Amplified predation after fire suppresses rodent populations in Australia's tropical savannas

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Abstract

Context. Changes in abundance following fire are commonly reported for vertebrate species, but the mechanisms causing these changes are rarely tested. Currently, many species of small mammals are declining in the savannas of northern Australia. These declines have been linked to intense and frequent fires in the late dry season; however, why such fires cause declines of small mammals is unknown.

Aims. We aimed to discover the mechanisms causing decline in abundance of two species of small mammals, the pale field rat, *Rattus tunneyi*, and the western chestnut mouse, *Pseudomys nanus*, in response to fire. Candidate mechanisms were (1) direct mortality because of fire itself, (2) mortality after fire because of removal of food by fire, (3) reduced reproductive success, (4) emigration, and (5) increased mortality because of predation following fire.

Methods. We used live trapping to monitor populations of these two species under the following three experimental fire treatments: high-intensity fire that removed all ground vegetation, low-intensity fire that produced a patchy burn, and an unburnt control. We also radio-tracked 38 *R. tunneyi* individuals to discover the fates of individual animals.

Key results. Abundance of both species declined after fire, and especially following the high-intensity burn. There was no support for any of the first four mechanisms of population decline, but mortality owing to predation increased after fire. This was related to loss of ground cover (which was greater in the high-intensity fire treatment), which evidently left animals exposed to predators. Also, local activity of two predators, feral cats and dingoes, increased after the burns, and we found direct evidence of predation by feral cats and snakes.

Conclusions. Fire in the northern savannas has little direct effect on populations of these small mammals, but it causes declines by amplifying the impacts of predators. These effects are most severe for high-intensity burns that remove a high proportion of vegetation cover.

Implications. To prevent further declines in northern Australia, fire should be managed in ways that limit the effects of increased predation. This could be achieved by setting cool fires that produce patchy burns, avoiding hot fires, and minimising the total area burnt.

Introduction

Contemporary fire management seeks to manipulate fire regimes to protect biodiversity and societal values (Parr and Andersen 2006; Driscoll *et al*. 2010). Management of fire to maintain biodiversity will be best accomplished if we understand the mechanisms by which different fire regimes affect plant or animal populations. For animals, in particular, we often have a poor understanding of the nature of the impacts of fire on populations. Although it is often clear that abundance changes in response to fire (Layme *et al*. 2004; Letnic *et al*. 2005; Green and Sanecki 2006; Lindenmayer *et al*. 2008), in most cases, the

demographic processes that lead to these changes in abundance are unknown (Parr and Andersen 2006; Clarke 2008; Driscoll *et al*. 2010; Kelly *et al*. 2012; Zwolak *et al*. 2012).

Northern Australia is currently experiencing rapid declines in many species of native small mammals (Andersen *et al*. 2005; Woinarski *et al*. 2011*a*). Changed fire regimes may be contributing to these declines. In particular, there is evidence that declines of small mammals are exacerbated by a higher frequency of fires in the late dry season. This is presumably because these fires burn at a higher intensity and remove a higher proportion of ground vegetation from larger areas than

do low-intensity fires in the early dry season (Woinarski *et al.* 2004, 2011*a*; Andersen *et al.* 2005; Legge *et al.* 2008; Firth *et al.* 2010). Fires of greater extent may have large impacts on small mammals (Lawes *et al.* 2015, and such fires are more likely in the late dry season. A shift to burning in the early dry season has been promoted to reduce the incidence and extent of late-season wildfires and to create fine-scaled mosaics of burnt and unburnt habitats (Andersen *et al.* 2005; Driscoll *et al.* 2010; Legge *et al.* 2011*b*). Whether such fire management will be effective in slowing or reversing the decline of small mammals is not known because we have little information on the processes by which small mammals respond to contrasting fire regimes.

We investigated behavioural and demographic responses to contrasting fire regimes in two northern rodent species, the pale field rat, *Rattus tunneyi*, and the western chestnut mouse, *Pseudomys nanus*. These species are among many that have recently declined across northern Australia (Braithwaite and Griffiths 1996; Cole and Woinarski 2000; Woinarski *et al.* 2010). Several studies have shown that they decline following fire (White 1992; Andersen *et al.* 2005; Legge *et al.* 2008). For example, Legge *et al.* (2008) recorded a ~90% reduction in trap rates for both species 5 weeks after a large (736 710 ha) late dry-season fire in the central Kimberley.

Several mechanisms could act on individuals to cause declines in populations following fire. First, animals might be killed by the fire itself (Friend 1993); second, mortality might increase because of food shortages caused by fire (Morris *et al.* 2011*a*); third, reproductive success might decline because of shortages of food and other resources essential for reproduction, leading to deficits in recruitment and, thus, population decline (Begg *et al.* 1981; Cockburn *et al.* 1981; Morris *et al.* 2011*b*); fourth, animals might migrate from burnt and into unburnt areas, in response to shortages of food and other resources in burnt areas (Christensen 1980; Morris *et al.* 2011*a*); and fifth, mortality in burnt areas might increase because of higher predation rates, which could be caused by increased vulnerability of individuals to predators in the post-fire environment (Green and Sanecki 2006; Conner *et al.* 2011), or increased activity of predators on burnt areas (Soyumert *et al.* 2010; Birtsas *et al.* 2012; McGregor *et al.* 2014). These mechanisms are not necessarily mutually exclusive, and it is possible that more than one mechanism could affect the same population.

We tested for these mechanisms by monitoring *R. tunneyi* and *P. nanus* through experimental fires with the following two levels of fire intensity: a low-intensity fire that produced a patchy burn typical of a fire in the early dry season, and a more intense fire that removed all ground level vegetation, typical of a fire in the late dry season. To remove effects of season *per se*, we set both fires at the same time of the year, the difference in intensity being a function of conditions at the time each fire was ignited.

We monitored immediate and short-term changes in the relative abundance, age structure, recruitment and body condition of both species through the two fire treatments and in an unburnt control. We also fitted radio-collars to a sample of *R. tunneyi* to detect emigration and local home-range shifts in relation to the fire treatments, and directly monitored individual survival of radio-collared animals to determine the causes and timing of deaths. The study used a before–after control–impact design and fire treatments were not replicated. Previous studies have

already provided several independent tests of the effect of fire on relative abundance of populations of both species (White 1992; Andersen *et al.* 2005; Legge *et al.* 2008). Here, we wanted to intensively monitor a large sample of individuals so as to reveal the factors that operate on individual animals to produce changes at the population level.

Materials and methods

Study area and fire treatments

We worked at Mornington Wildlife Sanctuary (17.55°S, 126.17°E), in the central Kimberley region of Western Australia, between February and July 2013 (Fig. 1). This area has a monsoonal climate, with an average annual rainfall of 750 mm, mostly falling December–February. Mornington is a 320 000 ha former pastoral station managed for conservation by the Australian Wildlife Conservancy. In 2004, a 40 300 ha section of the property was fenced and destocked of introduced herbivores, mainly cattle (Legge *et al.* 2011*a*). The study site was a 45 ha area of open savanna grassland with sparsely distributed trees and shrubs, adjacent to the Fitzroy River in the destocked area (Fig. 1). It was last burnt in the early dry season 2 years before the study.

The study area was divided into three plots of 11.18 ha, 14.35 ha and 19.07 ha for the control, low-intensity burn and high-intensity burn treatments, respectively (Fig. 1). Fires were contained by an existing road and by 5-m wide firebreaks around the perimeters of the plots. The low-intensity burn was started on 4 April under cool, calm conditions and produced a patchy burn of the grass layer. The high-intensity burn was set on 23 April under strong wind conditions, and consumed all grass and most small trees and shrubs. No part of the control plot was burnt.

Vegetation surveys

We measured the structure of the ground-layer vegetation in each plot immediately before burning, 1 month after, and 3 months after burning. Six 10-m^2 permanent quadrats were established in each plot, three in each of two main grass communities characterised by dominance of either *Aristida holathera* or *Chrysopogon fallax*. Ground cover was estimated at three different height intervals (0–10, 10–30 and 30–100 cm) chosen to represent the grass heights likely to be significant for activity of small mammals and their predators, using a modified version of the point–height–intercept technique (Macarthur and Macarthur 1961; Spurr and Warburton 1991). A 1-m pole was held vertically to the ground at 50 random points in each quadrat, and the number of grass or forb stems intercepting the pole at each height interval was estimated and given a value of 0, 1, 3, 5, 8, 10, 15 or 20. Intercept scores were summed across the 50 points at each height interval for each survey quadrat. Aerial photographs of the study site were taken immediately following the high-intensity burn to derive the percentage cover of unburnt patches in each plot, georeferenced to >10 GPS control points using a second-order polynomial in ARCMAP 10 (Environmental System Research Institute Inc., Redlands, CA, USA).

Small-mammal trapping

Populations of small mammals in each plot were surveyed by trapping immediately before burning, 1 week after, and 8 weeks

Fig. 1. Location of the study site on Mornington Wildlife Sanctuary in the far north-west of Australia, the location of fire treatment plots and the distribution of burnt and unburnt patches of vegetation after fire.

after burning. Elliot traps were placed 10–20 m apart along four transects of 10–20 traps, with at least 20 m separating each transect in each plot, and deployed for periods of three to five nights. Additional traps were placed before burning for up to 16 nights around rat burrows to increase the sample of radio-collared *R. tunneyi* individuals (see below). Additional sites were not re-trapped after burning. In total, 481 trap-nights, 389 trap-nights and 510 trap-nights were completed in the before-fire survey and the first and second after-fire surveys, respectively. Traps were baited with rolled oats and peanut butter in the late

afternoon, then checked and closed before sunrise. Animals were temporarily marked by clipping a small patch of fur at different positions, namely, left rear flank, right rear flank or above the tail, for each plot (to minimise handling time, we did not permanently mark individuals). We recorded weight, gender, age class and reproductive status and animals were released at point of capture. Females >60 g and males >65 g were classed as adults for *R. tunneyi*. Females >22 g and males >35 g were classed as adults for *P. nanus* (Braithwaite and Griffiths 1996; Taylor and Calaby 2004*a*, 2004*b*). The study took place during

the breeding season for both species (Braithwaite and Griffiths 1996). Females were deemed to be in breeding condition if they were pregnant or had enlarged teats indicating lactation, and males deemed to be in breeding condition if they had enlarged testes (Braithwaite and Griffiths 1996). Changes in bodyweight after fire compared with the control were used to indicate changes in body condition.

Radio-tracking and survival

During the before-fire trapping session, radio-collars were placed on adult *R. tunneyi* individuals above 68 g (radio-collar <5% of bodyweight) and in good condition. The collars consisted of a Sirtrack© LTD ZV1C 115 VHF transmitter (Sirtrack, New Zealand) with a cable-tie attachment (2.6–3.2 g). When a radio-collared individual left the study, for example, as a result of mortality, another individual in the same plot was trapped and collared, where possible. In total, 38 *R. tunneyi* individuals were radio-collared and tracked from 2 days up to 14 weeks over the 17 weeks of the study, including 11 rats in each of the control and high-intensity plots and 16 in the low-intensity plot. Radio-collared rats were located at least every 3 days. During the day, rats were tracked to their burrows and the burrow location was recorded using GPS. Movements to new burrows were noted and the characteristics of burrows recorded (e.g. under a shrub thicket or grass tussock). Following the fires, burrows were recorded as being either under vegetation cover or in the open.

During the period before fire, rats were also tracked when they were active at night to characterise movement patterns in each treatment plot. Radio-collared rats were approached quietly on foot and a GPS fix was taken as close as possible to the estimated location of the rat. To minimise spatial autocorrelation of successive locations, only two or three fixes were taken per night at intervals of at least 1 h (Puckey *et al.* 2004; Körtner *et al.* 2007). Following the fire treatments, night tracking was minimised to avoid excessive disturbance to the rats. Night tracking was undertaken only to check survival of individuals who had not moved burrow for at least 2 weeks.

Day tracking was used to determine mortality throughout the study, and to place rats into the following four categories: alive at the end of the study; confirmed dead during the study; no signal detected, fate unknown; and collar recovered but fate of rat unknown. If the collar was found on the surface, we attributed mortality when there were either clear signs of predation, the collar was directly under a perch or roost of a bird of prey, or was inside a predator (i.e. a snake). If there were no signs of predation, the rat was classed as 'fate unknown'. If the radio-collar could not be found on the surface, the site was confirmed as a burrow location. If a radio-signal was consistently located at the same burrow location during a 2-week period that included day and night-time tracking, the burrow was excavated. In the event that the collar was found underground but not associated with any remains of the rat, we assumed the rat had slipped the collar over its head and the rat was classed as 'fate unknown'. When no radio-signal could be detected for a collar, a thorough search over a larger area was conducted on foot, by tracking a set grid over the study area. Aerial searches by helicopter were undertaken three times to search for radio-collars that could not be located on foot. A 3 × 3 km area surrounding the study area was flown in a

regularly spaced grid. Four radio-collars were located outside the study area in this way. The remaining radio-collars that could not be found were classed as 'missing' from the last date they were located.

Predator activity

Remote sensor cameras (PC800 infrared sensor cameras, Reconyx, USA) were placed along the road leading through the study site and along the sand banks of the Fitzroy River, parallel to the study site. The aim was to measure changes in local activity of terrestrial mammalian predators (i.e. cats and dingoes) after fire treatments at the scale of the study site, rather than each treatment plot. Cameras were deployed for 2 weeks at the beginning of March, before burning, and then continuously for 8 weeks following the low-intensity burn, from 8 April until 11 June, except for the day on which the high-intensity burn was set. Between three and eight cameras were deployed during these periods, with at least six cameras deployed between April and June. Camera deployment was inconsistent during the study because of technical problems with cameras. Cameras were positioned on trees or stakes with the sensor aimed ~30 cm above the ground, with no baits or lures. The cameras were unlikely to detect avian predators (barn owls *Tyto alba* and boobook owls *Ninox novaeseelandiae*), which were noted in the area from opportunistic auditory and visual observations.

Data analysis

We used permutational multivariate analysis of variance (PERMANOVA) to test for differences in ground-cover scores between plots before fire. A second PERMANOVA tested differences within low-intensity and high-intensity plots at 1 and 3 months after fire, to measure changes in ground cover with fire. Bray–Curtis dissimilarities were computed among plots and permutations were constrained within sessions (before fire, 1 month after fire and 3 months after fire) to account for potential correlations across sessions owing to repeated sampling. PERMANOVAs were run with 9999 permutations using the 'adonis' function of the 'vegan' package in R ver.3.1.2 (R Core Team 2014).

Trapped rats were not individually marked; therefore, the probability of capture (detection probability) was used as a proxy for abundance. The probability of capture was modelled using a binomial general linear model (GLM) as a function of treatment (control, low-intensity fire, high-intensity fire), trap session (before fire, 1 week after fire and 8 weeks after fire) and their interaction. Separate analyses were conducted for each species and age class (adults, subadults). Captures of other species, empty traps and recaptures were recorded as 'failures'. Effects of treatment and trap session on log-transformed adult weights were analysed using a two-way ANOVA. The assumptions of the GLMs and ANOVAs were checked using standard procedures, and the results of the GLMs were visualised using the 'effects' package. All analyses were undertaken using R ver. 3.1.2 (R Core Team 2014).

Home ranges of *R. tunneyi* before fire were calculated by generating minimal convex polygons (MCP) using the Geospatial Modelling Environment (Version 0.7.2.1 in ESRI ARCMAP 10.0), combining day and night fixes (in the control plot, the

before fire period was considered to extend to 23 April). Rats with no night-time fixes, or fewer than three fixes, were excluded. Before fire MCPs were compared between sexes using a one-way ANOVA. For rats tracked both before and after fire ($n = 14$; 7 in the low-intensity plot and 7 in the high-intensity plot), a central location point, or centroid, was calculated from total day- and night-time fixes for the period before and the period after fire. Before the fire, there was a higher proportion of night-time fixes obtained when rats were active; night-time fixes represented 49.5% of total before-fire location fixes. After fire, night-time surveys were minimised to avoid disturbance to rats and potential predators; night-time fixes represented 23% of total after-fire location fixes. The distance between before and after-fire centroids was calculated as a displacement vector and compared with the radius of each individual's before-fire MCP to determine whether a shift in range had occurred following fire. The radius was calculated by treating MCPs as a circle. Individual range shifts were then examined in ARCMAP 10.0, to determine whether rats had moved into or out of burnt areas.

The Cox proportional hazards regression model, implemented in the 'survival' package of R, was used to analyse the distribution of survival times of radio-tracked *R. tunneyi* individuals (Hosmer *et al*. 2008). Rats were classed as either 'alive' or 'dead' at the end of the study. Those individuals that left the study (i.e. 'missing' or 'fate unknown') and those alive at the end of the study were right-censored at the last point that the animal was reliably recorded as alive (e.g. the last location before going missing). Fire treatment was included as a time-dependent covariate. The effect of treatment on mortality was measured at Time t for each individual, where t = number of days since entering the study. The observation period of rats in the burnt plots was split into two time periods, namely, before and after fire. Before fire, the covariate fire treatment was coded as unburnt, and after fire, it was coded as either 'low' or 'high' intensity. Rats in the control plot had one observation period and were classed as 'unburnt' for the entire study. To test whether mortality differed between sexes, a Cox proportional hazards model was run with one time-independent covariate sex for all individuals pooled. The assumption of proportional hazards for the covariates and the model was tested by correlating the corresponding set of scaled Schoenfeld residuals against time (Hosmer *et al*. 2008).

To account for differences in the number of cameras deployed during the study, a standardised activity index was calculated for cats and dingoes for each night of camera deployment as follows: the number of passes of each species per night was divided by the number of cameras deployed for that night. The 10 weeks of camera deployment was divided into five fortnights (a–e) to examine changes in activity before and with time since each fire. The mean standardised activity for each fortnight was compared using a one-way ANOVA for each species, with a square-root transformation to control heteroscedasticity.

Results

Effects of fire on ground-vegetation structure

Before burning, ground-vegetation cover and height did not vary significantly by grass community ($F_{1-12} = -0.0007$, $P = 0.98$),

plot ($F_{2-12} = 0.28$, $P = 0.95$) or their interaction ($F_{2-12} = 0.53$, $P = 0.77$). The two fire treatments had different effects on ground vegetation. The low-intensity fire burnt 78.8% of the plot. Unburnt patches ranged from 64 to 10 913 m^2, with a median patch size of 502 m^2. The high-intensity fire burnt 100% of the plot (Fig. 1). Overall, ground cover was lower in the high-intensity than the low-intensity plot at 1 month and 3 months after fire ($F_{2-24} = 23.61$, $P = 0.0001$). Total ground cover (the combined summed scores for the three height intervals) was 1.9% of pre-burn levels in the high-intensity plot at 1 month after fire and 7.4% at 3 months after fire, compared with 12.7% and 20.3%, respectively, for the low-intensity plot.

Changes in relative abundance and age structure

In total, there were 282 captures of the two species from 1380 trap-nights. *R. tunneyi* were trapped more frequently than were *P. nanus* (166 captures, including 98 within-session recaptures, *versus* 116 captures, including 46 recaptures). Movement of animals among plots within trapping sessions was rare; only nine cases were recorded. Adult and subadult *R. tunneyi* showed different patterns of capture success. For adult *R. tunneyi*, treatment plot had a strong effect on the probability of capture, being highest in the low-intensity fire plot and lowest in the high-intensity fire plot relative to the control ($G^2 = 35.2$, d.f. = 2, $P < 0.001$; Fig. 2). Fire treatment interacted weakly with the capture session ($G^2 = 8.0$, d.f. = 4, $p = 0.09$). In the high-intensity fire plot, the probability of capture success decreased; the odds of capture success were 0.22 times (95% CI: 0.05–0.8) lower at 1 week after fire ($P = 0.03$), and remained low at 8 weeks after fire (Fig. 2). In contrast, the probability of capture success in the control and low-intensity plots remained similar across all trapping sessions (Fig. 2). The probability of capture of subadult rats increased with each successive trapping session ($G^2 = 11.74$, d.f. = 2, $P = 0.002$); odds of capture success were 2.7 (95% CI: 1.13–7.19) times higher in trapping session two and 4.1 (95% CI: 1.88–10.24) times higher in trapping session three. The size of this increase did not depend on the fire treatment (interaction between treatment plot × session: $G^2 = 3.85$, d.f. = 4, $P = 0.43$). The probability of capture of *P. nanus* (pooled across age cohorts) depended on the interaction between trapping session and fire ($G^2 = 14.43$, d.f. = 4, $p = 0.006$). The odds of capture success were 0.23 (95%: 0.05–0.77) times lower 1 week after the high-intensity fire ($P = 0.03$) and remained low at 8 weeks after fire (Fig. 3). There were insufficient captures of subadult *P. nanus* to examine differences in response by age cohorts.

Reproductive condition and bodyweight

Before the fire treatments, 94% of all male and 90% of all female *R. tunneyi* and 75% of male and 71% of female *P. nanus* adults were in breeding condition. For both species, the proportion of adults in breeding condition did not vary with fire treatment. In the second trapping session, the proportion in breeding condition had declined from the beginning of the study across all treatments (63% of male and 32% of female *R. tunneyi*; 50% of male and 18% of female *P. nanus*). By the third trapping session, 8 weeks after the fire, the breeding season had ended for *R. tunneyi*, with no adult females and only 6% of adult males being in breeding condition, whereas for *P. nanus*, 14% of adult

females but no adult males were recorded in breeding condition. Weights of both female and male *R. tunneyi* rats declined significantly over time (females: $F_{2,58} = 0.05$, $P < 0.001$, males: $F_{2,32} = 3.573$, $P = 0.04$), but there was no change in weight attributable to the fire treatments (females: $F_{2,58} = 0.49$, $P = 0.75$, males: $F_{2,32} = 1.1$, $P = 0.39$; Fig. 4). We found no effects of time, treatment or their interaction on weights of

female *P. nanus*. There were insufficient captures of adult male *P. nanus* for analysis.

Movements

During the 17 weeks of the study, 38 *R. tunneyi* rats were radio-collared and tracked over periods from 2 days up to 14 weeks, including 11 rats in each of the control and high-intensity plots
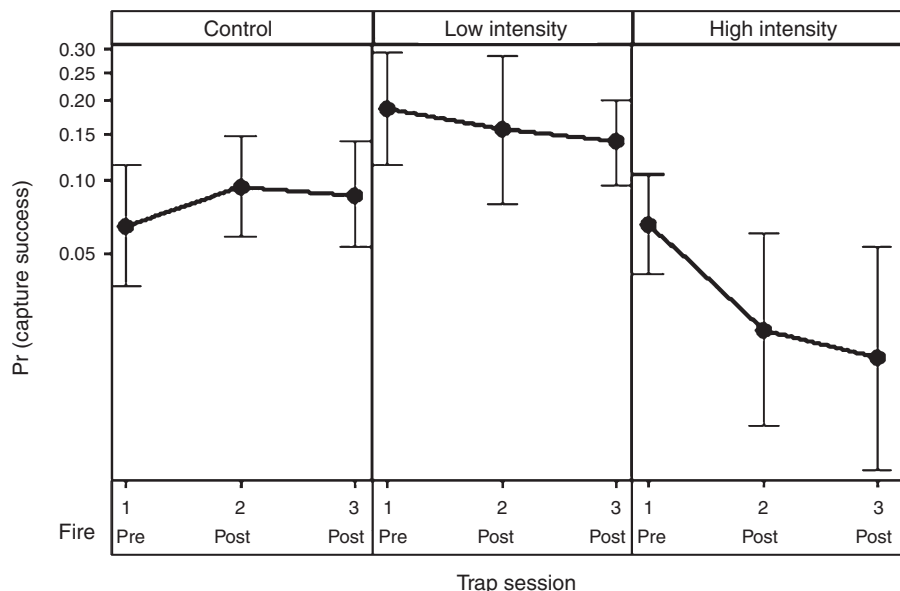

Fig. 2. Probability of capture success for adult *Rattus tunneyi* in three fire-treatment plots at the following three trapping sessions: 1 = before fire, 2 = 1 week after fire, 3 = 8 weeks after fire. Including 95% CI on fitted probabilities. *n* = 166.
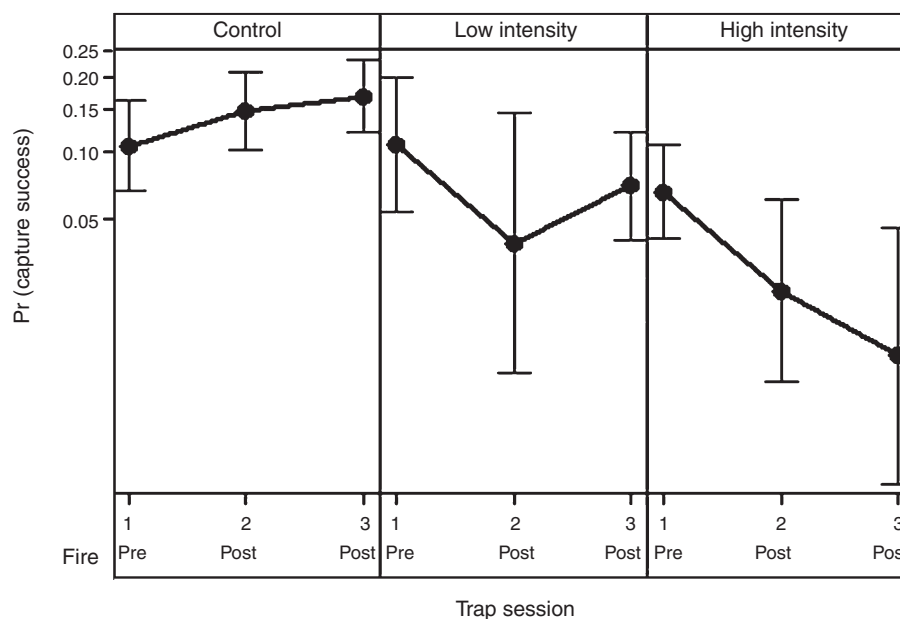

Fig. 3. Probability of capture success for *Pseudomys nanus*, pooled across age classes in three fire-treatment plots in three trapping sessions, where 1 = before fire, 2 = 1 week after fire, 3 = 8 weeks after fire. 95% fitted probabilities included. *n* = 116.
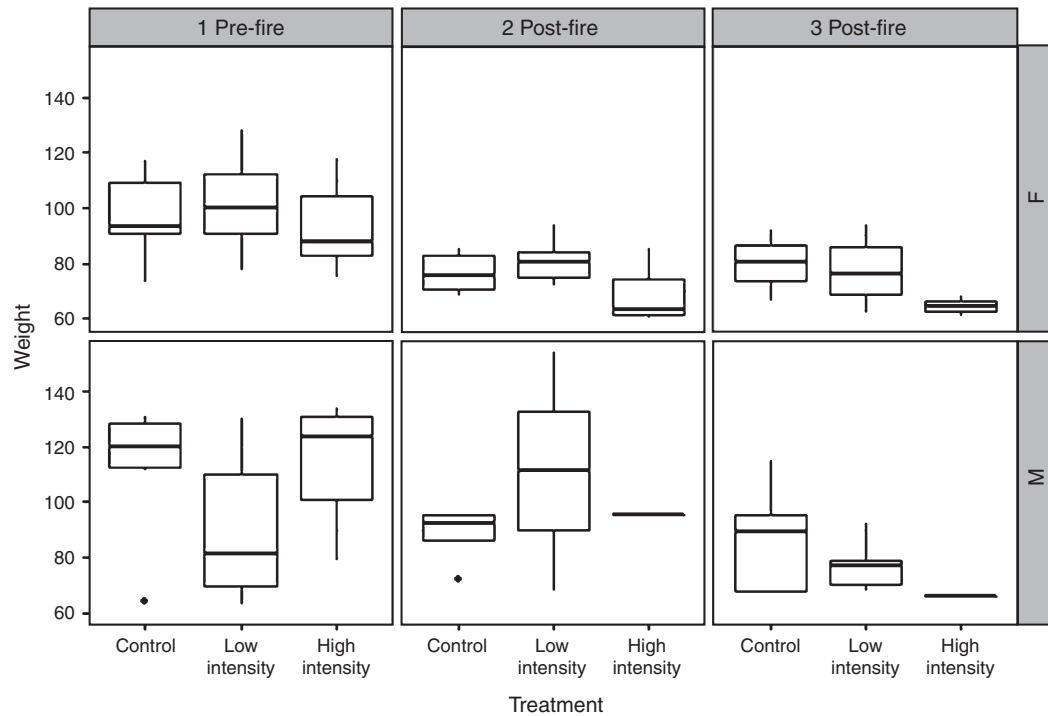
Fig. 4. Mean (± s.e.) weight of male and female *Rattus tunneyi* trapped in three fire-treatment plots in three trapping sessions, where 1 = before fire, 2 = 1 week after fire and three = 8 weeks after fire. Number of female captures = 68, number of male captures = 41.

and 16 in the low-intensity plot. We obtained a total of 892 location fixes, including 520 daytime and 372 night-time fixes. Totals for individual rats included in the analysis ranged from between 6 and 64 fixes, with a median value of 20.5 fixes. Individual rats used several (typically two or three) burrows. They moved short distances to change burrows, and did so every 2–3 weeks. Home ranges before the fire measured over periods of 2–5 weeks ranged from 0.02 to 1.01 ha (total $n = 22$; control = 6, high-intensity plot = 8, low-intensity plot = 8). Males had larger ranges than did females (0.39 ± 0.12 ha, $n = 8$, *versus* 0.09 ± 0.02 ha, $n = 14$; $F_{1,20} = 12.09$, $P = 0.002$). Fourteen individual rats, seven in each of the fire-treatment plots, were tracked both before and after fire. Of these, 12 did not shift their home ranges following the fire (Fig. 5; three rats included in this total did displace their range centroids by more than the radius of the before-fire home range, but by a distance of less than 2 m, which, being within GPS error (~5 m), was not deemed a home-range shift). Of the two rats that did move from the before-fire home range, one resident of the high-intensity plot (Rat 3) shifted its range by 35 m, but this shift resulted in the animal remaining in the high-intensity burned area (Fig. 5). A second rat (Rat 33) shifted its home range 103 m from the control plot into a patch of unburnt vegetation in the low-intensity plot 11 days after fire (Fig. 5). This was the longest movement by a rat during the study.

Survival

No radio-collared rats died during the fires and none showed obvious signs of physiological stress or starvation. There was no evidence of radio-collar failure; no rats were re-trapped with a failed radio-collar and the study ended within the expected life of the radio-transmitters.

In total, we recorded 12 mortalities, all attributed to predation. Eight mortalities (three in the low-intensity plot and five in the high-intensity plot) occurred in the first month after fire (Table 1). Two mortalities were recorded before fire treatments took place, occurring in the high-intensity plot. Two mortalities were recorded in the control plot, in Weeks 7 and 11 of the study. Four rats went missing during the study, but were recovered by helicopter tracking between 400 m and 1.5 km from their last recorded location and recorded as mortalities; the cause of these mortalities was most likely predation by wide-ranging avian predators (Table 1). Six mortalities were attributable to mammalian predators as collars were found in the open, i.e. not under an owl roost or perch branch, and with blood, fur or bone remains surrounding the collar. One mortality was suspected to be caused by a python because the collar was tracked to a tree hollow with evidence of python activity (a shed python skin and snake scat) at the entrance. One radio-collar was tracked to a king brown snake, *Pseudechis australis*, and it was assumed that the snake had eaten the rat. In addition, another 11 rats went missing from the study site and were never recovered. Five of these 11 rats went missing in the first 2 weeks following fire. It is plausible that these rats were also taken by wide-ranging avian predators or they were taken by mammalian predators who subsequently destroyed the radio-collar.

In the time-dependent covariate model, mortality risk in the low-intensity plot increased 4.9 times (95% CI: 0.99–24.31) relative to the unburnt control plot ($\chi^2 = 1.95$, $P = 0.052$). However, the confidence interval includes the null value,
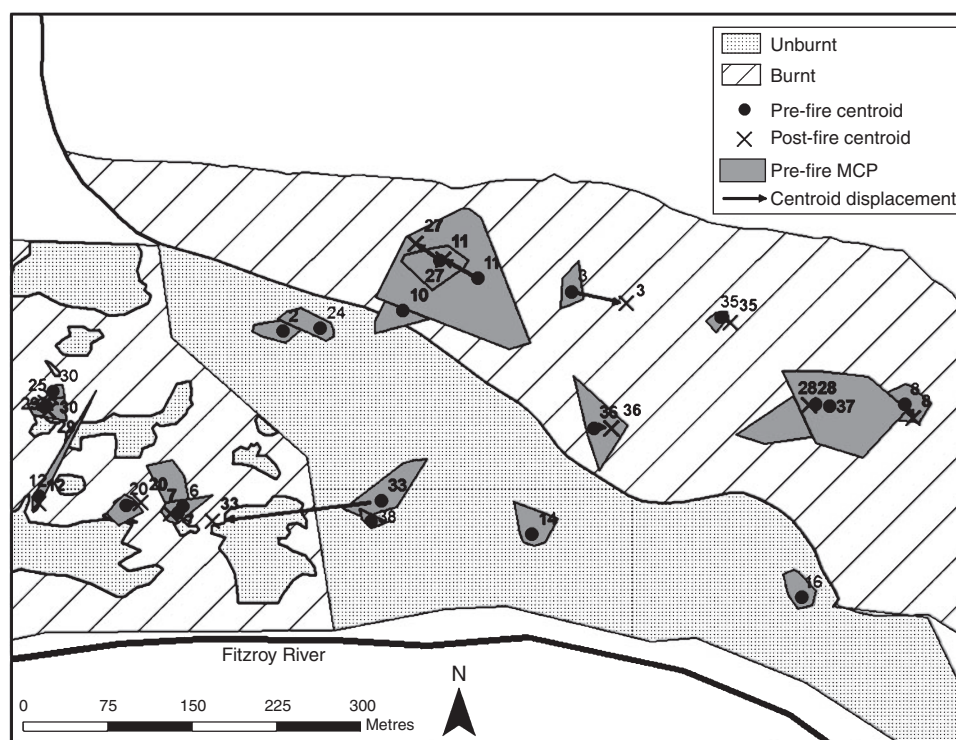
Fig. 5. Minimal convex polygon for *Rattus tunneyi* for a 2–5-week period before fire treatments for 22 animals and centroid displacements between before and after fire-location fixes for 14 animals.

Table 1.   Details of mortalities for 12 radio-collared *Rattus tunneyi*

Low-intensity fire was set on the 4 April 2013, high-intensity fire was set on the 23 April 2014. Date is when the animal was found dead or the date from which it first went missing

Rat ID	Treatment plot	Sex	Date	Comments
10	Control	M	18 April 2013	Matted fur stuck to collar with blood, close to burrow.
1	Control	F	12 May 2013	Fur and bone scattered around collar, 150 m from regular burrow.
20	Low intensity	F	6 April 2013	Missing. Collar located on 26 April 2013 by helicopter, 3 m high inside a hollow branch of a tree across the river from the study site. Python skin and snake scats located in hollow of tree.
9	Low intensity	F	12 April 2013	Body parts and fur remaining next to collar, 30 m from regular burrow.
30	Low intensity	F	15 April 2013	Missing. Collar located on 24 April 2013 by helicopter, 1.5 km from regular burrow.
18	High intensity	M	9 March 2013	Missing. Collar located on 26 April 2013 by helicopter. Located in river, 650 m from regular burrow.
22	High intensity	F	15 March 2013	Skull found next to collar underneath tree, 50 m from regular burrow.
11	High intensity	M	24 April 2013	Located beside river, 382 m from regular burrow directly under owl perch.
3	High intensity	F	28 April 2013	Radio-signal tracked to a king brown snake, *Pseudechis australis*.
8	High intensity	F	1 May 2013	Blood on collar, fur scattered around collar, located in open burnt area, 10 m from regular burrow.
35	High intensity	F	5 May 2013	Blood on collar, open burnt area. Located 50 m from regular burrow.
34	High intensity	M	14 May 2013	Missing. Collar located on 29 May 2013 by helicopter, 515 m from burrow.

suggesting no support for a significant change in mortality risk in the low-intensity plot. Animals in the high-intensity plot had a 20.8 times (95% CI: 4.95–87.47) higher mortality risk than did animals in the control ($\chi^2 = 4.142$, $P < 0.0001$). Males and females had similar mortality risks ($\chi^2 = 0.72$, $P = 0.47$) when individuals were pooled across the treatment plots. Survival was contingent on access to groundcover after fire. All collared rats that survived the first month following fire in the low-intensity plot ($n = 4$) and

in the high-intensity plot ($n = 1$) occupied burrows located under unburnt grass cover or under dense tree-canopy cover.

Activity of mammalian predators

We recorded a total of 36 cat passes and 264 dingo passes on camera traps. Dingo activity was significantly higher during the fortnight immediately after the high-intensity fire and 2 weeks
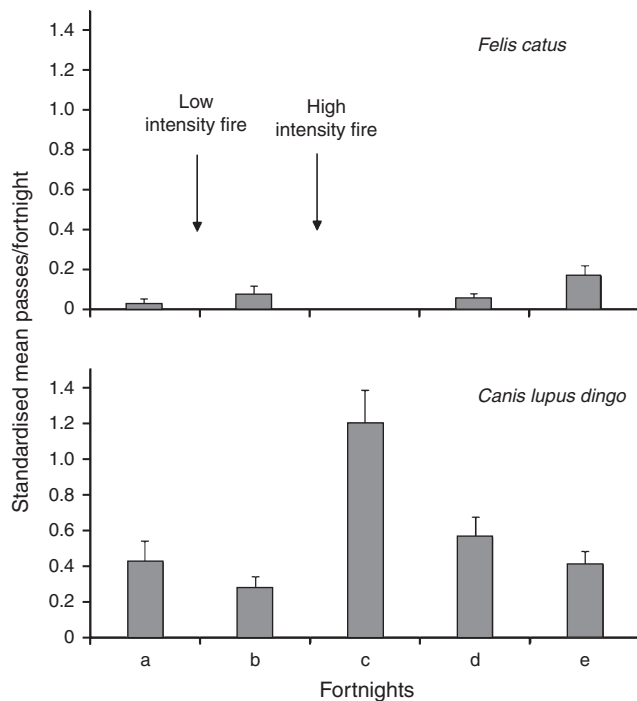
Fig. 6. Mean (+ s.e.) fortnightly cat, *Felis catus* (top), and dingo, *Canis lupus dingo* (bottom), passes per night standardised by the number of cameras deployed per night along the road and along the river front, both of which bordered the study area along the edge of all three fire treatments (low intensity, high intensity, control).

after the low-intensity fire (fortnight 'c': $F_{5-78} = 12.99$, $P < 0.001$; Fig. 6). Cat activity was significantly higher 1 month after the high-intensity fire and 6 weeks after the low-intensity fire (fortnight 'e': $F_{4-65} = 4.44$, $P = 0.003$; Fig. 6) than the fortnight before fire (fortnight 'a') and the fortnight immediately after the high-intensity fire (fortnight 'c'). No cats were recorded on any cameras for the fortnight immediately after the high-intensity fire (fortnight 'c'), when dingo activity was highest (Fig. 6). At least six different cats were known to use the study area, identified from distinct pelage patterns recorded on cameras. Two were identified using the area before burning and an additional four cats were identified using the area after burning. One of the identified cats was photographed along the river front in the low-intensity plot with a dead rat in its mouth on 14 June. In addition, one male cat, which was not photographed during the camera survey, was confirmed as visiting the site because it had been fitted with a GPS collar in a concurrent study. This cat traveled a distance of 12 km from its usual home range to the study site on 4 June and remained there for 3 weeks (H. McGregor, unpubl. data). Hourly GPS fixes showed this cat moving around the high-intensity burn scar at night and retreating to an adjacent unburnt patch during the day.

Discussion

Our study showed that the mortality risk to small rodents increased strongly after high-intensity fire, with less evidence for an increase after low-intensity fire. Increased mortality was due to increased predation, and was associated with evidence of

a decline in abundance. We found no evidence that fire caused starvation, emigration, direct mortality or depressed breeding. The elevated predation in the fire treatments was related to the availability of patches of unburnt vegetation; survival was more likely for individuals with access to such ground cover. Elevated predation rates were apparently driven by increased local activity of predators, including feral cats and dingoes.

The broad pattern of small mammals declining with intense fire in northern savannas is well documented (Andersen *et al.* 2005; Legge *et al.* 2008; Firth *et al.* 2010). The present study observed the same pattern of localised decline with intense fire, and demonstrated that the underlying mechanism was amplified predation in places where intense fire removed all vegetation cover. We demonstrated this by showing that mortality increased after fire, by recording a post-fire increase in the local activity of predators, specifically of cats and dingoes, and by providing direct evidence of predation of small mammals after fire.

The pattern of increased predation pressure following fire reported here is consistent with results of studies from northern Australia and other regions (Ogen-Odoi and Dilworth 1984; Derrick *et al.* 2010; Morris *et al.* 2011*a*; McGregor *et al.* 2014). Our results supported the hypothesis that declines of small mammals in northern Australia could be driven by increased predation facilitated by fire, particularly from feral cats (Woinarski *et al.* 2011*a*, 2011*b*; Fisher *et al.* 2013; Frank *et al.* 2014; McGregor *et al.* 2014). However, the lack of replication in the present study prevents further generalisation of the results. An additional study involving greater replication of sites and possible predator exclusion could determine whether this mechanism is operating more broadly across northern Australia, and the role of feral cats and dingoes.

It is possible that in other species of small mammals, fire might have different effects. For example, species that den on the ground rather than in burrows might be more likely to suffer immediate mortality from fire. *R. tunneyi* feeds mainly on roots (Braithwaite and Griffiths 1996) so its food source may have persisted after fire, whereas for other species, food availability might decline more strongly after fire. Griffiths and Brook (2015) showed that recurrent fires caused declines in recruitment in several species, including the northern brown bandicoot, *Isoodon macrourus*, brushtail possum, *Trichosurus vulpecula*, and northern quoll, *Dasyurus hallucatus*. Nonetheless, our results provide evidence that elevated predation can be an important mechanism by which fire affects populations of small mammals in the northern savannas.

Why does fire cause mortality?

We found no evidence for direct mortality caused by the fire. All radio-tracked *R. tunneyi* rats survived the fire by sheltering in burrows, and this was probably also the case for *P. nanus*, also a burrowing species (Layme *et al.* 2004; Derrick *et al.* 2010; Morris *et al.* 2011*b*). Burning was not associated with decline in bodyweight of animals in either fire treatment, indicating that the main impact of fire was not through reduced food resources. Bodyweight in *R. tunneyi* did decline through the study, but this was probably related to the cessation of breeding and to seasonal changes in food availability in the transition from the wet to the dry season (Braithwaite and Griffiths 1996). By the end of the

study, recruitment of subadults in the plot burned at high intensity offset the decline of adults after fire, perhaps as a compensatory response to the low density of adults. We do not know whether subadults recruited to the burned plots were the offspring of resident adults or immigrants from surrounding unburned areas (Banks *et al*. 2011), so we could not directly test whether *in situ* survival of juveniles varied with fire treatment (Morris *et al*. 2011*b*; Zwolak *et al*. 2012). Individual animals did not shift their home ranges in response to fire, consistent with other studies on Australian small mammals (Christensen 1980; Conner *et al*. 2011; Morris *et al*. 2011*a*; MacGregor *et al*. 2013). The only two home-range shifts that we recorded did not accomplish movements from the burnt into unburnt areas. Capture probability was used as a proxy for abundance, which limits the conclusions of the trapping study. However, the decline in abundance following fire reported here has been observed in other studies of this species (White 1992; Legge *et al*. 2008). Declines were likely due to increased mortality attributable to predation, as shown by the radio-tracked individuals, in the weeks and months after the fire.

Given the fidelity of *R. tunneyi* to its home range, the availability of refuge around the home range was a key determinant of survival after fire in the face of intensified predation risk. Refuges that persist after fire, whether these are unburnt patches or structural habitat features such as rocks, provide some protection from predators (Swinburn *et al*. 2007; Banks *et al*. 2011; Conner *et al*. 2011; Pereoglou *et al*. 2011). This explains the higher survival in the plot burnt at low intensity, where more unburnt vegetation remained to provide such refuge and which could have allowed rats to forage while remaining concealed. Furthermore, the role of refugia in protecting small mammals from predation explains how all collared rats alive in both burnt plots at the end of the study were those that had shifted burrows into small unburnt refugia within their pre-established home ranges, or whose burrows happened to be located in unburnt refugia.

How do predators interact with fire to result in increased predation?

Mortality was highest in the first month following fire. This is a common pattern in other studies (Christensen 1980; Begg *et al*. 1981; Legge *et al*. 2008; Conner *et al*. 2011; Morris *et al*. 2011*a*), suggesting that the period immediately after fire is especially risky. Several different predators, including owls, falcons, snakes and mammals, used the study area. Local activity of feral cats and dingoes increased after burning and two deaths were attributed to snakes.

Cats were infrequently detected on camera traps, whereas the rate of detection of dingoes was highest soon after fire. This is consistent with evidence from other studies that have found that cats avoid dingoes (Edwards *et al*. 2002; Brook *et al*. 2012; Kennedy *et al*. 2012). The low rate of detections could suggest that cat activity on the study area was low soon after fire, but we know that cats were present on the area throughout the study, including the period soon after fire. This was indicated by opportunistic observations of cat tracks during the period after the fire. The case of the GPS-collared cat who hunted regularly on the study area for 17 nights but was not detected

on camera suggests that detectability of cats was low despite their activity in the area.

Cat detections increased after the intense fire once dingo detections fell, probably increasing the predation pressure on small mammals. Small mammals between 50 and 100 g are preferred prey for feral cats and there is experimental evidence of cats directly causing localised extirpations of a population of small mammals in northern Australia (Kutt 2011, 2012; Frank *et al*. 2014). The intense fire would have created ideal hunting conditions for cats, because cats in the study area have been found to select strongly for such habitats (McGregor *et al*. 2014); further evidence of this was provided by a GPS-collared cat whose home range was 12 km away, but who traveled to the scar of the intense fire to hunt.

We do not know whether dingoes were hunting small mammals in the study area. Dingo activity was highest in the first month after fire when mortality of radio-collared individuals was highest. However, it is possible that they were attracted by an increased density of agile wallabies (*Macropus agilis*) on the grass regrowth after fire rather than by the opportunity to hunt rodents. In a northern Australian study, 51% of dingo diet consisted of large and medium macropods and only 1.7% was contributed by rodents (Brook and Kutt 2011). However, dingoes are opportunistic hunters and can alter their diet according to prey availability (Corbett and Newsome 1987; Brook and Kutt 2011). The role of dingoes in the environment after fire either as major predators of small mammals, or perhaps as protectors of small mammals via mesopredator suppression of feral cats, requires further investigation (Johnson *et al*. 2007; Woinarski *et al*. 2011*a*; Brook *et al*. 2012).

Conclusions

Predation pressure following fire from native predators such as snakes, owls and dingoes, combined with predation pressure from cats attracted to the recently burnt area, caused a local population decline of small mammals in the present study. Evidence suggests that predation, especially by feral cats, is playing a central role in the decline of small mammal species in northern Australia (Woinarski *et al*. 2011*a*, 2011*b*; Fisher *et al*. 2013; Frank *et al*. 2014; McGregor *et al*. 2014). Our study supports the hypothesis that feral cat predation is facilitated by high-intensity fire to the detriment of small-mammal species (Woinarski *et al*. 2011*a*; Fisher *et al*. 2013; Frank *et al*. 2014; McGregor *et al*. 2015), by showing that mortality due to predation increased post-fire, that cats increased their use of recently burnt sites, and by demonstrating predation of small mammals by cats in this situation. Intensive use of recently burned areas by cats could provide a mechanisms by which they could have large impacts on small-mammal populations, despite their generally low densities in the northern savannas (McGregor *et al*. 2015). However, we also demonstrated an increase in dingo activity immediately following fire, which requires further investigation.

This has implications for further research into declines of small mammals, and recommendations for management. In particular, it will be useful to determine the characteristics of fires that benefit (or disadvantage) predators of small mammals, and use that knowledge to manage fire in ways that mitigate

the impacts of predators, particularly feral cats. The present study supports other recent work showing that prescribed burning in the early dry season should be undertaken to avoid intense wildfires in the late dry season (Legge *et al.* 2011*b*; Andersen *et al.* 2012; McGregor *et al.* 2014). At the same time, prescribed burning should conducted in ways that maximise the retention of vegetative refuges at spatial scales relevant to the home ranges of declining species.

Acknowledgements

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