Evidence that post-fire recovery of small mammals occurs primarily via in situ survival

Susannah Hale | Lorissa Mendoza | Tom Yeatman | Raylene Cooke | Tim Doherty | Dale Nimmo | John G. White

1School of Life and Environmental Sciences, Deakin University, Geelong, Vic., Australia
2School of Environmental Science, Institute for Land, Water and Society, Charles Sturt University, Albury, NSW, Australia

Correspondence
John G. White, School of Life and Environmental Sciences, Deakin University, Geelong, Vic., Australia. Email: john.white@deakin.edu.au

Present address
Tim Doherty, School of Life and Environmental Sciences, The University of Sydney, Sydney, NSW, Australia

Funding information
Department of Environment and Primary Industries, Grant/Award Number: 10005800 and 10007121

Editor: Alan Andersen

Abstract
Aim: As climate change intensifies and wildfire frequency and scale increase, it is critical we develop a robust understanding of how species recover from these major disturbances. Here, we aim to determine whether source populations for recovery following large-scale intense wildfires are derived from either in situ survival, or immigration from surrounding unburnt areas (ex situ). Secondly, we sought to determine whether habitat elements (e.g., logs) within the landscape facilitate in situ survival of small mammals during fires.

Location: Grampians National Park, south-eastern Australia.

Methods: We used long-term post-fire small mammal monitoring to investigate sources of recovery for small mammals, and camera trapping and habitat surveys immediately following large intense wildfires to assess evidence for and drivers of post-fire survival.

Results: We found no relationship between distance to unburnt vegetation and the occurrence of any native species, suggesting that in situ survival is the probable mechanism for recovery of post-fire mammal populations, compared with immigration from surrounding unburnt areas. We also show that key habitat elements such as rocks and large trees were associated with the occurrence of several species immediately post-fire, suggesting a role for these features in facilitating the survival of species during and following fire.

Main conclusions: We present evidence for post-fire recovery being driven by in situ survival. In situ survival is facilitated by small unburnt patches and habitat elements in burnt areas. These surviving individuals become the founders for subsequent post-fire population recovery. Given that globally we are seeing increasingly frequent large-scale wildfires driven by climate change, the capacity for in situ survival will help mitigate some of the fire-related impacts of climate change.

Keywords
climate change, disturbance, fire, recovery, refuge, small mammals, succession, survival
Fire shapes ecosystems around the world by consuming plant material and influencing the distribution and abundance of biota (Bond & Keeley, 2005; He et al., 2019). However, fire regimes across the world have changed dramatically over the past five centuries with the spread of colonialism and the displacement of Indigenous people (Liebmann et al., 2016; Nowacki & Abrams, 2008; Romanin et al., 2016). Fire regimes are also being pushed further from historical baselines by climatic changes (Mariani et al., 2018) and increased prescribed burning (Penman et al., 2011). In particular, climate change is resulting in longer fire seasons and larger and more intense fires in many fire-prone regions globally (Clarke et al., 2011; Jolly et al., 2015; Kirchmeier-Young et al., 2017). Altered fire regimes have far-reaching consequences for ecosystems (Bradstock, 2008; Briani et al., 2004), including changes in species’ abundance (Bliege Bird et al., 2018), ecosystem state shifts (Bowman et al., 2013) and increased extinction risk (Enright et al., 2015).

Fire-induced mortality of wildlife leads to longer-term population reductions (Banks et al., 2011; Hale et al., 2016), which can increase the risk of local extinction. While mortality during fires is poorly documented (Friend, 1993; Koprowski et al., 2006), there is a growing body of evidence to suggest many small mammals can initially survive the immediate impacts of fire and the riskiest time is soon after fire (Leahy et al., 2015). Mortality after fire is associated with post-fire conditions, such as elevated rates of predation leading to population reductions (Conner et al., 2011; Leahy et al., 2015; Morris et al., 2011). Post-fire environments also have substantially altered vegetation structure and resource availability, which can affect survival and recruitment (Morris et al., 2011; Sutherland, 1999). For instance, Sutherland (1999) found that post-fire food supplementation caused temporary increases in brown antechinus Antechinus stuartii abundance relative to areas without food supplementation.

Reversing the impacts of fire requires population recovery, and a key question for land managers and researchers is whether populations recover mainly from survivors within the fire ground via in situ survival and population growth (in situ recovery) or from individuals emigrating from nearby unburned areas (ex situ recovery) (Banks et al., 2017). In situ recovery may be spatially indistinct, whereby survival is dispersed and not related to specific landscape or habitat features, or nucleated, where populations grow from spatial refugia within the fire boundary where animals survived (Banks et al., 2017). While animals may die during fire, certain habitat elements such as logs, burrows and rocks can buffer animals from the direct impacts of fire, thus facilitating their survival and providing potential nuclei for in situ recovery (Begg et al., 1981; Sutherland & Dickman, 1999). This scenario of in situ survival is considered the most plausible mechanism for the recovery of mammals in landscapes which may be subject to natural disturbances such as wildfire (Lindenmayer et al., 2005) and has been suggested to be more important than ex situ recovery (Banks et al., 2011, 2017; Bradstock, 2008; Plavsic, 2014; Southgate & Masters, 1996), although there are exceptions. Puiggirones et al. (2018) found that while a small proportion of survivors were retained within burnt areas, the recovery process was also heavily assisted by recolonization from unburnt areas. The relative importance of in situ recovery may be dependent on the severity, intensity, or size of a fire event (Romme et al., 1998). Ecosystems exposed to large, high-intensity and relatively homogeneous fires may experience greater mortality and result in fewer small, unburned refuges (Collins et al., 2019), potentially leading to a greater reliance on an ex situ mode of post-fire recovery (Bradstock, 2008).

Recent mega-fires in Brazil, Australia, the USA and elsewhere point to a critical need to disentangle the relative importance of in situ and ex situ strategies in the post-fire recovery of mammal populations (Kganyago & Shikwambana, 2020; Nolan et al., 2020). Larger, more intense and homogeneous fires are becoming increasingly common (Clarke et al., 2011), leaving fewer small unburned refuges within fire-affected landscapes (Foster et al., 2017). These changes to fire regimes are combined with more frequent droughts (Cunha et al., 2019; Intergovernmental Panel on Climate Change 2013), which are known to drive severe reductions in mammal distributions within fire-prone landscapes, even in long unburnt areas (Crowther et al., 2018; Hale et al., 2016). Such interactions can have severe impacts on the rates of population recovery in post-fire landscapes (Hale et al., 2016).

Here, we use extensive sampling of mammal populations to test key questions relating to the mechanisms and drivers of post-fire population survival and recovery. The Grampians National Park in south-eastern Australia has experienced three large-scale (35,000–85,000 ha), high-intensity wildfires in recent years (2006, 2013, 2014), while also enduring highly variable climatic conditions, creating a unique opportunity to examine the post-fire recovery of small mammals under conditions mimicking those forecast by climate change models. Long-term small mammal research has also been undertaken in this region making it an ideal location to address the following two questions.

1.1 | Question 1: Are source populations for recovery derived from in situ survival or via immigration from surrounding unburnt areas (ex situ) following large-scale, high-intensity wildfires?

If the main mechanism for recovery is ex situ immigration, we would expect to see a clear spatial pattern of post-fire population recovery, with sites closer to large patches of unburnt vegetation outside of the fire perimeter recovering more quickly than isolated sites in the interior of the burn. This is due to the larger distances individuals would have to travel through the landscape in order to recolonize interior burnt areas. If recovery is largely driven by in situ survivors, we would expect recovery to be unrelated to distance to external unburnt patches, as founding individuals would be derived from within the burn boundary and not from surrounding unburnt areas (Banks et al., 2011).
1.2 | Question 2: Do habitat elements (e.g., logs) facilitate in situ survival of small mammals in burnt areas?

If there is evidence of in situ survival after high-intensity fires, there are likely to be habitat features that have influenced survival by providing individuals with places to seek shelter during fire events and persist in the post-fire environment for a period of time. We expect to see more individuals surviving in areas with a higher abundance of particular habitat elements that could act as in situ refuges, such as large trees and logs, as animals may be able to readily seek shelter provided by these habitat elements both during and immediately after the fire.

2 | METHODS

2.1 | Study area

The Grampians National Park (168,000 ha) is located in central western Victoria, Australia (~37.21, 142.40) and has highly diverse flora and fauna (Enright et al., 1994; Parks Victoria, 2011). In 2006, approximately 50% of the park was burnt by a severe wildfire (85,000 ha) and subsequently 36 long-term study sites were established in 2008 to investigate the post-fire environment and mammal recovery. In January 2013, the Victoria Valley in the west of the Grampians National Park experienced a 35,000 ha, high-intensity wildfire that burnt for approximately 2 weeks. Following this, in 2014, another extremely high-intensity wildfire burnt 55,000 ha of the northern Grampians over 5 days. Cumulatively, these fires burned 175,000 ha of the park in less than a decade, with some overlap occurring between fire boundaries, resulting in approximately 90% of the park being burnt. All three fires were characterized by near complete burning of all vegetation within the fire perimeter, and a very limited number of small unburnt patches. These fires provide a unique opportunity to investigate the spatial patterns of small mammal survival and recovery following fires, and whether those patterns relate to habitat elements that allow mammals to persist in burnt areas. We use multiple data sets to examine evidence of survival of small mammals and the effect of habitat elements on that survival as well as the drivers of recovery post-fire (Figure 1).

2.2 | Site selection and description

2.2.1 | Source of recovery studies (long-term small mammal trapping data)

A total of 36 sites were established in 2008 to monitor the response of small- and medium-sized mammal communities to the 2006 wildfires (Hale et al., 2016). Sites were predominately located in healthy woodland and sand heathland, the dominant vegetation classes in this landscape (Figure 2). Each study site comprised a 150 × 150-m grid of 49 Elliott traps (25 m spacing) and 16 cage traps (50 m spacing) and was surveyed for four consecutive nights between April and July of each year, resulting in 260 trap-nights per site per year. Each trap contained a bait and nesting material and was covered by plastic and checked twice per day.

The 36 sites were initially selected to span both burnt (n = 19) and unburnt (n = 17) vegetation (representing a post-fire gradient of ~50 years), and the following constraints were used for site selection: (a) sites were established at an elevation <470 m a.s.l.; (b)
sites were within an intensive long-term fox (*Vulpes vulpes*) baiting area (an introduced mesopredator); (c) sites were easily accessible by road; and (d) sites were separated by at least 2 km each (see Hale et al. (2016) for further details). In this paper, we use a subset of the small mammal trapping data also used in Hale et al. (2016). First, given our interest in the source of population recovery within the fire grounds, only those survey sites which were burnt in the 2006 wildfire (*n* = 19) and those burnt in the 2013 (*n* = 6) and 2014 (*n* = 4) wildfires are included (i.e., unburned sites were excluded from analysis). Second, we only included data collected between 2008 and 2012 for the sites burnt in 2006, data collected in 2013–19 for the sites burnt in 2013, and data collected in 2014–19 for the sites burnt in 2014, because we are investigating the short-term recovery of mammals after fire.

The 2006 Grampians wildfire was an extremely high-intensity fire which resulted in near complete burning of all vegetation within the fire perimeter. There were seven large patches of vegetation ranging from 15 to 419 ha (mean 270.1 ha) that did not burn in 2006 but had been subjected to fuel reduction burning in the 2 years prior to the 2006 fire. Due to the extreme drought conditions associated with the millennium drought these areas had not recovered and as such had no fuel to carry a fire. These sites were trapped in 2008 and demonstrated they were almost devoid of small mammals with only one site having *Pseudomys shortridgei* present, and a further site having *Trichosurus vulpecula* present. There were also several small patches of vegetation (mean 3.4 ha, range 3.2–3.7 ha) that did not burn in the fire. These areas were randomly distributed in the landscape and may have provided protection for some species. These sites were also trapped in 2008 with two of them having *Antechinus agilis* present, and one site having *T. vulpecula* present.

2.2.2 | Immediate post-fire survival studies (camera trapping in recent post-fire areas)

Two further field surveys were conducted in 2013 and 2014 following the occurrence of two large high-intensity wildfires. Camera trapping sites were established within 3 months (Figure 3) of the relevant fire within the burn perimeter (2013: *n* = 160, 2014: *n* = 161) (Figure 2). In 2013, camera traps were located in one of
two treatments: burnt sites \((n = 70)\) and very small unburnt patch sites within the burn perimeter \((n = 90)\). In 2014, 161 sites were established in the northern Grampians: burnt sites \((n = 119)\) and small unburnt patch sites within the burn perimeter \((n = 42)\). Sites were selected based on the following factors: (a) prior productivity of the vegetation, to ensure a range of prior productivity levels based on landscape scale NDVI; (b) each site was at least 500 m from any other site; and (c) on ground observations were used to confirm whether the site was burnt.

Infrared motion sensing ScoutGuard 550 cameras with a 2 GB memory card were used to monitor mammals. Cameras were programmed to take three five megapixel images over a 6 s period with a 30 s idle period between each set of images. At each camera point, a camera was fixed to a wooden stake at a height of approximately 1.3 m facing down to the ground (De Bondi et al., 2010). This downward facing camera technique results in less false triggers caused by vegetation and improves the ability to identify small mammal species (Rendall et al., 2014). To further improve our capacity to identify species and reduce the impact of moving vegetation, we cleared an area of approximately 1 m² of vegetation underneath each camera. Below each camera, a lure consisting of a highly perforated PVC pipe, was pegged to the ground. The lure was filled with polyester cushion stuffing soaked in a mixture of peanut butter, vanilla extract, linseed oil and tuna oil. In addition to the fixed oil-based lure, a handful of rolled oats was placed below the camera to encourage small mammals to remain in the field of view for an extended period of time. Each site was surveyed for eight nights. This duration was selected as it has been found to confidently determine absences of species at the study site (De Bondi et al., 2010).

2.3 | Dependent and independent variables

2.3.1 | Source of recovery studies (long-term small mammal trapping data)

For each site, we determined the presence and absence of species across the four nights of trapping each year. To assess the mechanisms driving recovery, we used four independent variables, (a) distance to the perimeter of continuously unburnt vegetation; (b) time since fire; (c) rainfall; and (d) vegetation productivity.

Distance to the continuous unburnt vegetation was measured from the centre of the trapping grid to the unburnt vegetation at the perimeter of the 2006, 2013 and 2014 fires using fire maps.
provided by Parks Victoria. We used distance to the unburnt perimeter as a metric to establish if recovery of small mammals is driven by proximity to unburnt areas. While there were some unburnt patches within the 2006 fire landscape, the majority of these had been subjected to fuel management burns in the 2 years prior to the fire and were not carrying significant small mammal populations due to the underlying extreme drought conditions and lack of vegetative cover (see Hale et al., 2016). Distance to unburnt vegetation did not change between 2008 and 2013 as there was no prescribed fire or wildfire experienced at or around the trapping sites (distance to unburnt vegetation ranged between 0.11 and 13.39 km). Time since fire (years since last fire), 18 month rainfall up to April each year and productivity (as inferred from Normalized Difference Vegetation Index [NDVI]) were measured using the methods outlined in Hale et al., (2016). The two additional wildfires in 2013 and 2014 shifted the dynamics of the system. Sites burnt in 2013 and 2014 were then included in the post-fire recovery data with new metrics of distance to the continuous unburnt perimeter calculated for each site.

2.3.2 | Immediate post-fire survival studies (camera trapping in recent post-fire areas)

For both data sets, we recorded the presence or absence of each species (where species were deemed to have sufficient occurrences for analysis) from camera traps over the duration of sampling at each site to assess how individuals survive wildfire. For the burnt sites within the 2013 fire perimeter (n = 70), we used three independent variables: (a) prior productivity (NDVI); (b) cover abundance of large rocks (>30 cm diameter); and (c) number of large trees (10 cm diameter). These variables were used as they have been shown to provide refuge to mammal species both during (e.g., protection from fire) and post-fire (e.g., shelter) (Robinson et al., 2013). The productivity of each site was calculated using 6 years (prior to the 2006 wildfire) of satellite data from the sum months (the most water stressed period of the year in southeastern Australia) and then averaged to produce a single NDVI value for each site using a 50 m buffer (Hale et al., 2016). The cover abundance of large rocks was measured within a 10 m quadrat centred on each camera location. The number of logs within the quadrat was also counted (McCarthy et al., 1999).

In 2014, at all of the burnt sites (n = 119) we measured four independent variables at each camera location: (a) large rock cover abundance (>30 cm diameter); (b) canopy cover; (c) the number of large trees (>40 cm diameter at breast height) and (d) prior productivity (NDVI). Rock cover abundance was measured in the 10 m quadrat centred on each camera location and canopy cover was estimated by observing the proportion of sky obscured by the canopy above the quadrat. Prior productivity for the site was measured as described above. We used a slightly different set of variables in 2014, because after 2013 we determined that measuring the number of large trees and canopy cover may provide a better metric of tree-based survival options than log cover on the ground.

2.4 | Statistical analysis

2.4.1 | Source of recovery studies (long-term small mammal trapping data)

To examine the source of recovery of small mammals, we modelled the effects of time since fire, distance to unburnt vegetation, rainfall and productivity on the occurrence of six small mammal species using generalized additive mixed models (GAMMs). The response variable was the presence/absence of the species across the four nights of trapping conducted annually at each site, modelled as a binomial distribution of errors. We used mixed models as they allow for the inclusion of a random factor that accounts for repeated measurements (Zuur et al., 2009), which was required due to the repeated sampling of the same sites each year following fires. As our primary interest was in the role of distance to unburned vegetation on post-fire recovery, we considered three models, all of which included rainfall and NDVI in addition to (a) a time since fire x distance interaction, to examine whether distance to unburned vegetation modified species’ recovery trajectories, (b) time since fire and distance as main effects (i.e. no interaction), to examine whether time since fire and distance to unburned vegetation have additive effects, or (c) only time since fire (no distance variable), which would be supported if distance to unburned vegetation has little influence on post-fire recovery. Time since fire was treated as a smoothed variable, and all other variables were included as linear terms. Site identity was included as a random factor due to the repeated sampling of sites through time. We assessed which of these models was most supported by the data using Akaike’s Information Criteria (AIC).

2.4.2 | Immediate post-fire survival studies (camera trapping in recent post-fire areas)

To establish whether there was a difference in the ratio of the presence or absence of a species in burnt and unburnt sites we utilized a chi-square test of independence. We then used occupancy modelling to assess relationships between habitat variables and the persistence of each species immediately post-fire. We analysed the 2013 and 2014 data separately and only included burnt sites in the analyses. Predictor variables for 2013 dataset were NDVI, large rock cover abundance and a count of logs. For 2014, the predictor variables were large rock cover abundance, canopy cover, number of large trees and NDVI. The response variable was a matrix of species presence/absence at each site for each survey night (n = 8 per year). We fitted a global model for each species and year with main effects of the habitat variables, which we scaled and centred prior to analysis. We also included a detection
covariate of survey night (1–8) to account for potential changes in lure attractiveness over time. We present model coefficients and 95% confidence intervals. We excluded Antechinus mimetes for 2014 because the model did not converge.

3 | RESULTS

3.1 | Question 1: Are source populations for recovery derived from in situ survival or via immigration (ex situ) from surrounding unburnt areas following large-scale, high-intensity wildfires?

There was little evidence of a spatial pattern in the persistence or recovery of native mammals in relation to distance to unburned vegetation: the model which included time since fire only was the most parsimonious model for every species, except for R. rattus which also included an additive effect of distance to unburnt vegetation (Table 1). Time since fire was significant for all species (Table 2), and all species aside from M. musculus were least common immediately after fire and increased in their probability of occurrence thereafter (Figure 4). Rainfall was positively associated with M. musculus occurrence, and NDVI was positively associated with A. agilis, P. shortridgei and R. lutreolus occurrence (Table 2).

### Question 2: Do habitat elements (e.g., logs) facilitate in situ survival of small mammals in burnt areas?

Camera trapping within the fire perimeters of both the 2013 and 2014 wildfire revealed evidence of survival of small numbers of small mammals (Table 3). The species with the most detections were arboreal, including Antechinus agilis (present at 12.5%–16.6% of cameras), Antechinus flavipes (25.8%–29.4%) and Trichosurus vulpecula (10.4%–25.6%), or the invasive Rattus rattus (13.8%–22.1%) and M. musculus (13.1%–39.9%), whereas terrestrial native rodents were detected in low numbers (1.2%–7.5%; Table 3). For most species, there was little difference in presence/absence ratios between sites that were burnt and the very small unburnt patches within the fire boundary (Table 3). The native rodent P. shortridgei was more likely to be present in unburnt patches than in burnt sites in 2013 (Table 3). There was also a weak signal for a similar trend towards higher presence in unburnt patches for A. flavipes in 2014 (Table 3). A different trend occurred in the invasive M. musculus with it being more likely to be present in burnt areas than unburnt patches (Table 3). Surviving individuals were also detected at our long-term trapping sites soon after they were burnt during the 2013 (n = 6 burnt) and 2014 (n = 4 burnt) wildfires (e.g., A. agilis and P. shortridgei) (Appendix: Table A1).

For 2013, post-fire occupancy of A. flavipes at burnt sites was positively related to rocks and negatively to logs, whereas R. rattus occurrence was positively related to logs (Table 4). For 2014, occurrence of A. agilis was positively related to large trees, M. musculus responded negatively to canopy cover, and R. rattus responded positively to both rocks and NDVI (Table 5). There were no effects for the remaining combinations of species and habitat variables (Table 5).

### 4 | DISCUSSION

We sought to determine the relative importance of in situ survival and ex situ emigration to small mammal population recovery following wildfires and the influence of habitat variables in facilitating survival. We did not find a relationship between distance to the continuous unburnt vegetation and the occurrence of any native species, suggesting that in situ survival is a more likely mechanism for the recovery of post-fire mammal populations than immigration from the continuous unburnt habitat. We acknowledge that this research did not begin until 2 years after the 2006 wildfire and that small mammals could have moved long distances in this period. However, as discussed in detail below, the system was in extreme long-term drought conditions and small mammal abundances were extremely low across the landscape and vegetation recovery was extremely slow (Hale et al., 2016) and we saw the same recovery trend in sites.
burnt in 2013 and 2014 where we use data from immediately after the sites were burnt.

The occurrence of a further two high-intensity wildfires provided the opportunity to investigate survival of small mammals soon after the fires. While we could not commence field surveys until almost 3 months after the fire, we consider it unlikely native small mammals had rapidly invaded the burnt landscape, as most of the small mammal species in the system have a requirement for structurally complex ground vegetation which was missing immediately after the fires (Hale et al., 2016). The potential for extremely rapid colonization of the burnt landscape by animals from the unburnt vegetation at the perimeter of the fire cannot be discounted as a possible explanation of the patterns observed, but given the habitat requirements of the species being studied we consider it unlikely.

We found no evidence for continuous unburned habitat being the primary source of small mammal population recovery post-fire, with species occurrence being similar between sites near and far from continuous unburned vegetation (spanning distances 0.1–13 km from the burn edge). The lack of a spatial signal in small mammal population recovery across three high-intensity, large-scale fires across the landscape suggests that this mesic ecosystem is largely recovering internally via in situ survival rather than externally through emigration from unburned areas (Banks et al., 2017; Lindenmayer et al., 2008; Recher et al., 2009). Our results support the prediction of Banks et al. (2011) that residual populations made up of animals that survived the wildfires will be more important than emigration for population recovery of many species following wildfires. However, as mentioned previously, we note that our study did not commence until 2 years post-fire; therefore, evidence for recovery in the landscape was limited to the starting point of sites burnt in 2006 but was not limited in the sites burnt in 2013 and 2014. At the commencement of this research, small mammal populations were extremely suppressed in the time between the 2006 fire and when data collection began due to the extreme drought conditions in the region from 2001 to 2009 (Hale et al., 2016). As such, we do not expect there to have been significant immigration into the burned

### TABLE 2 Results of generalized additive mixed models describing the distribution of mammals post-fire. Details of smoothed terms for time since fire are shown for each species

| Species            | Smoothed term for time since fire | Rainfall | NDVI | Unburnt |
|--------------------|----------------------------------|----------|------|---------|
|                    | edf | Chi.sq | p-value | Estimate | SE | Estimate | SE | Estimate | SE |
| Antechinus agilis  | 2.36 | 14.76 | <0.01 | −0.07 | 0.30 | 2.46 | 0.62 | − | − |
| Antechinus flavipes| 1.00 | 12.38 | <0.001 | −0.03 | 0.37 | −1.34 | 0.75 | − | − |
| Pseudomys shortridgei | 1.00 | 29.50 | <0.001 | 0.08 | 0.43 | 2.27 | 0.95 | − | − |
| Rattus lutreolus   | 1.00 | 11.76 | <0.001 | 0.36 | 0.38 | 2.17 | 0.76 | − | − |
| Sminthopsis murina| 1.00 | 1.00 | <0.01 | 0.40 | 0.26 | 0.34 | 0.52 | − | − |
| Mus musculus       | 3.54 | 25.09 | <0.001 | 0.99 | 0.31 | 0.16 | 0.32 | − | − |
| Rattus rattus      | 1.00 | 1.00 | <0.001 | 0.03 | 0.02 | 2.11 | 9.28 | 0.17 | 0.08 |

Note: Coefficients of linear terms also included in the models (18 month rainfall, NDVI, and distance to unburnt vegetation). Bold values indicate relationships with a \( p \)-value < 0.05.

### FIGURE 4 Response curves of small mammal recovery following high-intensity wildfires
TABLE 3 Percentage of burnt or unburnt sites that were occupied and the site occupancy for all sites combined, following the 2013 and 2014 wildfires

| Species                | 2013 Unburnt (n = 90) | 2013 Burnt (n = 70) | Total (n = 160) | Chi-square (df = 1) | 2014 Unburnt (n = 42) | 2014 Burnt (n = 121) | Total (n = 163) | Chi-square (df = 1) |
|------------------------|-----------------------|---------------------|-----------------|---------------------|-----------------------|---------------------|-----------------|---------------------|
| Antechinus agilis      | 11.1% (n = 10)        | 14.3% (n = 10)      | 12.5% (n = 20)  | 0.363, p = .547     | 14.3% (n = 6)         | 17.4% (n = 21)      | 16.6% (n = 27) | 0.213, p = .645   |
| Antechinus flavipes    | 27.8% (n = 25)        | 31.4% (n = 22)      | 29.4% (n = 47)  | 0.253, p = .613     | 35.7% (n = 15)        | 22.3% (n = 27)      | 25.8% (n = 42) | 2.927, p = .087   |
| Antechinus mimetes     | 2.2% (n = 2)          | 4.3% (n = 3)        | 3.1% (n = 5)    | ID                  | 4.8% (n = 2)          | 1.7% (n = 2)        | 2.5% (n = 4)    | ID                  |
| Rattus lutreolus       | 4.4% (n = 4)          | 0.0% (n = 0)        | 2.5% (n = 4)    | ID                  | 2.4% (n = 1)          | 0.8% (n = 1)        | 1.2% (n = 2)    | ID                  |
| Pseudomys shortridgei  | 12.2% (n = 11)        | 1.4% (n = 1)        | 7.5% (n = 12)   | 6.612, p = .010     | 7.1% (n = 3)          | 0.0% (n = 0)        | 1.8% (n = 3)    | ID                  |
| Trichosurus vulpecula  | 23.3% (n = 21)        | 28.6% (n = 20)      | 25.6% (n = 41)  | 0.564, p = .452     | 16.7% (n = 7)         | 8.3% (n = 10)       | 10.4% (n = 17)  | 2.356, p = .125   |
| Rattus rattus          | 15.6% (n = 14)        | 11.4% (n = 8)       | 13.8% (n = 22)  | 0.565, p = .452     | 28.6% (n = 12)        | 19.8% (n = 24)      | 22.1% (n = 36)  | 1.383, p = .240   |
| Mus musculus           | 7.8% (n = 7)          | 20.0% (n = 14)      | 13.1% (n = 21)  | 5.159, p = .023     | 14.3% (n = 6)         | 48.8% (n = 59)      | 39.9% (n = 65)  | 9.093, p = .003   |

Where "n" equals the number of sites species were present at. Chi-square analysis establishes whether there is a difference in the ratio of presence/absence of a species and whether the site was burnt or unburnt.

Abbreviation: ID, Insufficient Data.

*Species not native to Australia.

TABLE 4 Modelling results for the effects of habitat variables on postfire occupancy in 2013 and 2014 wildfires

| Species                 | Variable | Estimate | LCI     | UCI     |
|-------------------------|----------|----------|---------|---------|
| Antechinus flavipes     | NDVI     | -0.15    | -1.01   | 0.76    |
| Antechinus agilis       | NDVI     | -0.17    | -0.43   | 1.39    |
| Rattus rattus           | Rocks    | 0.42     | 0.35    | 0.54    |
| R. lutreolus            | Rocks    | 0.49     | 0.34    | 0.68    |
| Pseudomys shortridgei   | Rocks    | 0.42     | 0.35    | 0.54    |
| Trichosurus vulpecula   | Rocks    | 0.38     | 0.31    | 0.46    |
| Mus musculus            | Rocks    | 0.78     | 0.60    | 0.96    |

Note: Bold text indicates variables where the 95% confidence intervals do not include zero. Abbreviations: LCI, lower 95% confidence interval; UCI, upper 95% confidence interval.
fire due to a lack of resources (Dickman et al., 1999) or elevated predation rates within the burn area (Leahy et al., 2015; Russell et al., 2003). While the Grampians is subjected to long-term intense fox baiting, both foxes and cats still have relatively high occupancy across the entire landscape (Geyle et al., 2020) suggesting that predation pressure likely remains high in burnt areas. A fruitful area for future research is to measure the post-fire survival and population recovery of small mammals in areas with and without effective predator control.

Previous studies have shown that post-fire population recovery of bush rats occurred from topographic drainage lines (Banks et al., 2017); Antechinus agilis abundance increased in gullies immediately post-fire (Swan et al., 2016); and elephant shrews in in South Africa survived fire by sheltering in termite mounds (Yarnell et al., 2008). We found mixed support for particular habitat elements influencing the occurrence of small mammals in the months following wildfire. The cover of rocks and logs was important for the invasive black rat, whereas the marsupial A. flavipes showed a negative response to logs and A. agilis a positive response to the number of large trees. The lack of response of the remaining species suggests that the measured habitat variables are not key to their post-fire persistence, at least in the context of this study.

It is essential to take into account the state of the landscape prior to a fire event when considering the timeframe and method of recovery. Post-fire recovery of small mammals in mesic systems has often been considered a product of waves of immigration from unburnt areas and having a strong link with time since fire and vegetation recovery (Fox, 1982). However, for our mesic study system, rainfall has a more prominent role in recovery than time since fire alone (Hale et al., 2016). During periods of below average rainfall, systems become depleted of mammals (Crowther et al., 2018; Hale et al., 2016; Meserve et al., 2011) and resources (Dickman et al., 1999) leaving a smaller pool of animals in the environment that have the potential to survive fire. The interplay between fire and underlying climatic conditions, exacerbated by climate change, may substantially alter how species recover post-fire, resulting in an increasingly dynamic system.

With small mammal recovery varying with the prevailing climatic conditions (Hale et al., 2016; Recher et al., 2009), it may be that the mode of recovery will shift as climatic conditions across the globe continue to change. Many species are likely to recover through in situ survival, at least during the initial stages of recovery, especially species that are less fire sensitive (e.g., A. agilis) as they are able to survive more readily in the post-fire environment (Banks

| Species                  | Variable      | Estimate | LCI   | UCI   |
|-------------------------|---------------|----------|-------|-------|
| Antechinus agilis       | Canopy cover  | 0.20     | -0.25 | 0.66  |
|                         | Rocks         | 0.60     | -0.01 | 1.21  |
|                         | Large trees   | 0.97     | 0.22  | 1.71  |
|                         | NDVI          | 0.54     | -0.08 | 1.15  |
| Antechinus flavipes     | Canopy cover  | -0.41    | -1.06 | 0.25  |
|                         | Rocks         | 0.37     | -0.23 | 0.96  |
|                         | Large trees   | 0.20     | -0.33 | 0.73  |
|                         | NDVI          | -0.37    | -0.98 | 0.24  |
| Trichosurus vulpecula   | Canopy cover  | 0.63     | -0.48 | 1.74  |
|                         | Rocks         | 0.48     | -0.38 | 1.35  |
|                         | Large trees   | -1.03    | -2.56 | 0.50  |
|                         | NDVI          | 0.46     | -0.36 | 1.28  |
| Felis catus             | Canopy cover  | 0.05     | -0.86 | 0.97  |
|                         | Rocks         | 0.66     | -0.31 | 1.62  |
|                         | Large trees   | -0.12    | -1.30 | 1.06  |
|                         | NDVI          | 0.98     | -0.09 | 2.04  |
| Mus musculus            | Canopy cover  | -0.73    | -1.29 | -0.17 |
|                         | Rocks         | -0.44    | -0.89 | 0.01  |
|                         | Large trees   | 0.18     | -0.27 | 0.62  |
|                         | NDVI          | 0.21     | -0.23 | 0.66  |
| Rattus rattus           | Canopy cover  | 0.36     | -0.15 | 0.88  |
|                         | Rocks         | 1.35     | 0.77  | 1.93  |
|                         | Large trees   | -0.24    | -0.76 | 0.28  |
|                         | NDVI          | 0.83     | 0.21  | 1.44  |

Note: Bold text indicates variables where the 95% confidence intervals do not include zero.
Abbreviations: LCI, lower 95% confidence interval; UCI, upper 95% confidence interval.
et al., 2017). The more sensitive species (such as *R. lutreolus*) may initially disappear from burnt areas and therefore rely more heavily on immigration for recovery once landscape conditions become more suitable (Banks et al., 2017). Following this logic, it may be that recovery occurs in a step-wise nature with initial recovery a result of individuals surviving within the burnt landscape which eventually build up populations as conditions improve (e.g. increased rainfall, available habitat). As these populations increase in size and burnt areas begin to recover, it is likely that individuals will subsequently disperse into the broader landscape.

The changes in fire regimes and rainfall observed in the study area are predicted to become increasingly “normal” under future climate change scenarios, with more intense and frequent wildfires paired with periods of below average rainfall punctuated by flooding events (Clarke et al., 2011; Intergovernmental Panel on Climate Change 2013). Even areas of the landscape which are long unburnt have suppressed animal populations during drought periods (Hale et al., 2016). We present strong evidence for post-fire recovery being driven largely by in situ survival. In situ survival is facilitated by small unburnt patches and key habitat elements in burnt areas and presumably prior populations (Hale et al., 2016). Given that south-eastern Australia and many other parts of the world are seeing increasingly frequent large-scale wildfires due to climate change, the capacity for species to survive fires via the mechanism of in situ survival and then become the foundation of population recovery will mitigate some of the critical impacts of climate change.

ACKNOWLEDGEMENTS

We thank and acknowledge the traditional owners and custodians, past, present and emerging of the Gariwerd landscape. We gratefully acknowledge funding and field support that was provided by Parks Victoria, Deakin University and the Holsworth Wildlife Research Endowment. We thank the Grampians research team and volunteers who assisted with this research. This study was carried in accordance with the regulations of the Animal Ethics Committee at Deakin University and research permits from the Department of Environment and Primary Industries (permit numbers 10005800 and 10007121).

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ddi.13283.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Raylene Cooke https://orcid.org/0000-0002-8843-7113
Tim Doherty https://orcid.org/0000-0001-7745-0251
John G. White https://orcid.org/0000-0002-7375-5944

REFERENCES

Banks, S. C., Dujardin, M., McBurney, L., Blair, D., Barker, M., & Lindenmayer, D. B. (2011). Starting points for small mammal population recovery after wildfire: Reconciliation or residual populations? *Oikos*, 120, 26–37. https://doi.org/10.1111/j.1600-0706.2010.18765.x

Banks, S. C., McBurney, L., Blair, D., Davies, I. D., & Lindenmayer, D. B. (2017). Where do animals come from during post-fire population recovery? Implications for ecological and genetic patterns in post-fire landscapes. *Ecography*, 40, 1325–1338. https://doi.org/10.1111/ecog.02251

Begg, R. J., Martin, K. C., & Price, N. F. (1981). The small mammals of little Nourlangie rock, N. T. IV. The effects of fire. *Wildlife Research*, 8, 515.

Bliege Bird, R., Bird, D. W., Fernandez, L. E., Taylor, N., Taylor, W., & Nimmo, D. (2018). Aboriginal burning promotes fine-scale pyrodiversity and native predators in Australia’s Western Desert. *Biological Conservation*, 219, 110–118. https://doi.org/10.1016/j.biocon.2018.01.008

Bond, W. J., & Keeley, J. E. (2005). Fire as a global ‘herbivore’: The ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution*, 20, 387–394. https://doi.org/10.1016/j.tree.2005.04.025

Bowman, D. M. J. S., Murphy, B. P., Boer, M. M., Bradstock, R. A., Cary, G. J., Cochrane, M. A., Fensham, R. J., Krawchuk, M. A., Price, O. F., & Williams, R. J. (2013). Forest fire management, climate change, and the risk of catastrophic carbon losses. *Frontiers in Ecology and the Environment*, 11, 66–68. https://doi.org/10.1890/13.WB.005

Bradstock, R. A. (2008). Effects of large fires on biodiversity in south-eastern Australia: Disaster or template for diversity? *International Journal of Wildland Fire*, 17, 809–822. https://doi.org/10.1071/WF07153

Briani, D., Palma, A. T., Vieira, E., & Henriques, R. B. (2004). Post-fire succession of small mammals in the Cerrado of central Brazil. *Biodiversity & Conservation*, 13, 1023–1037. https://doi.org/10.1023/B:BIOC.0000014467.27138.0b

Clarke, H. G., Smith, P. L., & Pitman, A. J. (2011). Regional signatures of future fire weather over eastern Australia from global climate models. *International Journal of Wildland Fire*, 20, 550–562. https://doi.org/10.1071/WF101070

Collins, L., Bennett, A. F., Leonard, S. W. J., & Penman, T. D. (2019). Wildfire refugia in forests: Severe fire weather and drought mute the influence of topography and fuel age. *Global Change Biology*, 25(11), 3829–3843. https://doi.org/10.1111/gcb.14735

Connor, J. M., Castlesberry, S. B., & Derrick, A. M. (2011). Effects of mesopredators and prescribed fire on hisdopon cotton rat survival and cause-specific mortality. *Journal of Wildlife Management*, 75, 938–944.

Crowther, M. S., Tulloch, A. I., Letnic, M., Greenville, A. C., & Dickman, C. R. (2018). Interactions between wildfire and drought drive population responses of mammals in coastal woodlands. *Journal of Mammalogy*, 99, 416–427. https://doi.org/10.1093/jmammal/gyy003

Cunha, A. P. M. A., Zeri, M., Leal, K. D., Costa, L., Cuartas, L. A., Marengo, J. A., Tomassella, J., Vieira, R. M., Barbosa, A. A., Cunningham, C. Cal García, J. V., Broedel, E., Alvalá, R., & Ribeiro-Neto, G. (2019). Extreme drought events over Brazil from 2011 to 2019. *Atmosphere*, 10(11), 642. https://doi.org/10.3390/atmos10110642

De Bondi, N., White, J. G., Stevens, M., & Cooke, R. (2010). A comparison of the effectiveness of camera trapping and live trapping for sampling terrestrial small-mammal communities. *Wildlife Research*, 37, 456–465. https://doi.org/10.1071/WR100046

Dickman, C. R., Mahon, P. S., Masters, P., & Gibson, D. F. (1999). Long-term dynamics of rodent populations in arid Australia: The influence of rainfall. *Wildlife Research*, 26, 389–403. https://doi.org/10.1071/WR97057

Enright, N. J., Fontaine, J. B., Bowman, D. M. J. S., Bradstock, R. A., & Williams, R. J. (2015). Interval squeeze: Altered fire regimes and
to European land management in a Tasmanian eucalypt savanna. *Australian Journal of Botany*, 64, 427–440. https://doi.org/10.1071/ BT16032

Romme, W. H., Everham, E. H., Frelich, L. E., Moritz, M. A., & Sparks, R. E. (1998). Are large, infrequent disturbances qualitatively different from small, frequent disturbances? *Ecosystems*, 1, 524–534. https://doi.org/10.1007/s100219900048

Russell, B. G., Smith, B., & Augee, M. L. (2003). Changes to a population of common ringtail possums (*Pseudocheirus peregrinus*) after bushfire. *Wildlife Research*, 30, 389–396. https://doi.org/10.1071/WR01047

Southgate, R., & Masters, P. (1996). Fluctuations of rodent populations in response to rainfall and fire in a central Australian hummock grassland dominated by *Plectrachne schinzii*. *Wildlife Research*, 23, 289–303. https://doi.org/10.1071/WR9960289

Sutherland, E. F. (1999). Fire, resource limitation and small mammal populations in coastal eucalypt forest. PhD thesis, The University of Sydney. Retrieved from https://ses.library.usyd.edu.au/handle/2123/5344

Sutherland, E. F., & Dickman, C. R. (1999). Mechanisms of recovery after fire by rodents in the Australian environment: A review. *Wildlife Research*, 26, 405–419. https://doi.org/10.1071/WR97045

Swan, M., Galindez-Silva, C., Christie, F., York, A., & Di Stefano, J. (2016). Contrasting responses of small mammals to fire and topographic refugia. *Austral Ecology*, 41, 443–451. https://doi.org/10.1111/aec.12331

Yarnell, R. W., Mcalfe, D. J., Dunstone, N., Burnside, N., & Scott, D. M. (2008). The impact of fire on habitat use by the short-snouted elephant shrew (*Elephantulus brachyrhynchus*) in North West Province, South Africa. *African Zoology*, 43, 45–52.10.3377/1562-70 20(2008)43[45:TIOFOH]2.0.CO;2

**BIOSKETCH**

The Grampians Fire, Climate and Biodiversity Project is a collaboration between Deakin University, Charles Sturt University and Parks Victoria. Our team is focussed on unpacking how animals respond to fire and climatic conditions through time. With climate change intensifying, our long-term small mammal research is designed to provide a view into how climate change is influencing biodiversity in fire-prone landscapes.

**How to cite this article**: Hale S, Mendoza L, Yeatman T, et al. Evidence that post-fire recovery of small mammals occurs primarily via in situ survival. *Divers Distrib*. 2021;00:1–13. https://doi.org/10.1111/ddi.13283

**APPENDIX**

**TABLE A1** The number of long-term monitoring sites burnt in the 2013 and 2014 wildfires and the presence of species at these sites (no other species were detected within these sites)

| Year of burn | Number of sites burnt | Year of occupancy | Number of sites species were detected at | Antechinus agilis | Antechinus flavipes | Mus musculus | Pseudomys shortridgei |
|--------------|-----------------------|-------------------|----------------------------------------|-------------------|-------------------|---------------|----------------------|
| 2013         | 6                     | 2013              | 3                                      | 0                 | 0                 | 0             | 0                    |
|              |                       | 2014              | 1                                      | 0                 | 5                 | 2             | 0                    |
| 2014         | 4                     | 2014              | 1                                      | 1                 | 2                 | 0             | 0                    |
|              |                       | 2015              | 1                                      | 0                 | 3                 | 0             | 0                    |