

The short-term responses of small mammals to wildfire in semiarid mallee shrubland, Australia

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Abstract

Context. Wildfire is a major driver of the structure and function of mallee eucalypt- and spinifex-dominated landscapes. Understanding how fire influences the distribution of biota in these fire-prone environments is essential for effective ecological and conservation-based management.

Aims. We aimed to (1) determine the effects of an extensive wildfire (118 000 ha) on a small mammal community in the mallee shrublands of semiarid Australia and (2) assess the hypothesis that the fire-response patterns of small mammals can be predicted by their life-history characteristics.

Methods. Small-mammal surveys were undertaken concurrently at 26 sites: once before the fire and on four occasions following the fire (including 14 sites that remained unburnt). We documented changes in small-mammal occurrence before and after the fire, and compared burnt and unburnt sites. In addition, key components of vegetation structure were assessed at each site.

Key results. Wildfire had a strong influence on vegetation structure and on the occurrence of small mammals. The mallee ningai, *Ningai yvonneae*, a dasyurid marsupial, showed a marked decline in the immediate post-fire environment, corresponding with a reduction in hummock-grass cover in recently burnt vegetation. Species richness of native small mammals was positively associated with unburnt vegetation, although some species showed no clear response to wildfire.

Conclusions. Our results are consistent with the contention that mammal responses to fire are associated with their known life-history traits. The species most strongly affected by wildfire, *N. yvonneae*, has the most specific habitat requirements and restricted life history of the small mammals in the study area. The only species positively associated with recently burnt vegetation, the introduced house mouse, *Mus domesticus*, has a flexible life history and non-specialised resource requirements.

Implications. Maintaining sources for recolonisation after large-scale wildfires will be vital to the conservation of native small mammals in mallee ecosystems.

Additional keywords: conservation, fauna, fire, disturbance, habitat, marsupials.

Introduction

Fire is an ecological process that shapes ecosystems worldwide (Bowman *et al.* 2009) and is a major driver of the structure and function of many arid and semiarid landscapes (Pausas and Bradstock 2007; Turner *et al.* 2008). In the 'mallee' shrublands of semiarid Australia, for example, wildfires exceeding 100 000 ha typically occur every 10–20 years (Noble and Vines 1993; Bradstock and Cohn 2002). Smaller fire events take place more frequently (LCC 1987). The prevailing fire regime strongly influences vegetation composition and structure (Bradstock 1989), which provide important resources for fauna, such as food, cover and nest sites (Menkhorst and Bennett 1990; Brown *et al.* 2009). Consequently, fire is widely used as a management tool in mallee ecosystems to protect natural

and built assets, and to maintain and create faunal habitats (Bradstock and Cohn 2002; Sandell *et al.* 2006).

Since European settlement, there has been a marked decline in the native mammal fauna of mallee shrublands, an ecosystem that covers 250 000 km² of southern Australia (Australian Native Vegetation Assessment 2001). Of note has been the regional extinction of one-third of the historical mammal assemblage (Bennett *et al.* 1989). Other species have declined in range and abundance (Seebeck and Menkhorst 2000; Bennett *et al.* 2006). These changes have been attributed to several factors acting in concert, including land clearing, grazing by introduced stock and European rabbits, *Oryctolagus cuniculus*, predation by introduced cats, *Felis catus*, and foxes, *Vulpes vulpes*, and inappropriate fire regimes (Dickman *et al.* 1993; Lunney 2001;

Bennett *et al.* 2006). Ongoing concern about the impact of fire regimes on small mammals inhabiting semiarid mallee vegetation (Tulloch 2004; Bennett *et al.* 2006) highlights the need for a better understanding of how fire affects small-mammal populations, if ecological and conservation-based management is to be enhanced.

Several studies have examined small-mammal responses to fire in the hummock (or spinifex) grasslands of arid Australia (e.g. Southgate and Masters 1996; Letnic *et al.* 2004), whereas little is known of the fire response of small-mammal communities characteristic of extensive mallee environments. In a review of vertebrate response to fire in mallee shrublands and temperate heathlands, Friend (1993) proposed that the fire-response patterns of small mammals could be predicted by their shelter, food and breeding requirements. Thus, small mammals with high specificity and limited flexibility in life-history traits (e.g. seasonal breeders and species that rely on particular vegetation characteristics) are likely to be strongly negatively affected when a wildfire occurs, but persist in later post-fire ages (Friend 1993). In contrast, small mammals positively associated with early post-fire ages would more likely be generalist omnivores with a flexible life history (e.g. opportunistic breeders and species able to construct burrows and persist in a range of vegetation types) (Friend 1993).

In the present study, we took advantage of a major wildfire that burnt 118 000 ha of mallee shrubland in southern Australia. Prior

to the fire, we had established faunal survey sites, and completed a round of small mammal surveys, as part of a broad-scale investigation into the region's biodiversity. The unplanned fire produced a mosaic of burnt and unburnt sites, providing an excellent opportunity to examine small-mammal responses to wildfire. In all, 26 sites were surveyed concurrently before the fire, and on four occasions following the fire (including 14 sites that remained unburnt). Thus, we were able to document changes before and after the fire, in addition to comparing burnt and unburnt sites. Here, we examine the following two key questions: (1) what are the short-term responses of small mammals to wildfire in semiarid mallee shrubland, and (2) are species' responses to wildfire consistent with their life-history traits, as proposed by Friend (1993)?

Materials and methods

Study area

The study was undertaken at Gluepot Reserve, South Australia, an area of 55 000 ha managed primarily for biodiversity conservation since 1997 (Fig. 1) (Department for Environment and Heritage 2008). The vegetation is characterised by eucalypt-dominated mallee shrubland (i.e. vegetation dominated by *Eucalyptus* spp. with a multi-stemmed growth form). Common canopy species include *Eucalyptus dumosa*, *E. socialis*, *E. leptophylla*, *E. gracilis* and *E. oleosa*. The hummock grass,

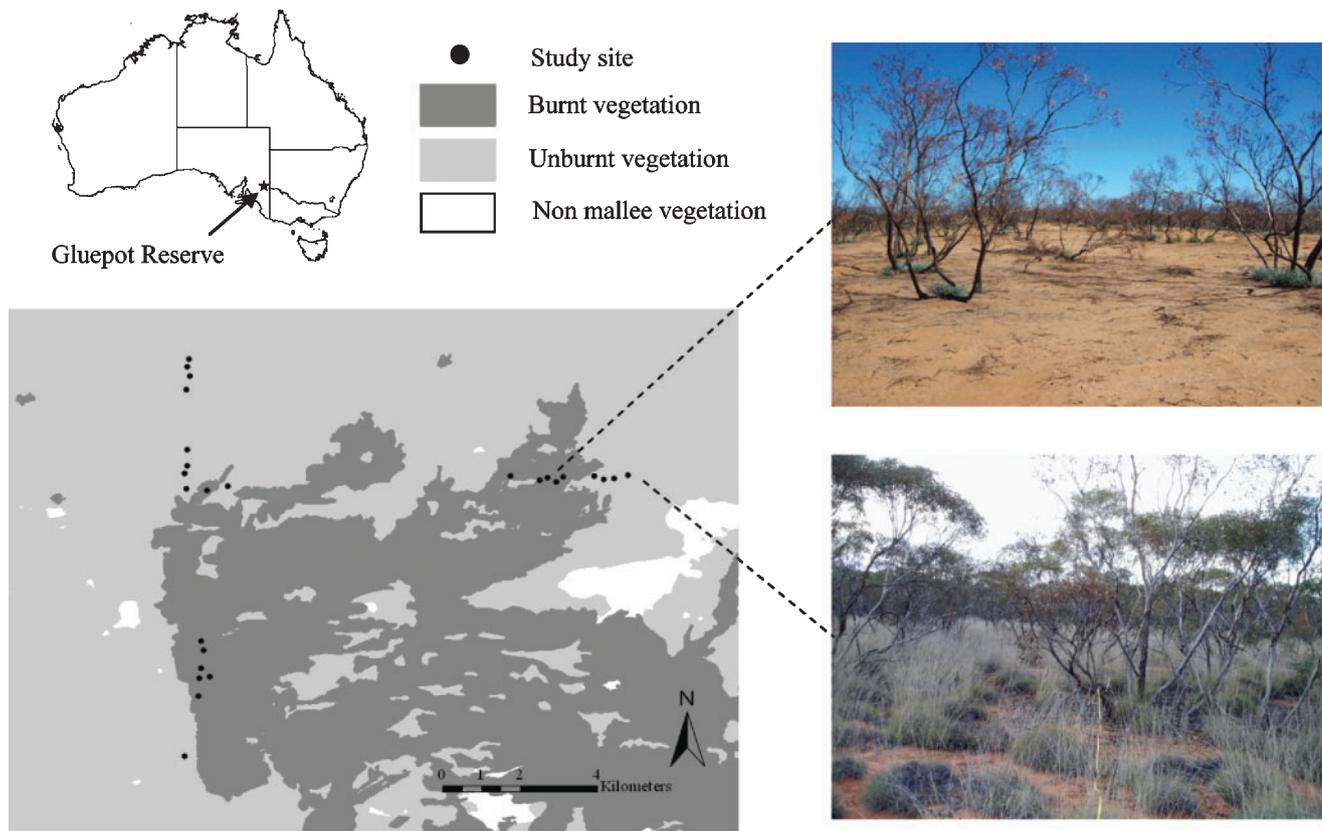


Fig. 1. The location of Gluepot Reserve, South Australia (33.76°S, 140.13°E). Recently burnt vegetation is shown in the top right (photograph taken 4 months post-fire), and unburnt vegetation is shown in the bottom right (photograph of vegetation >35 years post-fire).

Triodia scariosa, is widespread on sandy soils, whereas *Maireana* spp., *Atriplex* spp. and *Zygophyllum* spp. are common understorey species on soils with a heavier texture. Mallee eucalypts are the primary source of surface fuel and flammable *Triodia* hummocks play a major role in fire spread (Bradstock and Cohn 2002). The wildfire of December 2006 burnt 8000 ha within Gluepot Reserve. Previous wildfires in the region occurred in 1917 and in the 1950s (Department for Environment and Heritage 2008). Mean annual rainfall is 229 mm. Mean daily maximum temperature in summer is 33°C and temperatures >40°C are common. Winters are mild (mean daily maximum temperature 18°C) (Australian Bureau of Meteorology, <http://www.bom.gov.au/>).

Study design and analysis

Small-mammal surveys were conducted at 26 sites (14 unburnt and 12 burnt). Each site was surveyed five times, including November 2006 (pre-fire), February 2007 (3 months post-fire), October 2007 (11 months post-fire), November/December 2007 (12 months post-fire) and January/February 2008 (14 months post-fire). We established a line of pitfall traps comprising 10 20-L plastic buckets, spaced 5 m apart, connected by a continuous 300-mm-high flywire drift-fence at each site. Each survey period consisted of five consecutive nights of trapping and the traps were checked daily. Elliot traps (33 × 10 × 10 cm) were used to complement pitfall surveys in the spring sampling periods of November 2006, October 2007 and November/December 2007. On these occasions, five Elliot box traps were placed adjacent to the pitfall line at each site. Hair clipping was used to identify recaptures during each survey period and small mammals were released at the point of capture. Elliot traps were not employed in January/February sampling periods to ensure the welfare of animals during months with high daily temperatures. The mean distance between neighbouring sites was 0.3 km (range = 0.2–1.6 km) and all sites were located >50 m from access tracks. We completed a total of 6500 pitfall trap-nights and 1950 Elliot trap-nights.

We measured several key attributes of vegetation structure at each site, assessed once in August 2007 (9 months post-fire). Ground cover (litter, bare ground and herbs) and the presence of *Triodia* hummocks were recorded at 1-m intervals on a 50-m transect at each site. Attributes of mallee eucalypts encountered on the transect were measured (stem diameter and the presence of stems with hollows). Logs (woody debris >10 cm in diameter) were counted on an adjoining 50 × 10 m belt transect. Average canopy height was estimated for the dominant eucalypt cohort at each site. Mallee shrubland comprises several local vegetation types. However, here we retain the use of this broad vegetation association because exploratory analysis indicated that a further division of sites on the basis of vegetation types, or spatial location, was uninformative at the scale of the present study.

For each survey period, we calculated the proportion of sites at which a species was present in each fire-history category (unburnt or burnt). We quantified the response to fire of each species by using Fisher's exact test of independence (Crawley 2007), testing the null hypothesis that the proportion of sites at which a species was present is the same in each fire category. We carried out this test for each species, for each survey period for which the species

was captured at four or more sites in either fire category (i.e. the minimum number of sites required to demonstrate a significant result).

We examined how species richness responded to fire by using a generalised linear mixed model (GLMM) with Poisson errors and a log-link function (Zuur *et al.* 2009). Species richness, the response variable, was the number of species of native small mammals recorded at each site for each post-fire survey period. Site was entered as a random effect in the regression model to account for repeated-measures at the same site, which can lead to non-independent error structure in the data (Zuur *et al.* 2009). Fire history was entered into the model as a categorical predictor variable (unburnt or burnt). We present the estimated parameter coefficient, standard error, *t*-value (i.e. the parameter coefficient divided by its standard error) and corresponding *P*-value for this model (Zuur *et al.* 2009). We quantified the response of vegetation structure to fire history by using a Wilcoxon rank-sum test (Crawley 2007). A *P*-value of <0.05 was used to indicate significance in all statistical tests.

In addition, we plotted temporal profiles of each species' response to the wildfire. We examined the percentage of burnt and unburnt sites at which each species was present for each survey period. We also plotted the total number of native small-mammal species captured in each fire category for each survey period. These qualitative results complement statistical models.

Statistical analysis was undertaken in the R statistical package version 2.10.1 (R Development Core Team 2009). GLMMs were run in the extension package MASS version 7.3-5 (Venables and Ripley 2002).

Results

Vegetation structure

The wildfire had a marked effect on vegetation structure (Fig. 1). Hummock grass was not recorded at recently burnt sites (Table 1). In contrast, the mean cover of *Triodia* hummocks at unburnt sites was ~19%. Litter cover, large trees and canopy height had greater values at unburnt sites. At burnt sites, the extent of bare ground was much higher than it was at unburnt sites (Table 1). A low level of herb cover was recorded in recently burnt areas, whereas herbs were not recorded from unburnt sites (Table 1).

Small mammals

Fauna surveys resulted in 291 captures of five mammal species. The small-mammal assemblage was composed of the following: two species of insectivorous/carnivorous marsupials, the mallee ningaui, *Ningaui yvonneae* (139 captures at 22 sites), and common dunnart, *Sminthopsis murina* (21 captures at 13 sites); an insectivore/nectarivore, the western pygmy possum, *Cercartetus concinnus* (75 captures at 24 sites); an omnivorous rodent, Bolam's mouse, *Pseudomys bolami* (4 captures at 4 sites); and an omnivorous introduced rodent, the house mouse, *Mus domesticus* (52 captures at 18 sites). We did not undertake statistical analyses on *P. bolami* because it was captured at few sites.

Ningaui yvonneae was present before the fire at a similar proportion of the sites as after fire, which later were classified as unburnt and burnt sites (64% and 67%, respectively) (*P* = 1.00).

Table 1. Comparison of vegetation characteristics at unburnt and burnt sites (mean ± s.d.)

Difference = (mean value at unburnt sites) – (mean value at burnt sites). n.a., not assessed with Wilcoxon test because of low data values

Vegetation characteristic	Measure	Unburnt (n = 14)	Burnt (n = 12)	Difference	P
Bare ground	%cover	25.7 ± 11.4	82.8 ± 11.1	-57.1	<0.0001
Litter	%cover	31.0 ± 8.7	8.7 ± 8.4	22.3	<0.0001
Herbs	%cover	0.0 ± 0.0	1.9 ± 2.2	-1.9	n.a.
Hummock grass	%cover	19.1 ± 13.3	0.0 ± 0.0	19.1	<0.001
Logs	Number per hectare	20.0 ± 28.3	10.0 ± 18.1	10	0.461
Mallee tree stems	Maximum diameter of living stems >1.5 cm	12.3 ± 4.5	0.0 ± 0.0	12.3	<0.0001
Canopy height	Average height (m)	4.7 ± 0.9	0.6 ± 0.2	4.1	<0.0001
Hollow stems	Proportion of stems with hollows	0.1 ± 9.6	0.0 ± 1.9	0.1	n.a.

Following the wildfire, this species was not recorded at a single burnt site (Fig. 2A). It remained common at unburnt sites, occurring at 43–93% of these sites over the four post-fire surveys (Fig. 2A). Fisher’s exact test confirmed this pronounced decline, with *N. yvonneae* present at a lower proportion of surveys at burnt sites than at unburnt sites. This pattern was evident across all post-fire survey periods, i.e. at 3 months post-fire ($P < 0.0001$), 11 months post-fire ($P = 0.002$),

12 months post-fire ($P = 0.017$) and 14 months post-fire ($P < 0.0001$).

Before the wildfire, *Mus domesticus* was present at 36% of unburnt sites and 33% of later-burnt sites ($P = 1.00$). Three months post-fire, the percentage occurrence of *M. domesticus* was higher in recently burnt vegetation (42%) than in unburnt vegetation (21%), although this difference was not significant ($P = 0.401$). In surveys undertaken at 11, 12 and

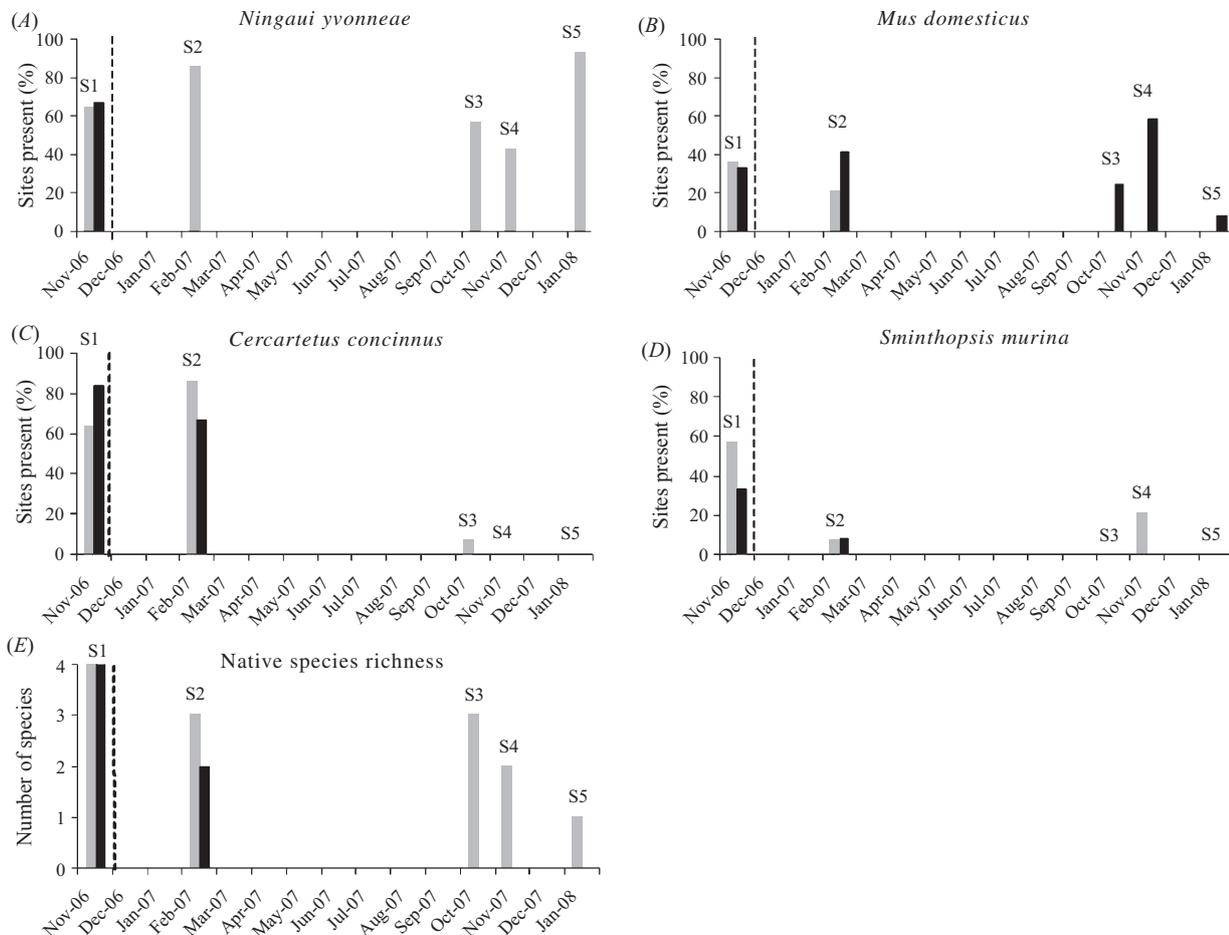


Fig. 2. (A–D) Temporal profiles of species presence at unburnt (grey bars) and burnt (black bars) sites during the survey period: S1, pre-fire; S2, 3 months post-fire; S3, 11 months post-fire; S4, 12 months post-fire; and S5, 14 months post-fire. (E) Species richness of native small mammals. A dashed line separates pre- and post-fire surveys.

14 months post-fire, *M. domesticus* was captured only in burnt areas, reaching a peak occurrence of 58% of burnt sites 12 months post-fire (Fig. 2B). Fisher's exact test confirmed that *M. domesticus* was positively associated with burnt sites 12 months post-fire ($P=0.001$). Comparisons were not made for this species at survey periods 11 and 14 months post-fire because of the low numbers of animals captured. *M. domesticus* was the only species regularly captured in Elliot traps. This survey method was used (in addition to pitfall traps) in Survey periods 1, 3 and 4 only. Consequently, the lower capture rates of *M. domesticus* 14 months post-fire (Fig. 2B) may be a result of reduced survey effort for this species.

Cercartetus concinnus was common at all sites before the wildfire (64% and 83% of later-burnt and unburnt sites, respectively) ($P=0.391$). Three months post-fire, there was a slight decrease in percentage occurrence at sites that were burnt, and an increase at unburnt sites (Fig. 2C); however, this difference was not significant ($P=0.365$). Notably, *C. concinnus* was still present at 67% of burnt sites at this time. Surveys undertaken at 11, 12 and 14 months post-fire indicated a marked decline in records of *C. concinnus* across all sites. We do not attribute this overall decline to the wildfire (see Discussion).

Sminthopsis murina was captured most frequently in the first survey period, occurring at 33% and 57% of later-burnt and unburnt sites, respectively ($P=0.267$). During Surveys 2, 3 and 4, it was relatively uncommon at all sites and we did not undertake statistical analysis. However, we note that between 11 and 14 months after fire, *S. murina* was not captured in recently burnt vegetation, whereas it was recorded at 20% of unburnt sites 12 months post-fire (Fig. 2D).

Regression modelling indicated that species richness of native small mammals was positively associated with unburnt vegetation (parameter estimate = 1.69, s.e. = 0.27, t -value = 6.17, $P < 0.0001$). Although this result was largely driven by the negative response of *N. yvonneae* to burnt sites, we did not capture a single native small mammal at burnt sites in the last three survey periods (11, 12 and 14 months post-fire) (Fig. 2E). Conversely, *N. yvonneae*, *C. concinnus*, *S. murina* and *P. bolami* were each captured at unburnt sites at this time (Fig. 2E).

Discussion

The present study is one of the first to document the response to wildfire of a semiarid small-mammal community in Australia. It provides clear evidence that fire has a strong influence on small-mammal assemblages in semiarid mallee shrublands. The occurrence of *N. yvonneae* and the species richness of native small mammals were both positively associated with unburnt vegetation. The introduced *M. domesticus* was the only species to show a positive association with recently burnt vegetation.

Small-mammal responses to wildfire

Previous studies of the habitat requirements of *N. yvonneae* have reported a consistent positive association with the cover of hummock grass (Bennett *et al.* 1989; Bos *et al.* 2002), and have shown that the species regularly forages in ground litter (Bos and Carthew 2003). *N. yvonneae* breeds predictably in spring each year, with females producing up to seven young in a single litter. Individuals rarely participate in a second breeding season

(A. F. Bennett, unpubl. data; Bos and Carthew 2001). Thus, *N. yvonneae* has relatively specific habitat requirements and a restricted life history. *N. yvonneae* was not recorded at any sites burnt by wildfire, despite survey effort continuing up to 14 months post-fire. This response is likely to be driven by post-fire changes in vegetation structure. *Triodia* hummocks and ground litter covered extensive areas of unburnt vegetation, whereas both were much reduced at recently burnt sites. Hummock grass offers a range of resources to *N. yvonneae*, including food, shelter, protection from predators and a suitable microclimate (Bos *et al.* 2002; Bos and Carthew 2003).

Mus domesticus was positively associated with recently burnt vegetation. Higher capture rates were apparent 3 months post-fire and remained relatively high during all post-fire surveys. Recently burnt sites were characterised by large areas of bare ground, reduced canopy cover and the presence of ephemeral herbs and grasses. *M. domesticus* is well documented as a coloniser of recently burnt vegetation in temperate Australia (Fox 1996; Recher *et al.* 2009). Interestingly, the positive relationship between *M. domesticus* and recently burnt vegetation does not appear to extend to central Australia, where the species is generally uncommon during periods of average or below-average rainfall (Masters 1993; Southgate and Masters 1996).

Recently burnt vegetation in mallee shrubland may provide *M. domesticus* with enhanced foraging opportunities; it has an omnivorous diet and is likely to feed on the ephemeral herbs and grasses which become available following fire (Land Conservation Council 1987; Cohn *et al.* 2002). It has a flexible life history, characterised by a high reproductive potential: opportunistically breeding females can produce several litters of 4–9 young per year in agricultural areas of semiarid Australia (Singleton *et al.* 2001). It can excavate and live in burrows in areas of limited vegetation cover (Menkhorst 1996), so sparse vegetation cover may not be an impediment to persisting at burnt sites. Individuals of *M. domesticus* are also capable of making long-range movements (up to 1 km: Chambers *et al.* 2000). Pocock *et al.* (2005) noted that *M. domesticus* individuals are often 'pulled' towards more suitable habitat. This may explain why the species was not captured in unburnt vegetation in the final three survey periods, whereas it was regularly encountered in the immediate post-fire environment.

The relationship between *C. concinnus* and wildfire was less conclusive. *C. concinnus* was common at all sites before the wildfire, and 3 months post-fire it was still captured at several burnt sites. While this demonstrates that individuals persisted in the post-fire environment for up to 3 months, numbers were markedly reduced at all sites in later surveys, with only one capture (in unburnt vegetation) of the species in three surveys at 11, 12 and 14 months post-fire. This is indicative of a region-wide change in the abundance over this time period, rather than a negative response to wildfire. Short-term changes in the capture rates of this species have been recorded in other areas of semiarid Australia (Carthew *et al.* 2008) and any response to wildfire may have been masked by this broad-scale change. Similarly, *S. murina* and *P. bolami* were captured in low numbers after the fire at all sites, complicating assessment of the effect of wildfire on these species.

Pooling the data to calculate species richness offered additional insights. Species richness of native small mammals was positively associated with unburnt vegetation. No native small mammals were captured in burnt vegetation over the last three survey periods (11, 12 and 14 months post-fire) despite a survey effort of 2400 pitfall trap-nights and 900 Elliot trap-nights at this time, whereas each of *N. yvonneae*, *C. concinnus*, *S. murina* and *P. bolami* was captured in unburnt vegetation during this time.

Comparisons between mallee shrubland and hummock grassland

Spinifex is a prominent feature of both mallee shrublands and hummock grasslands. Several genera of native small mammals are common to the two vegetation types, including *Ningauai*, *Sminthopsis* and *Pseudomys* (Van Dyck and Strahan 2008). In the grasslands of arid central Australia, a series of studies examined the response of small-mammal communities to broad-scale wildfire (Letnic *et al.* 2004, 2005; Letnic and Dickman 2005). Several species displayed a preference for long-unburnt vegetation (e.g. desert mouse, *Pseudomys desertor*), whereas other species appeared largely unaffected by fire (Letnic and Dickman 2005; Letnic *et al.* 2005). Letnic *et al.* (2005) reported that wildfire had a large impact on arid-zone vegetation, and attributed the negative association of *P. desertor* with recently burnt areas to the reduced cover of hummock grass. The Wongai ningauai, *Ningauai ridei*, also typically preferred older sites where hummock grass is common (Letnic *et al.* 2004). We observed a similar pattern. Small-mammal species dependent on the cover of spinifex appear to be particularly sensitive to large wildfire events in both mallee shrubland and hummock grassland.

Fire responses and life-history characteristics

Friend (1993) concluded that the fire-response patterns of small mammals are closely related to their shelter, food and breeding requirements. According to this hypothesis (Friend 1993), we expected that small mammals displaying a negative short-term response to wildfire would have specific habitat requirements and a restricted life history. In addition, species associated with the immediate post-fire environment would more likely be generalist omnivores with a flexible life history. Our results supported this hypothesis. The species most strongly affected by wildfire, *N. yvonneae*, has the most specific habitat requirements and restricted life history of the small-mammal assemblage in the study area (Bennett *et al.* 1989). Further, the only species positively associated with recently burnt vegetation, *M. domesticus*, has a generalist diet, a high reproductive potential and the ability to excavate burrows in a range of vegetation formations.

These results indicated that there is merit in pursuing the framework outlined by Friend (1993). However, for several species, we were unable to determine clear responses to wildfire. In part, this is likely to be a result of the low densities of small mammals recorded during much of our study. Low capture rates are typical of small-mammal communities in semiarid Australia (Bennett *et al.* 1989). Nevertheless, we have focussed here on comparisons between relatively simple and discrete representations of the post-fire environment, namely

burnt and unburnt vegetation. Further development of a framework to predict small-mammal responses to fire in mallee shrublands would be aided by examining (1) responses to fire regimes over extended temporal scales, (2) the influence of spatial aspects of fire history on small mammals and (3) the movement, behaviour and reproductive status of individuals in relation to fire history. In addition, it is likely that other processes, such as rainfall and predation, will be relevant to understanding and predicting small-mammal distribution in mallee shrublands (Letnic and Dickman in press). For example, in the present study, species richness of native small mammals was highest in unburnt vegetation during Survey period 1, which was preceded by a 24-month cumulative rainfall total of 559 mm. By contrast, species richness was much reduced in Survey period 5, which was preceded by a 24-month cumulative rainfall total of 395 mm (Australian Bureau of Meteorology, <http://www.bom.gov.au/>).

Management implications

Recently burnt mallee vegetation is unsuitable as habitat for *N. yvonneae* and has a reduced number of species of native small mammals. In addition, wildfire has a strong immediate impact on key components of mallee vegetation, including a reduction in the cover of *Triodia* hummocks, leaf litter and mallee eucalypts. This is an important first step in developing an understanding of how small mammals respond to wildfire in mallee shrublands. Fire is widely used as a management tool in mallee ecosystems, to protect natural and built assets, to restrict the size of wildfires and to maintain habitat for species dependent on particular seral stages (Bradstock and Cohn 2002; Sandell *et al.* 2006). The results of the present study have indicated that maintaining sources for recolonisation after large-scale wildfires (i.e. unburnt patches of vegetation) will be vital to the conservation of native small mammals in mallee ecosystems.

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References

- Australian Native Vegetation Assessment (2001). 'Australian Native Vegetation Assessment.' (National Land and Water Resources Audit and Commonwealth of Australia: Canberra.)
- Bennett, A. F., Lumsden, L. F., and Menkhorst, P. W. (1989). Mammals of the mallee region of south-eastern Australia. In 'Mediterranean Landscapes in Australia: Mallee Ecosystems and their Management'. (Eds J. C. Noble and R. A. Bradstock.) pp. 191–220. (CSIRO: Melbourne.)

- Bennett, A. F., Lumsden, L. F., and Menkhorst, P. W. (2006). Mammals of the mallee region, Victoria: past, present and future. *Proceedings of the Royal Society of Victoria* **118**, 259–280.
- Bos, D. G., and Carthew, S. M. (2001). Population ecology of *Ningaii yvonneae* (Dasyuridae: Marsupialia) in the Middleback Ranges, Eyre Peninsula, South Australia. *Wildlife Research* **28**, 507–515. doi:10.1071/WR00021
- Bos, D. G., and Carthew, S. M. (2003). The influence of behaviour and season on habitat selection by a small mammal. *Ecography* **26**, 810–820. doi:10.1111/j.0906-7590.2003.03584.x
- Bos, D. G., Carthew, S. M., and Lorimer, M. F. (2002). Habitat selection by the small dasyurid *Ningaii yvonneae* (Marsupialia: Dasyuridae) in South Australia. *Austral Ecology* **27**, 103–109. doi:10.1046/j.1442-9993.2002.01163.x
- Bowman, D. M. J. S., Balch, J. K., Artaxo, P., Bond, W. J., Carlson, J. M., et al. (2009). Fire in the earth system. *Science* **324**, 481–484. doi:10.1126/science.1163886
- Bradstock, R. A. (1989). Dynamics of a perennial understorey. In 'Mediterranean Landscapes in Australia: Mallee Ecosystems and their Management'. (Eds J. C. Noble and R. A. Bradstock.) pp. 141–154. (CSIRO: Melbourne.)
- Bradstock, R. A., and Cohn, J. S. (2002). Fire regimes and biodiversity in semi-arid mallee ecosystems. In 'Flammable Australia: The Fire Regimes and Biodiversity of a Continent'. (Eds R. A. Bradstock, J. E. Williams and M. A. Gill.) pp. 238–258. (Cambridge University Press: Cambridge, UK.)
- Brown, S., Clarke, M., and Clarke, R. (2009). Fire is a key element in the landscape-scale habitat requirements and global population status of a threatened bird: the mallee emu-wren (*Stipiturus mallee*). *Biological Conservation* **142**, 432–445. doi:10.1016/j.biocon.2008.11.005
- Carthew, S. M., Cadzow, B. R., and Foulkes, J. N. (2008). Western pygmy-possum *Cercartetus concinnus*. In 'The Mammals of Australia'. (Eds S. Van Dyck and R. Strahan.) pp. 215–217. (New Holland Publishers: Sydney.)
- Chambers, L. K., Singleton, G. R., and Krebs, C. J. (2000). Movements and social organization of wild house mice (*Mus domesticus*) in the wheatlands of northwestern Victoria, Australia. *Journal of Mammalogy* **81**, 59–69. doi:10.1644/1545-1542(2000)081<0059:MASOOW>2.0.CO;2
- Cohn, J. S., Bradstock, R. A., and Burke, S. (2002). Effects of time since fire, topography and resprouting eucalypts on ephemeral understorey species composition, in semi-arid mallee communities in NSW. *Cunninghamia* **7**, 579–600.
- Crawley, M. J. (2007). 'The R Book.' (Wiley: Chichester, UK.)
- Department for Environment and Heritage (2008). 'Bookmark Mallee Fire Management Plan.' (Department for Environment and Heritage: Adelaide.)
- Dickman, C. R., Pressey, R. L., Lim, L., and Parnaby, H. E. (1993). Mammals of particular conservation concern in the western division of New South Wales. *Biological Conservation* **65**, 219–248. doi:10.1016/0006-3207(93)90056-7
- Fox, B. J. (1996). Long-term studies of small-mammal communities from disturbed habitats in eastern Australia. In 'Long-term Studies of Vertebrate Communities'. (Eds M. L. Cody and J. A. Smallwood.) pp. 467–501. (Academic Press: San Diego, CA.)
- Friend, G. R. (1993). Impact of fire on small vertebrates in mallee woodlands and heathlands of temperate Australia: a review. *Biological Conservation* **65**, 99–114. doi:10.1016/0006-3207(93)90439-8
- Land Conservation Council (1987). Report on the mallee area review. Land Conservation Council, Victoria, Melbourne.
- Letnic, M., and Dickman, C. R. (2005). The responses of small mammals to patches regenerating after fire and rainfall in the Simpson Desert, central Australia. *Austral Ecology* **30**, 24–39. doi:10.1111/j.1442-9993.2004.01410.x
- Letnic, M., and Dickman, C. R. (In press). Resource pulses and mammalian dynamics: conceptual models for hummock grasslands and other Australian desert habitats. *Biological Reviews of the Cambridge Philosophical Society*. doi:10.1111/j.1469-185X.2009.00113.x
- Letnic, M., Dickman, C. R., Tischler, M. K., Tamayo, B., and Beh, C. L. (2004). The responses of small mammals and lizards to post-fire succession and rainfall in arid Australia. *Journal of Arid Environments* **59**, 85–114. doi:10.1016/j.jaridenv.2004.01.014
- Letnic, M., Tamayo, B., and Dickman, C. R. (2005). The responses of mammals to La Niña (El Niño Southern Oscillation)-associated rainfall, predation, and wildfire in central Australia. *Journal of Mammalogy* **86**, 689–703. doi:10.1644/1545-1542(2005)086[0689:TRO MTL]2.0.CO;2
- Lunney, D. (2001). Causes of the extinction of native mammals of the western division of New South Wales: an ecological interpretation of the nineteenth century historical record. *The Rangeland Journal* **23**, 44–70. doi:10.1071/RJ01014
- Masters, P. (1993). The effects of fire-driven succession and rainfall on small mammals in spinifex grassland at Uluru National Park, Northern Territory. *Wildlife Research* **20**, 803–813. doi:10.1071/WR9930803
- Menkhorst, P. W. (1996). House mouse *Mus musculus*. In 'Mammals of Victoria'. (Ed. P. W. Menkhorst.) pp. 210–212. (Oxford University Press: Melbourne.)
- Menkhorst, P. W., and Bennett, A. F. (1990). Vertebrate fauna of mallee vegetation in southern Australia. In 'The Mallee Lands: A Conservation Perspective'. (Eds J. C. Noble, P. J. Joss and G. K. Jones.) pp. 39–53. (CSIRO Publishing: Melbourne.)
- Noble, J. C., and Vines, R. G. (1993). Fire studies in mallee (*Eucalyptus* spp.) communities of western New South Wales: grass fuel dynamics and associated weather patterns. *The Rangeland Journal* **15**, 270–297. doi:10.1071/RJ9930270
- Pausas, J. G., and Bradstock, R. A. (2007). Fire persistence traits of plants along a productivity and disturbance gradient in Mediterranean shrublands of south-east Australia. *Global Ecology and Biogeography* **16**, 330–340. doi:10.1111/j.1466-8238.2006.00283.x
- Pocock, M. J. O., Hauffe, H. C., and Searle, J. B. (2005). Dispersal in house mice. *Biological Journal of the Linnean Society, London* **84**, 565–583. doi:10.1111/j.1095-8312.2005.00455.x
- R Development Core Team (2009). 'R: A Language and Environment for Statistical Computing.' (R Foundation for Statistical Computing: Vienna.)
- Recher, H. F., Lunney, D., and Matthews, A. (2009). Small mammal populations in a eucalypt forest affected by fire and drought. 1. Long-term patterns in an era of climate change. *Wildlife Research* **36**, 143–158. doi:10.1071/WR08086
- Sandell, P., Tolhurst, K., Dalton, J., Scott, B., and Smith, M. (2006). Fire management prescriptions for the Victorian Mallee parks. *Proceedings of the Royal Society of Victoria* **118**, 395–412.
- Seebeck, J., and Menkhorst, P. (2000). Status and conservation of the rodents of Victoria. *Wildlife Research* **27**, 357–369. doi:10.1071/WR97055
- Singleton, G., Krebs, C. J., Davis, S., Chambers, L., and Brown, P. (2001). Reproductive changes in fluctuating house mouse populations in southeastern Australia. *Proceedings of the Royal Society of London. Series B. Biological Sciences* **268**, 1741–1748. doi:10.1098/rspb.2001.1638
- Southgate, R., and 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. doi:10.1071/WR9960289
- Tulloch, A. (2004). The importance of food and shelter for habitat use and conservation of the burramyids in Australia. In 'The Biology of Australian Possums and Gliders'. (Eds R. L. Goldingay and S. M. Jackson.) pp. 268–284. (Surrey Beatty: Sydney.)

- Turner, D., Ostendorf, B., and Lewis, M. (2008). An introduction to patterns of fire in arid and semi-arid Australia, 1998–2004. *The Rangeland Journal* **30**, 95–107. doi:[10.1071/RJ07039](https://doi.org/10.1071/RJ07039)
- Van Dyck, S., and Strahan, R. (Eds) (2008). 'The Mammals of Australia.' (New Holland Publishers: Sydney.)
- Venables, W. N., and Ripley, B. D. (2002). 'Modern Applied Statistics with S.' 4th edn. (Springer: New York.)
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., and Smith, G. M. (2009). 'Mixed Effects Models and Extensions in Ecology with R.' (Springer: London.)

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