponds to a decrease in perceived predation risk (Brown 1988). We conducted a 2-factor field experiment in long unburnt (> 40 years since last fire) and recently burnt (9-13 years) shrublands with open and sheltered microhabitats and predicted that: 1) GUDs will be higher in recently burnt compared to long unburnt vegetation because the shorter and sparser vegetation in younger areas will provide rodents with less refuge from predators; 2) GUDs will be higher in open microhabitat when compared to sheltered microhabitat because open areas will make rodents more vulnerable to predation; and 3) the effect of microhabitat on GUDs will be weaker in long unburnt vegetation when compared to recently burnt because the taller and denser vegetation in older habitat will mediate predation risk and hence microhabitat structure will be less important there.

MATERIALS AND METHODS

Study site and species.—We conducted this study at Charles Darwin Reserve, a ~68,000 ha pastoral lease 350 km northeast of Perth in the northern "wheatbelt" region of Western Australia (29°35′S, 116°58′E), managed for conservation by Bush Heritage Australia and destocked of goats and sheep since 2003 (Fig. 1). The climate is semiarid Mediterranean, with cool winters, hot summers, and unreliable, low rainfall (mean

306 mm/year; long-term average at the adjacent Wanarra station-Australian Bureau of Meteorology 2014). Mixed Acacia spp. shrublands make up 50% of the reserve's area and the remainder is a mixture of eucalypt woodlands and other shrubland types (Braun 2006). A history of unplanned fire has created a series of fire ages across the landscape: the most recent fires in Acacia shrubland occurred between 2000 and 2004 inclusive ("recently burnt": 9-13 years since last fire at time of sampling), and the oldest recorded fire age is estimated at 1969 ("long unburnt": > 40 years—Braun 2006). Wildfire dramatically reduces vegetation cover in Acacia shrublands and vegetation attributes like canopy height and density recover over successional timeframes of decades (Parsons and Gosper 2011; Dalgleish et al. 2015). Fire history information was extracted from spatial data layers in ArcMap (ESRI 2012) that were drawn from satellite imagery and aerial photography of historical fire scars around 2005 (Braun 2006). There have been no fires at the study site since that time.

Mitchell's hopping mouse N. mitchellii and the sandy inland mouse P. hermannsburgensis are small native rodents found in arid and semiarid parts of Australia (van Dyck and Strahan 2008). The hopping mouse (40-60 g) is bipedal and has large back legs, whereas *P. hermannsburgensis* is smaller (9–14.5 g) and quadrupedal (van Dyck et al. 2013). They inhabit woodlands, shrublands, and hummock grasslands and forage exclusively at night mostly on seeds and other plant material, but also insects to a lesser extent (van Dyck and Strahan 2008). The life history, feeding ecology, and ecological role of P. hermannsburgensis are very similar to those of the introduced house mouse *M. musculus* (up to 30 g), which is widespread throughout most of Australia and encompasses the distributions of both N. mitchellii and P. hermannsburgensis (van Dyck and Strahan 2008). Potential predators of rodents in the study area include the feral cat and the barn owl Tyto alba, and also to a lesser extent the dingo Canis dingo, the introduced red fox, elapid snakes, and other birds of prey.

Foraging experiments.—We established 144 feeding trays across 6 long unburnt and 6 recently burnt sites in Acacia shrublands in 2013. All sites were separated by a minimum distance of 1 km, except for 1 pair that was separated by 800 m (Fig. 1). The long unburnt sites were situated in continuous patches of vegetation (> 40 years since last fire) ranging in size from 20 to > 200 ha and the recently burnt sites were situated in continuous areas of vegetation > 200 ha (9–13 years since last fire). At each site 6 trays were placed in "open" microhabitat consisting of a clearing at least 3 m in diameter with no vegetation cover. Generally these clearings were naturally devoid of vegetation cover, although at some sites a small amount of dead vegetation was manually removed. The remaining 6 trays were placed in "sheltered" microhabitat, which was positioned directly under the cover of a live shrub. All trays were separated by a minimum distance of 20 m. Feeding trays consisted of round plastic containers 5-cm deep and of 19-cm diameter. Trays were half buried in the ground and filled with 1 liter of sifted sand with 20 peanut quarters randomly mixed in. The sand in and around each tray was smoothed to detect foraging activity. Trays were



Fig. 1.—Location of recently burnt (black circles) and long unburnt (white circles) giving-up density experiment sites. Additional sites where pitfall trapping was undertaken are shown with square symbols. Small gray diamonds represent the location of remote cameras. The gray shading represents the distribution of shrublands that were last burnt 9-13 years prior to sampling, and most other areas were unburnt for > 40 years.

checked for footprints and tracks the next morning and the remaining peanuts were counted. The GUD was recorded as the number of peanuts remaining in the tray after each night. Any missing peanuts were replaced and the sand was smoothed again. We repeated this for 6-8 nights, with the first 3-5 nights used as prebaiting to allow animals to become accustomed to feeding at trays, thus giving 3 nights of useful data for each sampling period (n = 864 tray-nights). We conducted 1 sampling period each in February and April 2013±5 days from the new moon phase to prevent lunar illumination from influencing foraging activity (Prugh and Golden 2014). Lids were placed on trays and trays were left in situ between sampling periods. During all experiments we identified the species responsible for foraging events based on footprints and tracks left in the sand surrounding the tray. N. mitchellii prints were identified by 2 long hind foot tracks > 25 mm and the imprint of the heel, while P. hermannsburgensis and M. musculus tracks were identified by their small size (< 20 mm) and imprint of 5 hind toes (Triggs 2004). It was not possible to distinguish between *P. hermanns*burgensis and M. musculus based on footprints and tracks, so we refer to them collectively as "mouse group" in the results.

Rodent abundance.—We conducted pitfall trapping at the study site in the austral spring 2012 (October prior to February GUD experiments) and autumn 2013 (concurrent with April GUD experiments) to determine if there were differences in rodent abundance between 8 long unburnt and 8 recently burnt sites. This included the same 12 sites at which foraging experiments were conducted, plus 2 additional sites in each fire history (Fig. 1). Although the October surveys were not

concurrent with the GUD surveys, they were still in the same spring–summer activity period and life-history stage of rodent populations at the site, so we do not feel that this represents an issue in data interpretation. Each site had 2×60 -m aluminum drift fences with 6 pitfall traps positioned at 10-m intervals along each fence. Traps were open for 10 nights in October and 8 nights in April and any captured animals were identified to species, temporarily marked with a nontoxic paint pen and then released at the site of capture. Pitfall trapping is highly effective at catching our target species and has been found to be an effective method for surveying arid-zone rodents in general (Dickman et al. 2011).

Predator abundance.--We measured the relative abundance of dingoes and feral cats using 20 Scoutguard 560PV (HCO, China) and 20 Moultrie i60 (EBSCO, Birmingham, Alabama) remote cameras. Cameras were mounted ~30 cm above the ground and positioned along vehicle tracks, each separated by at least 2 km and encompassing the same area where rodents were surveyed (Fig. 1). At half of the camera stations, we used a raw chicken wing encased in a PVC bait holder pegged to the ground as a scent lure and at the remaining cameras we used an electronic device that emitted the sound of a bird tweeting as an audio lure (Lucky Duck, Baldwin, Wisconsin). Lures were swapped between cameras half way through each monitoring period (2 weeks in February 2013 and 4 weeks in May 2013). Cameras were programmed to take 3 consecutive photographs each time the heat-in-motion sensor was triggered, with a minimum 1-min delay between photo sets.

Research methods followed the American Society of Mammalogists guidelines for use of live animals (Sikes et al. 2011) and were approved by the Edith Cowan University Animal Ethics Committee (permits 8501 and 8875). A field research permit was issued by the Western Australian Department of Parks and Wildlife (permit SF008871).

Habitat structure.—We measured vegetation structure using 2×30 -m transects at the 16 pitfall trapping sites. At 1-m intervals we counted the number of vegetation touches on a 4-m pole in the following strata: 0–50, 50–100, 100–200, and 200–400 cm above the ground. Every 2 m we measured canopy cover using a spherical densiometer and made visual percentage estimates of bare ground and litter cover in a 50×50-cm square.

Statistical analyses.—For the GUD data, we used individual tray-nights as data points (Hinkelman et al. 2011) and analyzed the 2 species/groups separately. We excluded data points where neither species/group visited the tray in a night, and data points where both species/groups visited the same tray in a night, because it was not possible to determine which species had visited last. We transformed GUDs to a proportion ("prop-GUD") by dividing values by 20 and used generalized linear mixed models (GLMMs), assuming a binomial error distribution, to assess the influence of fire history and microhabitat on foraging activity. Fire history, microhabitat, and the interaction term were included in the model as fixed effects with 2 levels per factor: long unburnt and recently burnt, and sheltered and open, respectively. Sampling period (February or April) and the individual tray were specified as random effects to account for variation caused by differences between sampling periods or trays. We report 95% confidence intervals (CIs) for the fixed effects and interaction term. Given the complications associated with calculating denominator d.f. and hence performing significance tests in a mixed modeling framework (Pinheiro and Bates 2000), we inferred "significant" effects where the CIs did not overlap zero, which is equivalent to an alpha level of 0.05. The residuals were inspected visually and there were no problematic residual distributions for any of the models. We analyzed mixed models using the lme4 package version 1.0-5 in program R version 3.0.1 (Bates et al. 2013; R Core Team 2013).

We used GLMMs to test the response of rodent species abundance to vegetation fire history. To account for differences in sampling effort between seasons, we divided the number of animals caught at a site by the number of nights the traps were open and multiplied this by 100. Fire history was included in the model as a fixed effect (long unburnt or recently burnt) and models were fitted assuming a normal error distribution and using the identity link function. Site and trapping period were specified as random effects in the model to account for variation caused by trapping periods and repeat sampling of sites over time. We calculated 95% *CI*s for fire history and inferred "significant" differences in abundance where the *CI*s did not overlap zero.

We calculated indices of dingo and cat activity by summing the number of independent photos captured at each camera site in each month. We considered photos of the same species caught on the same camera to be independent when they were captured more than 15 min apart. To account for differing sampling effort between months and cameras (e.g., due to battery failure), we calculated a relative abundance index by dividing the number of independent photos taken by each camera by the number of nights it was active and multiplied this by 100. Using ArcMap (ESRI 2012), we calculated the proportion of habitat within a 500-m radius around each camera that was either recently burnt (9-13 years since last fire) or long unburnt (> 40 years). To determine whether dingo or cat activity was related to the fire history of vegetation at a camera site, we fitted GLMMs assuming a normal error distribution with dingo or cat activity as the response variable and the proportion of both long unburnt and recently burnt vegetation as predictor variables. We calculated 95% CIs for the predictor variables and inferred "significant" differences in activity where the CIs did not overlap zero.

We used multivariate analysis of variance (MANOVA) to test for significant differences in habitat structure between the 2 fire histories, with significance set at 0.05. A significant MANOVA was followed by univariate tests to identify which habitat variables differed between fire histories. We logit-transformed proportional variables (litter, bare ground, and canopy cover) and log-transformed pole count data to meet assumptions of normality (Zar 2010).

Results

GUD experiments.—GUDs were higher in long unburnt vegetation and in open microhabitat for both *N. mitchellii* and the mouse group (Tables 1 and 2). The interaction term was significant for the mouse group, but not *N. mitchellii* (Table 2). There was no microhabitat effect in long unburnt vegetation for either species/group, but in recently burnt vegetation GUDs were higher in open microhabitat when compared to sheltered for both species/groups (Fig. 2).

Rodent abundance.—Mean abundance of *P. hermannsburgensis* was 19.22 animals per 100 nights ($SE \pm 2.93$), whereas *M. musculus* was 4.77 (\pm 1.47) and *N. mitchellii* was 7.03 (\pm 1.83; Fig. 3). There was no difference in abundance between long unburnt and recently burnt sites for *P. hermannsburgensis* (model estimate = -0.31, CI = -9.55 to 8.93), *N. mitchellii* (model estimate = -1.56, CI = -8.21 to 5.09), or *M. musculus* (model estimate = -1.41, CI = -7.25 to 4.43; Fig. 3).

Predator abundance.—Mean cat activity was higher than dingo activity in February (cat: 3.36 photos per 100 nights \pm 1.20 *SE*; dingo: 2.19 \pm 0.99) and marginally higher in May (cat: 2.07 \pm 0.40; dingo: 1.88 \pm 0.82). Cat activity was not related to the proportion of recently burnt vegetation (estimate = 1.44, *CI* = -7.85 to 10.73) or long unburnt vegetation at camera sites (estimate = 0.79, *CI* = -8.47 to 10.04), nor was dingo activity (recently burnt: estimate = 0.88, *CI* = -8.06 to 9.82; long unburnt: estimate = 3.59, *CI* = -5.32 to 12.49).

Habitat structure.—Mean vegetation density and cover were significantly different between long unburnt and recently burnt

Notomys mitchellii ($n = 247$)	Mouse group ^a ($n = 266$)
14.86 (0.61)	14.79 (0.68)
16.34 (0.59)	16.44 (0.52)
16.38 (0.35)	17.03 (0.30)
16.83 (0.30)	16.55 (0.41)
	Notomys mitchellii (n = 247) 14.86 (0.61) 16.34 (0.59) 16.38 (0.35) 16.83 (0.30)

Table 1.—Mean giving-up densities in each combination of microhabitat and fire history treatments. SEs are in parentheses.

^a Mouse group = *Pseudomys hermannsburgensis* and *Mus musculus*.

Table 2.—Parameter estimates and 95% *CIs* for the fixed effects of fire history, microhabitat, and the interaction term on proportional giving-up densities, and the variance estimates for random effects of sampling period and tray. Significant effects (*) were inferred where *CIs* did not overlap zero. The intercept is the contrast level in the model.

Model term	Estimate	95% CI
Notomys mitchellii		
Fixed effects		
Intercept	1.22	0.71, 1.76
Microhabitat (open)*	0.75	0.14, 1.37
Fire history (unburnt)*	0.58	0.02, 1.17
Microhabitat by fire interaction	-0.53	-1.36, 0.28
Random effects variance		
Tray	0.84	
Sampling period	0.03	
Mouse group (<i>Pseudomys hermannsburgensis</i> and <i>Mus musculus</i>)		
Fixed effects		
Intercept	1.34	0.82, 1.47
Microhabitat (open)*	0.75	0.34, 1.18
Fire history (unburnt)*	0.98	0.74, 1.23
Microhabitat by fire interaction*	-0.99	-1.33, -0.65
Random effects variance		
Tray	0.69	
Sampling period	0.01	

sites (Pillai = 0.80, $F_{1,14}$ = 4.52, P = 0.025). Univariate tests showed that mean vegetation density at recently burnt sites was 70% higher in the 0- to 50-cm stratum and 35% higher in the 50- to 100-cm stratum when compared to long unburnt sites, whereas vegetation density in the 100- to 200-cm stratum at long unburnt sites was double that at recently burnt sites and was almost 100 times greater in the 200- to 400-cm stratum at long unburnt sites (Table 3). Mean canopy cover was almost 10 times higher at long unburnt sites and litter cover was 2.5 times higher, whereas bare ground at recently burnt sites was almost twice that at long unburnt sites (Table 3).

DISCUSSION

Fire history effect.—We expected that animals would prefer to forage in the denser, long unburnt habitat rather than in the recently burnt vegetation (hypothesis 1); however, the data did not support this prediction. There are a number of possible explanations for the lower GUDs in recently burnt areas. Firstly, food trays in recently burnt habitat may have been perceived as more valuable if background levels of food availability were lower and competition was higher in recently burnt habitat (Davidson and Morris 2001; Ylönen et al. 2002). Individuals living in a resource poor environment can be more likely to undertake risky foraging behavior compared to those in resource-rich environments (Olsson et al. 2002). If this was the case, we would expect GUDs to be lower in both the sheltered and open microhabitats in recently burnt compared to long unburnt areas. Although we did not measure food availability, this seems unlikely to be a significant explanatory variable because GUDs were only lower at sheltered trays in recently burnt areas, whereas open trays in recently burnt areas were similar to both sets of trays at long unburnt sites.

Alternatively, lower GUDs in recently burnt areas may occur if predator abundance and hence predation risk were lower there. However, there is little support for this idea, since remote camera monitoring showed that cat and dingo activity during the study period were similarly high irrespective of the amount of long unburnt or recently burnt vegetation around camera sites. These indices are able to provide data on the relative abundance of predators across the landscape; however, we acknowledge that they do not provide information on fine-scale movements or hunting strategies within different habitat types. Although difficult to obtain, direct measurements of the number of prey killed by predators in each habitat type could provide information on the actual predation pressure experienced in these different areas. Based on the data available, the observed pattern appears to be related to differences in the vertical distribution of vegetation structure and is linked to our 3rd hypothesis, which we discuss later.

Microhabitat effect.—GUDs were higher in open microhabitat, which supports our 2nd hypothesis. Use of complex microhabitats in this study suggests that rodents are using risk-aversive behavior by foraging in sheltered microhabitats to avoid encounters with predators and reduce their chance of being depredated. Indeed, cats are known to prey on all 3 species at the study site (T. Doherty, Edith Cowan University, pers. comm.) and were common during the study period, which suggests that they presented a genuine threat to the rodents studied here. The reduced



Fig. 2.—Plots of mean GUD values and *SE* bars for the effects of fire history and microhabitat on the "mouse group" (upper; *Pseudomys hermannsburgensis* and *Mus musculus*) and *Notomys mitchellii* (lower) foraging activity. Sample sizes are in parentheses. GUD = giving-up density.

foraging activity in open areas is consistent with the notion that animals perceive a greater predation risk in open areas since predator encounters are generally more likely to occur in the open (Kotler et al. 1988; Dickman et al. 1991; Janssen et al. 2007). In Australia's Simpson Desert, P. hermannsburgensis and N. alexis prefer to forage in complex microhabitats during periods of high predator activity (Dickman et al. 2010) and on Australia's Fraser Island, rodents reduced their foraging activity following experimental reduction of cover (Spencer et al. 2005). Stokes et al. (2004) also found that 2 dasyurid marsupial species had lower GUDs under artificial cover than in open habitats and inferred that this was due to predation risk. Risk-sensitive foraging behavior by rodents can vary with temporal changes in predator activity (Dickman et al. 2010, 2011), so future studies in this system could compare the use of sheltered and open microhabitats during times of low and high predator activity.

Combined effects of microhabitat and fire history.—Our results showed no effect of microhabitat in long unburnt areas, but clear differences between sheltered and open microhabitat in recently burnt areas. We expected GUDs to be lower overall in long unburnt areas and that microhabitat would be less important there because the taller and denser vegetation would impair visual detection of prey by predators and hence negate the need for additional refuge while foraging. However, our rejection of hypothesis 1 indicates that this may not be the case, since overall, GUDs were actually higher in long unburnt areas.

The absence of a microhabitat effect in long unburnt areas suggests that the study species perceive a similarly high predation risk when foraging at sheltered and open patches in long unburnt areas. This pattern appears to be related to the density of vegetation structure close to the ground, rather than in the canopy. Our vegetation measurements confirm the findings of previous studies that canopy cover increases and becomes more continuous with increasing time since fire in Acacia shrublands, whereas ground-level vegetation cover decreases, and the density of short shrubs in long unburnt areas is lower than that in recently burnt areas (Parsons and Gosper 2011; Dalgleish et al. 2015). Since the feral cat is a major predator of the study species and cats were common during the study period, it is intuitive that vegetation density in the lower stratum is more important than canopy cover in mediating predation risk. Sheltered microhabitats are expected to decrease predation risk for these small mammals by providing vegetation cover that hinders visual detection by predators



Fig. 3.—Mean and SE bars for the abundance of Notomys mitchellii, Pseudomys hermannsburgensis, and Mus musculus in spring (October) 2012 and autumn (April) 2013.

	Recently burnt mean	Long unburnt mean	$F_{1,14}$	Р
0–50 cm	2.32	1.36	5.00	0.042
50–100 cm	1.15	0.85	4.69	0.048
100–200 cm	0.63	1.52	13.74	0.002
200–400 cm	0.02	1.75	21.71	< 0.001
Canopy cover (%)	6.82	63.17	28.70	< 0.001
Litter cover (%)	19.00	49.39	22.71	< 0.001
Bare ground (%)	58.45	34.00	19.32	< 0.001

Table 3.—Mean vegetation density (number of touches in each strata) and percent cover for recently burnt and long unburnt sites and univariate analysis of variance tests for the effect of fire history. Mean variables are untransformed. Significance level is 0.05.

and provides shelter to escape to when threatened. Consequently, foraging in areas with dense vegetation close to the ground (e.g., areas 9–13 years since last fire) likely provides the rodents in our study system with improved survival rates (Torre and Díaz 2004).

Conservation and management implications.—Our findings have revealed that shrubland fire history can have a significant impact on the foraging behavior of small rodents. An unexpected finding was that rodents spent more time foraging in recently burnt rather than long unburnt areas. Vegetation patches in intermediate fire ages provide rodents with refuge and hence are likely to aid the persistence of rodents in these areas. However, the vegetation here has recovered over 9–13 years since being burnt and younger postfire ages (e.g., 0–3 years) are likely to present small mammals with greater predation risk since vegetation cover is greatly reduced immediately following a fire (Conner et al. 2011). Younger postfire ages were not available at the time of this study.

Although further studies across a wider range of fire ages will provide greater clarity, results from this and other studies suggest that a range of postfire successional stages should be maintained across such landscapes to conserve small mammal communities (Horn et al. 2012; Kelly et al. 2012; Doherty et al. 2015). Inappropriate fire regimes threaten small mammal communities in Australia (Woinarski et al. 2014) and elsewhere globally (Kelt and Meserve 2014; Plavsic 2014) and future increases in fire extent and severity in Australia will increase loss of protective cover and hence potentially exacerbate the impact of introduced predators like feral cats and foxes on small mammals (Conner et al. 2011; Woinarski et al. 2011; Radford et al. 2014). If the negative impacts of introduced predators and inappropriate fire regimes are to be reduced, land management actions must consider the behavioral, as well as population-level responses of small mammal communities to differing fire regimes.

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