RESEARCH ARTICLE

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Unburnt habitat patches are critical for survival and in situ population recovery in a small mammal after fire

Robyn E. Shaw[1] (iD) | Alex I. James[2] | Katherine Tuft[3] | Sarah Legge[4,5] (iD) |
Geoffrey J. Cary[5] (iD) | Rod Peakall[1] (iD) | Sam C. Banks[5] (iD)

[1]Research School of Biology, The Australian National University, Canberra, ACT, Australia

[2]Australian Wildlife Conservancy, Mornington Sanctuary, Derby, WA, Australia

[3]Arid Recovery, Olympic Dam, SA, Australia

[4]Threatened Species Recovery Hub, National Environmental Science Program, Centre for Biodiversity and Conservation Science, The University of Queensland, St Lucia, Qld, Australia

[5]The Fenner School of Environment & Society, The Australian National University, Canberra, ACT, Australia

Correspondence
Robyn E. Shaw
Email: robyn.shaw@murdoch.edu.au

Present address
Robyn E. Shaw, Murdoch University, Perth, WA, Australia
Sam C. Banks, Research Institute for the Environment and Livelihoods, Charles Darwin University, Darwin, NT, Australia

Abstract

1. Fire drives animal population dynamics across many ecosystems. Yet, we still lack an understanding of how most species recover from fire and the effects of fire severity and patchiness on recovery processes. This information is crucial for fire-mediated biodiversity conservation, particularly as fire regimes change globally.

2. We conducted an experiment to test whether post-fire recovery is driven by in situ survival or recolonisation, and to determine whether this varies with fires of increasing percentage area burnt (burn cover) and severity. We used the pale field rat *Rattus tunneyi* as a model, because it represents the extinction process for a suite of mammal species suffering population collapse across Australia's northern savannas. Our treatments spanned a gradient from patchy, low severity fires (simulating early dry season management burns) to thorough, high severity fires (simulating wildfires). We performed capture–mark–recapture, vegetation and aerial surveys before, 6 weeks after and 1 year after fire.

3. Six weeks after fire, pale field rats were only captured in unburnt patches of vegetation, and capture rates were proportional to the amount of unburnt habitat. One year later, both vegetation and pale field rat populations recovered across all sites. However, population recovery after low severity fires was likely achieved through in situ survival and reproduction in unburnt micro-refuges, compared to recolonisation driving recovery after high severity fires.

4. *Synthesis and applications.* Pale field rat persistence is strongly dependent on the retention of unburnt habitat patches within fire-affected areas. Management strategies that increase micro-refugia within burnt areas may facilitate pale field rat population recovery. Globally, building recovery mechanisms into fire management will be vital for supporting the long-term persistence of fire-affected species.

KEYWORDS

fire experiment, fire recovery, fire response, in situ survival, recolonisation, small mammals, vegetation associations

1 | INTRODUCTION

Fire is a key influence on biodiversity, shaping community structure, species distributions and abundance (Turner, 2010). Altered fire regimes can increase extinction risk for many species (Kelly et al., 2011). Consequently, fire management is recognised as a fundamental tool for biodiversity conservation globally, especially as climate change affects fire frequency and intensity in many ecosystems (Driscoll et al., 2010; Greenville et al., 2018).

There is a growing body of literature exploring faunal responses to fire (Leahy et al., 2016; Legge et al., 2008) and the relationship between pyrodiversity and biodiversity (Lindenmayer et al., 2016; Stillman et al., 2019; Tingley et al., 2016). However, many of these studies are correlative and experimental studies are crucial for identifying recovery mechanisms and linking pattern to process (Andersen, 2020). A key issue relating to wildfires and prescribed fire is how different kinds of fire events influence post-fire recovery by animal populations. In particular, the effects of frequency, severity and spatial pattern (extent and patchiness) on post-fire recovery remain largely unquantified.

Landscape fire management through prescribed burning often aims to implement low-intensity burns to avoid unplanned high-intensity wildfires, by burning during seasons not conducive to intense wildfire. Low intensity, patchy fires are typically assumed to have lesser effects on animal populations than higher intensity, thorough fires (Legge, Murphy, et al., 2011; Tingley et al., 2016). However, the importance of fire patchiness in facilitating the mechanisms underlying population recovery is largely unknown (Leahy et al., 2016; Russell-Smith & Edwards, 2006; Watson et al., 2012). Conceptual, mathematical and simulation models highlight the importance of in situ survival and recolonisation for animal population persistence in fire-prone landscapes (Amarasekare & Possingham, 2001; Banks et al., 2017; Romme et al., 1998). Therefore, there is a need for studies that experimentally measure how spatial patterns of prescribed fire affect population recovery so we are able to design effective conservation strategies by using prescribed fire in ways that maximise post-fire recovery.

Fire management is particularly pertinent for conservation in grassland savannas. Grassy biomes cover approximately 20% of vegetated land area globally and are one of the most actively fire-managed biomes in the world (Bond & Parr, 2010; Yates et al., 2008). In tropical savannas, the wet–dry season cycle generates high levels of vegetative biomass that fuels a regime of annual fire, and in the tropical savannas of northern Australia, early dry season, low-intensity burning is implemented to avoid large, intense late dry season fires. Mounting evidence suggests extensive, high-intensity fires interact with predation by feral cats and grazing by introduced herbivores to drive the broadscale declines and local extinctions of many once-common mammals across northern Australia (Leahy et al., 2016; Legge et al., 2019; McGregor et al., 2014, 2015; Ziembicki et al., 2015). Fire management is considered the most economically and logistically tractable 'lever' we can pull to manage these landscapes for both biodiversity conservation and greenhouse gas emissions (Legge, Murphy, et al., 2011; Radford et al., 2015; Williams et al., 2003; Yibarbuk et al., 2001).

Here, we use a manipulative fire experiment to investigate the response, recovery and fine-scale habitat requirements of the pale field rat *Rattus tunneyi* to different scenarios of severity and burn cover (percentage area burnt) of prescribed fire. Rodents are ideal for such studies, given their quick response to fluctuating resources driven by ecological disturbance (Monamy & Fox, 2000). The pale field rat was once widespread across much of Australia, but is now mostly restricted to the monsoonal tropics and continues to decline (Woinarski et al. 2014). The mechanisms driving this decline are representative of those affecting both rodents and marsupials more broadly. The ultimate objective of the study was to determine whether we can integrate recovery mechanisms into fire management to facilitate recovery and persistence at a whole-of-landscape scale.

## 2 | MATERIALS AND METHODS

2.1 | Study location

We conducted our study at the Mornington Wildlife Sanctuary (17.55°S, 126.17°E), in the central Kimberley, north-western Australia (Figure 1). This former pastoral station is managed for conservation by the Australian Wildlife Conservancy (AWC). The fire regime in this region involves frequent fires that typically scorch, rather than burn the canopy. Fire has been managed at a regional scale by AWC since 2007 to reduce the incidence of extensive, intense fires and increase the extent of long-unburnt habitat (Legge, Murphy, et al., 2011). Our study was carried out within an area destocked of introduced herbivores in 2004–2005 (Legge, Kennedy, et al. 2011), in tropical savanna woodland dominated by tussock and hummock grasses.

2.2 | Experimental design

In February 2015, we trapped pale field rats across 10 sites that had not been burnt for at least 2 years. Sites consisted of linear transects approximately 40 m wide and 1 km long, following the bank of a watercourse. These were allocated into experimental groups, consisting of a paired burnt and unburnt site (spaced 100–1 km apart), with two exceptions: a stand-alone control and a group of three sites where the original control later burnt (Figure 1).

Fire treatments were implemented in one site per group after the initial 2015 trapping session (Figure 1). Fires varied in burn cover (percentage area burnt; see Appendix A.S1 in Supporting Information) and severity (loss of above-ground vegetative cover from burning; quantified using vegetation surveys). Two sites were burnt with low severity fires that affected <50% of the site, containing small unburnt patches within the burnt footprint and simulating early dry season prescribed burns. A further three sites were burnt

FIGURE 1 Study location, site layout and experiment schematic. Sites with 0% burn cover were unburnt controls. Treatments with <50% burn cover simulated small-scale management burns, and >50% simulated thorough wildfires [Colour figure can be viewed at wileyonlinelibrary.com]
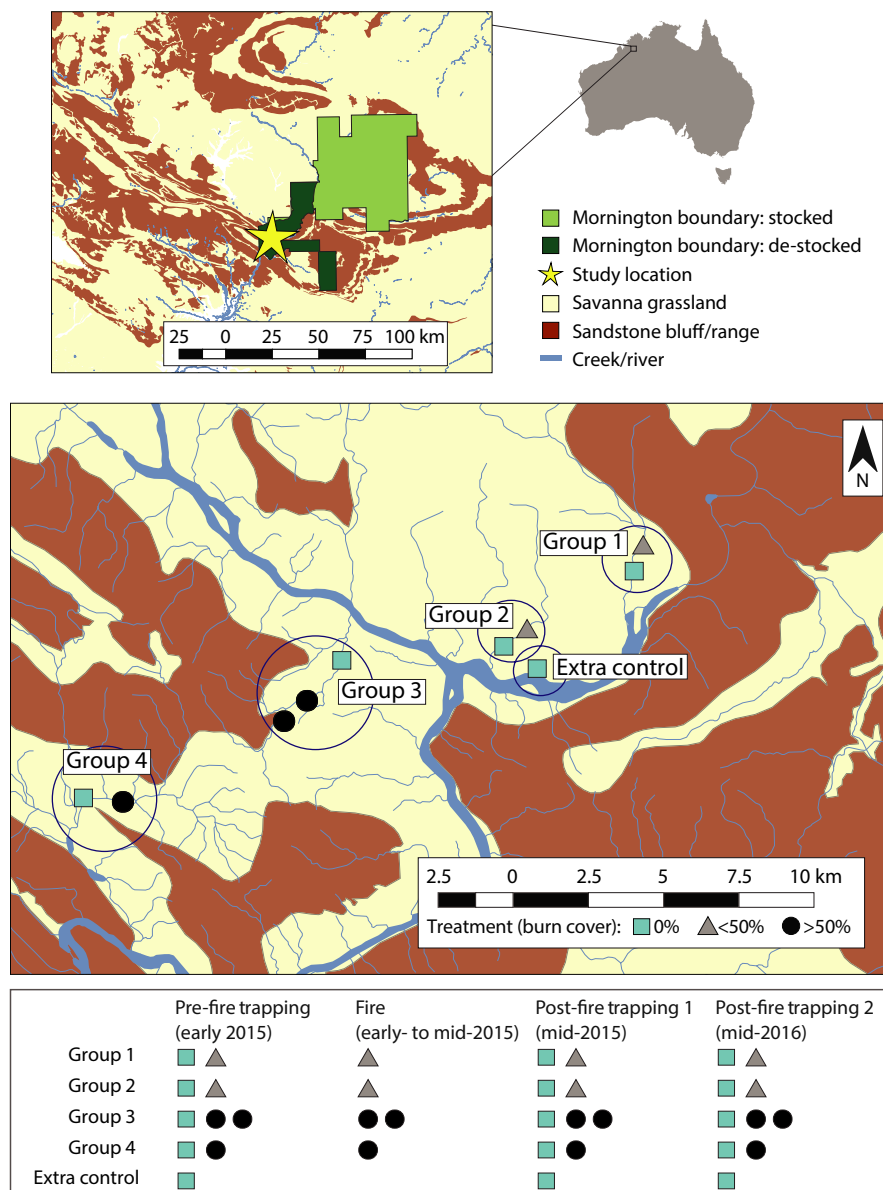
with high severity fires to simulate mid to late dry season fires, affecting over 50% of the site and containing little remnant unburnt vegetation within the burnt footprint. The remaining five sites were unburnt controls.

2.3 | Trapping protocol

We trapped pale field rats across three trapping sessions: immediately before (session 1: February–May 2015), 6 weeks after (session 2: May–July 2015) and 1 year after fire treatments (session 3: March–June 2016; Figure 1). The second trapping session took place 6 weeks after fire, as high predator activity 2–6 weeks after fire drives post-fire mortality (rather than the fire event itself; Leahy et al. 2016).

Sites were trapped using 100 steel Sherman Type A traps (30 × 10 × 8 cm) run along two transects, 30–40 m apart (comprising 50 traps at 20-m intervals). Each site was trapped for approximately five nights (range: four–six, due to inaccessibility and inclement weather), with paired sites trapped consecutively. Animals were identified to species and sex, weighed, implanted with Trovan ID100 Midi-Chips (Microchips Australia Ltd.), then released. Females over 60 g and males over 65 g were classified as adults (Leahy et al., 2016).

2.4 | Aerial mapping

We took helicopter aerial photographs before and immediately after fire treatments (processed in ARCMAP; Environmental System Research Institute Inc.). Vegetation (before fire) and fire scars (after fire) were digitised in a 50-m belt along each transect in QGIS, corresponding to mean home range size (males = 0.39 ha, females = 0.09 ha; Leahy et al. 2016; QGIS Development Team, Open Source Geospatial Foundation Project). The pale field rat is

associated with riparian and seep areas and eats high nutrient stem and leaf material from a number of native grasses (Braithwaite & Griffiths, 1996; Braithwaite & Muller, 1997). As such, we categorised four vegetation types distributed along a gradient of increasing distance to creek lines: riparian grassland, tussock grass, annual grassland and mixed grasses (see Appendix A.S1–S2). We determined the percentage area covered by the different vegetation types within a 20-m radius of each trap before and immediately after fire (corresponding to the distance between traps; referred to as '%trap veg type'). To quantify burn cover, we also determined the percentage area burnt at the site ('%site burnt') and within a 20-m radius of each trap ('%trap burnt'; see Appendix A.S3). Finally, we calculated a patchiness index following Donaldson et al., (2018). We recorded burnt/unburned patches at each trap and used aerial mapping to calculate the following equation: 1- (burnt points/total points – [unburnt points/total points × no. unconnected burn points/total points]). Preliminary analysis showed that patchiness was strongly correlated with burn cover (see Appendix A.S4), so in the following analyses we refer only to burn cover (as a representative of both spatial extent and patchiness).

2.5 | Vegetation surveys

We established eighty-two 10-m^2 vegetation quadrats (two per vegetation type per site), to assess the level of cover at 30–100 cm (an interval likely to provide the most cover from predators). We estimated the number of stems intercepting a pole held perpendicular to the ground (with the following scores: 0, 1, 3, 5, 8, 10, 15 or 20) 50 times per quadrat and used the quadrat sum total in analyses (referred to as 'vegetation density'). We measured vegetation density across the three trapping sessions to quantify fire severity, defined as the loss of ground-level vegetation caused by fire treatments, and to quantify subsequent vegetation recovery.

2.6 | Statistical analysis overview

We fit Poisson GLMMs using *lme4* (Bates et al., 2015) in R (R Core Team, 2019), and checked residuals with *DHARMa* (Hartig, 2017). Negative binomial models were fitted if data were overdispersed. Model fit was assessed by comparing differences in the Bayesian information criterion (ΔBIC) to the null model. Models with ΔBIC between 0 and 2 were considered equivalent. R code and tests of model assumptions can be found in see Appendix B in Supporting Information.

Pale field rat capture patterns were investigated using a per-trap night 'capture rate', which accounted for trapping effort and approximated abundance well (see Appendix A.S5–S6). We focused on two levels of analysi, namely; site-level 'capture rate' and trap-level 'capture rate'. Trap-level models included a spatial autocovariate (see Appendix A.S7). All model variables are summarised in Appendix A.S5.

2.7 | Do pale field rats have specific vegetation preferences?

We investigated whether local vegetation influenced pale field rat captures before fire, using a negative binomial GLMM. Trap-level 'capture rate' was modelled with 'spatial autocovariate' and '%trap veg type' as fixed effects. Spatial proximity of paired sites and differences in the timing of trapping were included as a random term 'group'. While the vegetation types are collinear (summing to 100%), our aim was to determine if these had a positive or negative effect on 'capture rate' and whether preferences are best summarised by a subset of variables. We performed model selection using the MUMIN package (Bartoń, 2016).

We tested whether pre-fire ground cover (response variable: 'vegetation density') varied among 'vegetation type' (fixed effect) by fitting an intercept-free negative binomial GLMM, with 'group' as a random effect.

2.8 | How is ground cover affected by fire?

Negative binomial GLMMs were used to explore fire severity by quantifying how ground cover changed with increasing burn cover, and if vegetation recovery differed with fires of increasing severity and burn cover. We fitted a three-way interaction with 'vegetation density' as the response variable, structured as 'session' × '%site burnt' × 'vegetation type', with 'group' as a random effect. '%site burnt' was continuous, with control sites represented as 0% burnt. The interaction term between '%site burnt' and session 1 (before the fire experiment was implemented) was used to establish a baseline, to ensure there was no pre-fire relationship between ground cover and burn cover, and as a comparison to determine whether ground cover returned to pre-fire levels 1 year after fire (this is also the case for 'capture rate' analyses below).

2.9 | How does the spatial pattern of fire affect pale field rat captures, recaptures and vegetation preference?

2.9.1 | Captures

To investigate the effect of fire on populations, we fitted a negative binomial GLMM using sex and age-specific site 'capture rates' as the response variable. Fixed effects in the global model included 'session', '%site burnt', 'sex' and 'age' and all interactions between these variables, with a random effect of 'group'. We compared all combinations in our model selection to determine which variables and interaction terms best predicted site 'capture rate'. This was then repeated at the trap level to determine whether these patterns were also important over local scales (tens of metres). Poisson GLMMs followed the same structure as the site-level analysis (with

the addition of the 'spatial autocovariate'), using trap-level 'capture rate' and '%trap burnt'. Random effects included 'trap' nested within 'group'.

2.9.2 | Recaptures

To determine whether post-fire recovery stemmed from in situ survival or recolonisation, we tested whether the proportion of recaptured individuals varied between trapping sessions and how this changed with fire. We fitted a binomial GLMM, comparing the number of recaptures to the total number of potential recaptures. We ran three GLMMs for recaptures from session 1 to 2, 2 to 3 and 1 to 3, with '%site burnt' as the fixed effect and a random effect of 'group'. We also calculated maximum distances travelled between traps by recaptured pale field rats within and between sessions.

2.9.3 | Vegetation preference

We explored how the area burnt and the remaining vegetation (20 m around each trap point) influenced pale field rat 'capture rate' 6 weeks after fire. Vegetation types were aggregated into preferred and non-preferred categories based on the pre-fire analysis. We carried out model selection using a Poisson GLMM with trap 'capture rate' as the response variable (treatment sites only). Fixed effects included '%trap burnt', '%preferred vegetation' and '%non-preferred vegetation', with a random term of 'group'. While the percentage of preferred and non-preferred vegetation types are collinear, our aim was to determine which variable best explained 'capture rate' using model selection, rather than to include both predictors in our final model.

3 | RESULTS

3.1 | Do pale field rats have specific vegetation preferences?

Model selection revealed strong support for two models (ΔBIC < 2; ΔBIC null model = 18.106; Table 1.1). The top-ranked model revealed significant, positive associations between 'capture rate' and the amount of both *riparian* and *tussock grass* vegetation within 20 m of each trap (BIC = 1,423.44; Table 1.1; see Appendix A.S8), while the second-ranked model showed a significant negative association with both *annual grassland* and *mixed grasses* (BIC = 1,424.228; Table 1.1; see Appendix A.S8.1a,b).

'Vegetation density' varied significantly among different 'vegetation types' (Figure 2; ΔBIC null model = 48.717; Table 1.2; see Appendix A.S8.2), being highest for *tussock grass*. 'Vegetation density' was similar between *Riparian*, *annual grassland* and *mixed grasses* (Figure 2; see Appendix A.S8.2). Thus, pale field rats prefer

riparian and tussock grass vegetation (the two vegetation types closest to the creek line), with the latter offering high density cover.

3.2 | How is ground cover affected by fire?

The percentage area burnt varied from 27% to 82% across treatment sites (see Appendix A.S1). Fire had a negative effect on 'vegetation density' across all 'vegetation types' in *session 2* (Figure 3; ΔBIC null model = 212.613; Table 1.3; see Appendix A.S8.3). However, 1 year after the experiment (*session 3*), 'vegetation density' did not differ significantly from pre-fire levels. Thus, as burn cover increased, so did fire severity (as ground cover was negatively affected by fire). However, vegetation recovered to pre-fire levels within 1 year, regardless of fire severity and burn cover.

3.3 | How does the spatial pattern of fire affect pale field rat captures, recaptures and vegetation preference?

3.3.1 | Captures

We caught 951 unique pale field rats over the fire experiment (see Appendix A.S9a).

We found strong support for models featuring 'session', '%site/ trap burnt' and an interaction between these variables at the site and trap level (site: BIC = 693.736, ΔBIC null model = 92.039; trap: BIC = 6,660.176, ΔBIC null model = 139.416; Table 1.4). Models featuring 'sex' and 'age' were not well-supported (ΔBIC > 2). Fire had a significant negative affect on 'capture rate'. In *session 2* (6 weeks after fire), predicted site 'capture rate' declined by 99% as the percentage of the site burnt increased from 0% to 100%. Predicted trap 'capture rate' was significantly greater at unburnt traps and declined by 95% as the percentage area burnt at the trap increased from 0% to 100%. However, 1 year after the experiment (*session 3*), pale field rat site and trap 'capture rate' did not differ significantly from pre-fire levels (Figure 4; see Appendix A.S8.4).

Collectively, these findings reveal a common broadscale (site) and local (trap) response, irrespective of age or sex, with full recovery to pre-fire levels within 1 year. However, patterns of short-term, post-fire abundance varied significantly with fires of increasing severity and burn cover.

3.3.2 | Recaptures

The percentage of the site that burnt ('%site burnt') had a significant, negative effect on the 'proportion of recaptures' from before (*session 1*), to immediately after fire (*session 2*; Figure 4b; BIC = 41.962, ΔBIC null model = 48.739; Table 1.5b; see Appendix A.S8.5). This suggests individual survival decreased as burn cover increased.

TABLE 1 Model structure, degrees of freedom (*df*), log-likelihood (log(L)), Bayesian information criterion (BIC), BIC difference from best model (ΔBIC), Akaike weight, conditional and marginal R^2 for models within ΔBIC = 2 and null models. Model fit was assessed using the ΔBIC comparison to the null model, as low R^2 reflects the highly stochastic system and low overall captures (regardless of the fire experiment)

Model	GLMM	Data subset	Analysis level	Response	Random	Fixed	Intercept	df	log(L)	BIC	ΔBIC	Akaike weight	Cond. R^2	Marg. R^2
1. Pre-fire vegetation preferences	Negative binomial	S1	Trap (n = 1,000)	Capture rate	Group	%Rip + %Tuss + AutCov	-3.982	6	-690.85	1,423.44	0	0.512	0.183	0.098
						%AG + %MG + AutCov	-2.923	6	-691.244	1,424.228	0.788	0.345	0.188	0.098
						AutCov (null)	-3.281	4	-706.86	1,441.545	18.106	0	0.133	0.064
2. Ground cover by vegetation type	Negative binomial	S1	Quadrat (n = 82)	Vegetation density	Group	Veg type	NA	6	-431.401	889.242	0	1	0.445	0.445
						Null model	NA	3	-462.369	937.959	48.717	0	0.065	0
3. Ground cover and fire	Negative binomial	S1, S2, S3	Quadrat (n = 246)	Vegetation density	Group	Session*%site burnt*VegType	4.323	26	-1280.607	2,704.247	0	1	0.747	0.733
						Null model	4.69	3	-1450.178	2,916.859	212.613	0	0.089	0
4. Capture rate and fire														
a) Site level	Negative binomial	S1, S2, S3	Site (n = 30)	Capture rate	Group	%site burnt*Session	-4.092	8	-327.718	693.736	0	0.603	0.248	0.166
						Null model	-4.021	3	-385.706	785.775	92.039	0	0.119	0
b) Trap level	Negative binomial	S1, S2, S3	Trap (n = 3,000)	Capture rate	Trap, Group	%trap burnt *Session + AutCov	-5.21	9	-3287.748	6,660.176	0	0.944	0.253	0.15
						AutCov (null)	-5.084	4	-3380.978	6,799.592	139.416	0	0.165	0.058
5. Recaptures and fire														
a) S1 to S2	Binomial	S1 to S2	Site (n = 10)	Proportion recaptures	Group	%site burnt	-0.719	3	-17.527	41.962	0	1	0.707	0.699
						Null model	-1.577	2	-43.048	90.7	48.739	0	0.097	0
b) S2 to S3	Binomial	S2 to S3	Site (n = 10)	Proportion recaptures	Group	%site burnt	-3.325	3	-11.792	30.491	0	0.642	NA	0.224
						Null model	-3.589	2	-13.528	31.662	1.171	0.358	0.022	0
c) S1 to S3	Binomial	S1 to S3	Site (n = 10)	Proportion recaptures	Group	%site burnt	-4.21	3	-6.193	19.294	0	0.603	NA	0.87
						Null model	-4.956	2	-7.761	20.127	0.832	0.397	0.176	0
6. Post-Fire Vegetation Preferences	Poisson	S2 treatment	Trap (n = 500)	Capture rate	Group	%PrefVeg	-4.95	3	-131.369	281.381	0	0.67	0.216	0.028
						Null model	-4.548	2	-136.386	285.202	3.821	0.099	0.297	0

Note: S = Session. %veg type within 20 m trap radius: Rip = Riparian; Tuss = Tussock grass; AG = Annual grassland; MG = Mixed grasses. AutCov = Spatial Autocovariate. %site burnt = percentage area burnt at site. %trap burnt = percentage area burnt within 20-m radius of trap. %PrefVeg = percentage riparian and tussock grass remaining after fire, within 20 m trap radius.
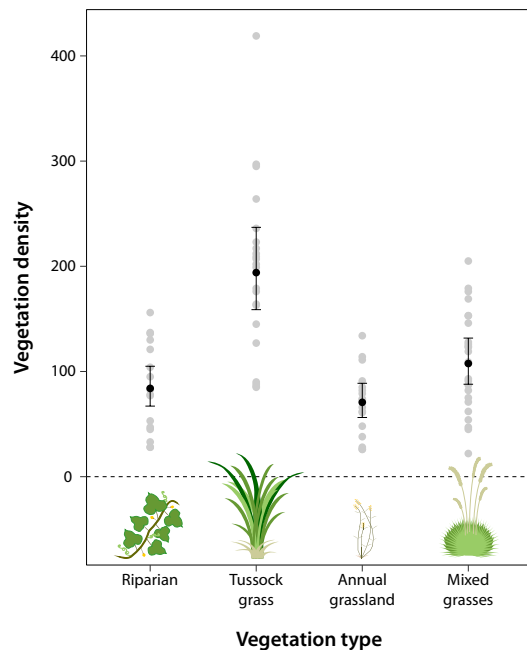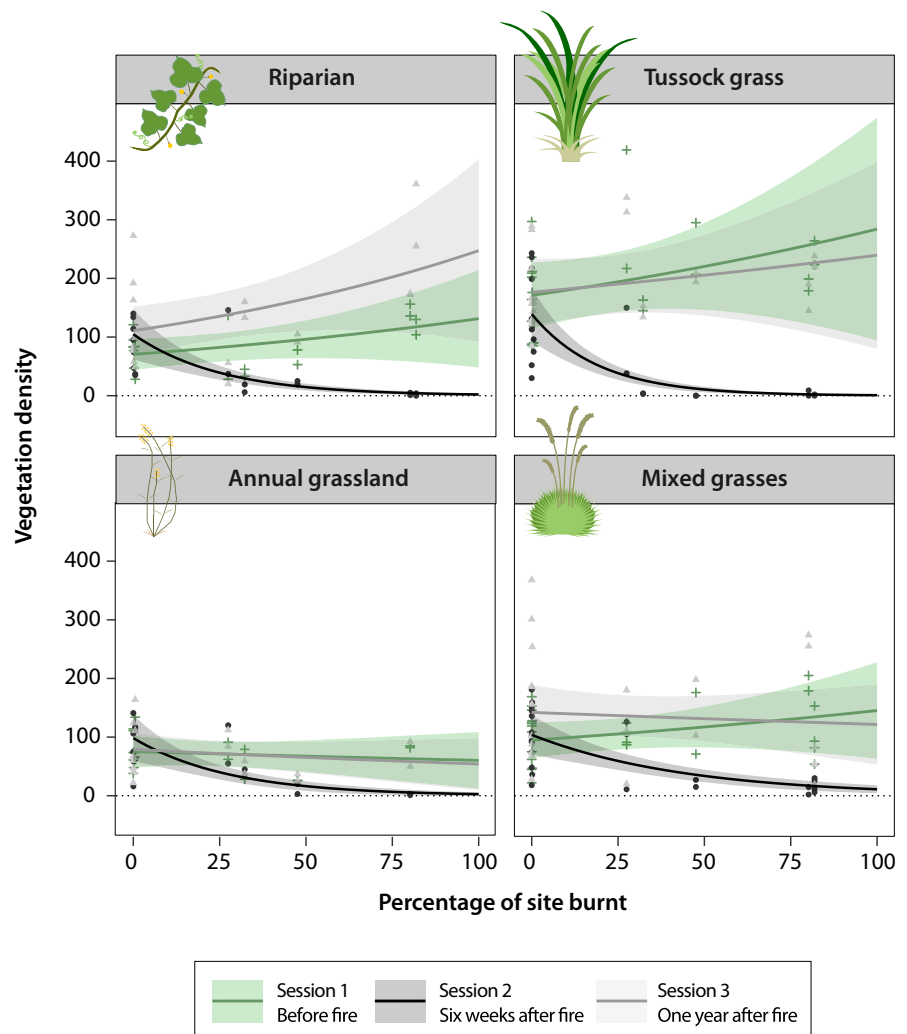
FIGURE 2 Model predictions with 95% confidence intervals of vegetation density across four different vegetation types (plots generated in *GGPLOT2*; Wickham, 2009) [Colour figure can be viewed at wileyonlinelibrary.com]

Models investigating the effect of fire on the 'proportion of recaptures' 1 year later (*session 2 to session 3* and *session 1 to session 3*) had low predictive ability, as recaptures were low in session 3 across both control and treatment sites (Figure 4b; null models within 2 ΔBIC; Table 1.5a–c).

The mean maximum distance moved by recaptured individuals within sessions was 33 ± 5 m (males = 53 ± 11 m; females = 21 ± 3 m; maximum = 522 m). Between sessions, this varied from 65 ± 32 m (maximum = 1,882 m; session 1 to session 2) to 1,630 ± 99 m, (maximum = 1,723 m; session 2 to session 3).

3.3.3 | Vegetation preference

Six weeks after fire, pale field rat 'capture rate' was significantly related to the remaining amount of preferred vegetation (the aggregate amount of tussock grass and riparian vegetation) within a 20-m radius of each trap ('%preferred vegetation'; see Appendix A.S8.6). While there was only moderate support for this model relative to the null model (BIC = 281.381; ΔBIC null model = 3.821; Table 1.6), alternative representations of post-fire burnt and unburnt vegetation condition ('%non-preferred vegetation' or the '%trap burnt')

FIGURE 3 Model predictions with 95% confidence intervals for the effect of fire (percentage of site burnt) on vegetation density at four different vegetation types, over three trapping sessions. Note that the 'session 1' × '%site burnt' interaction is presented to display baseline vegetation density before the fire experiment was implemented (i.e. percentage burnt refers to the future treatment) [Colour figure can be viewed at wileyonlinelibrary.com]
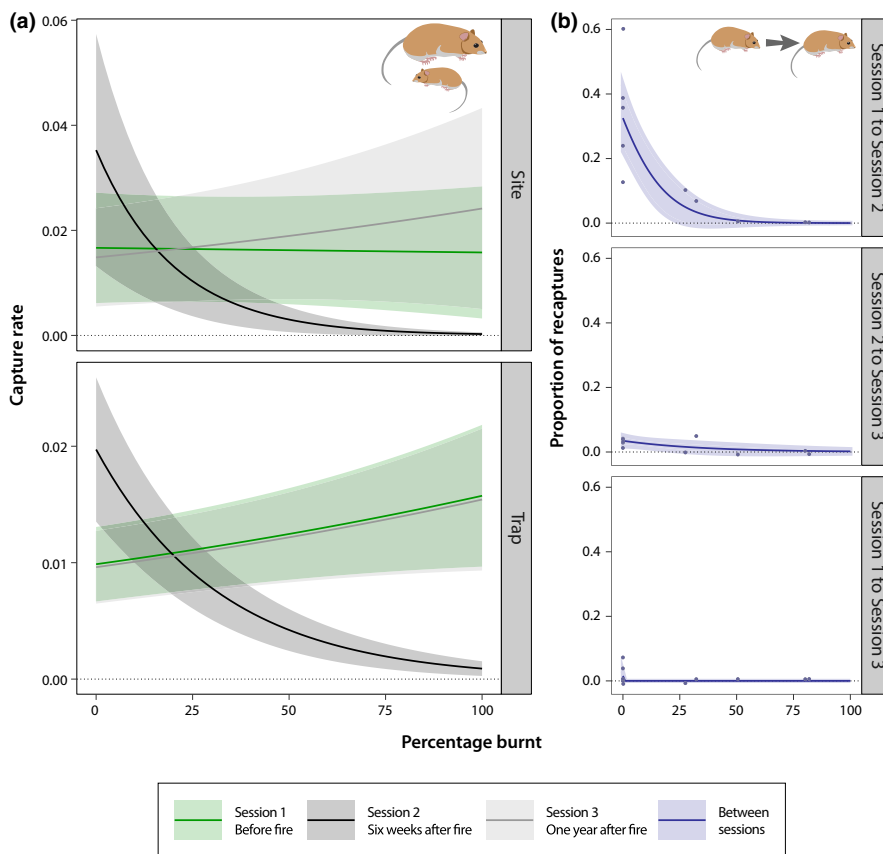
FIGURE 4 Model predictions with 95% confidence intervals over three trapping sessions, for the effect of burn cover on: (a) pale field rat site/trap capture rate (raw data visualised in Appendix A.S9b), and (b) the proportion of between session recaptured individuals. Note that the 'session 1' × '%site burnt' interaction is presented to display baseline capture rate before the fire experiment was implemented (i.e. percentage burnt refers to the future treatment) [Colour figure can be viewed at wileyonlinelibrary.com]

were not well-supported (ΔBIC > 2). Pale field rats are thus tied to unburnt patches of preferred vegetation and respond to conditions over a fine scale (20 m).

4 | DISCUSSION

Our results show that unburnt patches of vegetation are important for small mammal persistence after fire in tropical savannas and without this, populations are dependent on recolonisation for post-fire recovery. By understanding fire recovery in pale field rat populations, we demonstrate how recovery mechanisms can be incorporated into fire management strategies to facilitate landscape-level recovery.

4.1 | The density of vegetative ground cover influences savanna mammal occurrence

Subtle variation in geology, moisture and vegetation can strongly influence the local distribution of animal populations in otherwise uniform savanna landscapes (Woinarski et al., 2005). We found strong associations between pale field rat captures and two vegetation types closest to the creek line—riparian and tussock vegetation. These vegetation types are likely important for foraging (grass stems, roots and seeds, as well as invertebrates and fungi to a lesser extent; Braithwaite & Griffiths, 1996). Tussock grass also provides dense cover. While riparian

ground cover was similar to non-preferred vegetation, this habitat provides a canopy that likely provides protection from aerial predators (Leahy et al. 2016). Dense cover is well-recognised as an important feature for small, ground-dwelling mammals (Banks et al., 2011; Fordyce et al., 2016; Sutherland & Dickman, 1999).

4.2 | Vegetative ground cover recovers within 1 year of fire

We found that loss of above-ground vegetative cover (fire severity) increased with increasing burn cover, suggesting that our experimental fires were good representatives of low severity, patchy management burns compared to high severity, through wildfires. Fire severity had little bearing on the vegetation 1 year after fire, with all vegetation types recovering to pre-fire levels. Individual fire events within stable regimes often have relatively little effect on the structure of savanna vegetation, with inter-annual differences mostly driven by rainfall (Bowman et al., 1988; Plavsic, 2014; Williams et al., 2003).

4.3 | Unburnt preferred habitat patches facilitate in situ persistence following experimental fires

Pale field rat abundance was significantly affected within 6 weeks of fire. Both captures and recaptures declined as fire severity and burn cover increased, providing strong evidence for high mortality after

extensive, severe fires. This was likely driven by increased post-fire predation due to reduced cover. Feral cats in particular are known to target intense fire scars to take advantage of the newly open landscape for hunting (McGregor et al., 2014, 2016). Leahy et al. (2016) found that individual pale field rats did not shift territories if they were within burnt areas after fire. High home range fidelity after fire has been found across a number of small mammal species (MacGregor et al., 2013; Morris et al., 2011). In intensely burnt landscapes, this leaves animals with little shelter and thus exposed to predation.

Fire was also important over local scales, potentially indicating some avoidance of burnt areas by the pale field rat when unburnt refuges were present within the scale of a home range. Thus, after less extensive fires, lower pale field rat capture and recapture rates likely reflected both mortality and/or avoidance of burnt areas. This behaviour has been shown in the Australian bush rat *Rattus fuscipes*, with animals taking more convoluted paths to avoid patch edges after prescribed fire in south-eastern Australia (Fordyce et al., 2016).

Specific and restricted habitat preferences may be an important factor contributing to the pale field rat's vulnerability to fire, as our results suggest that dense vegetation close to watercourses is important for population persistence in the post-fire landscape. Similarly, Diffendorfer et al. (2012) found a positive influence of nearby riparian or rocky substrates on the abundance of many small mammal species after a large wildfire in California. The vegetation association found by Diffendorfer et al., (2012) affected long-term population recovery, highlighting the role of specific vegetation communities, rather than just unburnt vegetation, in supporting post-fire recovery.

4.4 | Is post-fire recovery driven by in situ survival or recolonisation, and does this change with increasing fire severity and burn cover?

Post-fire abundance of small mammals has been linked to the regeneration of vegetation and habitat structure (Crowther et al., 2018; Monamy & Fox, 2000). We found pale field rat populations fully recovered within 1 year, mirroring the regeneration of suitable vegetation (although recognising that unburnt vegetation outside of the experimental plot was within the dispersal range we measured, 1,882 m). However, differences in the spatial distribution of survivors suggest that our treatments had different 'starting points for recovery' (Banks et al. 2011), with the mechanistic response of pale field rats shifting from in situ survival and reproduction to recolonisation-driven recovery depending on fire severity and burn cover.

Post-fire recovery after patchy, low severity fires was likely driven by in situ survivors in unburnt patches (possibly augmented by immigration). These micro-refuges create the potential for population expansion from many dispersed nuclei once habitat becomes suitable (Banks et al., 2011, 2017; Robinson et al., 2013). Retaining refugia within disturbed areas can maintain stable populations at a landscape scale, through greater metapopulation connectivity. Research on grassland bird communities in the United States has shown that fire management actions that take these source-sink

dynamics into account may be important for reversing long-term population declines (Davis et al., 2016).

After high severity, extensive fires, pale field rat populations shifted to a recovery mechanism based on recolonisation from outside the burnt area. Large scale, high severity fires that typically do not contain unburnt refuges (Russell-Smith & Edwards, 2006) mean that pale field rat recovery is limited by restricted per generation colonisation. For example, late dry season wildfires in northern Australia can cover areas of 10,000 km^2 or more (Russell-Smith & Edwards, 2006; Russell-Smith et al. 2003). We predict this is a major contributing factor in the widespread decline of the pale field rat and other small mammals in northern Australia. Furthermore, many small mammal species show strong microhabitat associations, with recolonisation after fire only occurring once these microhabitats recover (Plavsic, 2014). For example, after a wildfire in Portugal, increased distance to the edge of the burn and the absence of preferred vegetation were factors that delayed recolonisation in the Cabrera vole (do Rosário & da Luz Mathias et al., 2007).

5 | CONCLUSIONS

Our results add to the growing body of research demonstrating important conservation benefits of reducing the size and severity of fires in tropical savannas, such that overall burn cover is reduced and appropriate remnant vegetation for small mammals is retained within fire scars at a fine scale (Legge, Kennedy, et al., 2011; McGregor et al., 2014; Radford et al., 2015).

Our study was performed in an area managed for conservation for the last decade, through fire management and the removal of introduced herbivores. As such, this is a best-case scenario landscape, without the additional pressures facing small mammals in many savanna ecosystems. Furthermore, our experimental fires were small compared to wildfires, which regularly cover thousands of square kilometres. Over a scale more representative of a wildfire, we may not expect such rapid post-fire recovery between successive fire events. In worst-case scenario landscapes dominated by frequent and extensive fire and grazing, small mammal populations may be at such low densities that recovery through recolonisation is no longer feasible over a landscape scale.

AUTHORS' CONTRIBUTIONS

R.E.S. collected the data, conducted the analyses and led the writing of the manuscript. All the authors contributed to conception and development of the project, contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.tmpg4f4xs (Shaw et al., 2021).

ORCID

Robyn E. Shaw (iD) https://orcid.org/0000-0002-7899-1743
Sarah Legge (iD) https://orcid.org/0000-0001-6968-2781
Geoffrey J. Cary (iD) https://orcid.org/0000-0002-6386-1751
Rod Peakall (iD) https://orcid.org/0000-0001-9407-8404
Sam C. Banks (iD) https://orcid.org/0000-0003-2415-0057

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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