**Small mammals decline with increasing fire extent in northern
Australia: evidence from long-term monitoring in Kakadu
National Park**

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Abstract

Small mammals (<2 kg) have declined dramatically in northern Australia in recent decades. Fire regimes, characterized by frequent, extensive, late season wildfires, are implicated in this decline. Here we compare the effect of fire extent, in conjunction with fire frequency, season and spatial heterogeneity (patchiness) of the burnt area, on mammal declines in Kakadu National Park over a recent decadal period. Fire extent – an index incorporating fire size and fire frequency – was the best predictor of mammal declines, and was superior to the proportion of the surrounding area burnt and fire patchiness. Point-based fire frequency, a commonly used index for characterizing fire effects, was a relatively weak predictor of declines. Small-scale burns affected small mammals least of all. Crucially, the most important aspects of fire regimes that are associated with declines are spatial ones; extensive fires (at scales larger than the home ranges of small mammals) are the most detrimental, indicating that small mammals may not easily escape the effects of large and less patchy fires. Notwithstanding considerable management effort, the current fire regime in this large conservation reserve is detrimental to the native mammal fauna, and more targeted management is required to reduce fire size.

Introduction

Biodiversity is declining severely in tropical areas world-wide, mostly due to rapid human population growth, habitat loss, hunting, invasive species and inadequate conservation reserves (Mack *et al.* 2000; Bradshaw *et al.* 2009). While the rate of biodiversity decline in tropical Australia may be comparable to that of other tropical areas, the principal factors driving declines elsewhere (broad-scale vegetation loss and hunting) are largely absent here (Woinarski *et al.* 2001), providing new insights to the natural and non-anthropogenic drivers of mammal declines and their synergies under global change (Brook *et al.* 2008). In the

absence of direct anthropogenic drivers of mammal declines, it is likely that landscape-scale factors are involved. There is increasing evidence that fire is such a factor (Russell-Smith *et al.* 2009a), but the manner in which fire effects biodiversity declines is poorly known. Here we seek to better resolve that causality to inform management.

Fire is ubiquitous in most Australian landscapes (Murphy *et al.* 2013) and fire regimes have changed dramatically since European arrival (Ward *et al.* 2001; Russell-Smith *et al.* 2003). In some tropical savanna regions of northern Australia, fire regimes are now dominated by large (>1000 km²) contiguous fires, occurring at short (~2–3 year) fire return intervals (Yates *et al.* 2008). Managing fire for desired environmental outcomes is an important conservation issue in Australia (Russell-Smith *et al.* 2003; Andersen *et al.* 2005; Russell-Smith *et al.* 2007; Di Stefano *et al.* 2011), requiring a clear understanding of the effects of the timing, frequency and scale of fires on biodiversity (Clarke 2008; Driscoll *et al.* 2010; Kelly *et al.* 2011).

In recent decades many small mammal species have declined dramatically in northern Australia, and while the causes are complex and synergistic, they most likely involve both adverse fire regimes and predation by feral cats *Felis catus* (Fitzsimons *et al.* 2010; Woinarski *et al.* 2011; Fisher *et al.* 2014). In northern Australia, there is evidence that many small mammal species, especially those that live in burrows or rock crevices, survive fires with declines in abundance occurring in the months after a fire (e.g., Legge *et al.* 2008), suggesting that the indirect effects of fire on survival and reproductive output are more important than direct fire-related mortality. These effects may be most severe if individual fires are large (much larger than individual home ranges) and further exacerbated by high fire frequency and/or an interaction with indirect effects that limit population recovery after fire, such as predation by feral cats (Williams *et al.* 2003; Legge *et al.* 2008; Andersen *et al.* 2012). Immediately after a fire, and prior to the onset of wet season rains, there is typically

reduced ground cover (e.g., Watson *et al.* 2012a) and abundance of food plants for small herbivorous mammals, increasing their risk of predation and starvation, reducing body condition and reproductive output (Sutherland and Dickman 1999). In the longer-term, frequent fires reduce the abundance of woody understorey and midstorey plants (Burbidge and McKenzie 1989; Woinarski and Ash 2002), leading to decreased overall availability of food resources such as fleshy fruits (Friend and Taylor 1985; Kerle 1985) and shelter and denning sites.

To date, investigations of fire have focused on the temporal aspects of fire regimes, mainly fire frequency and intensity (Woinarski *et al.* 2010). For example, high frequencies of fire, especially in the late dry season when fires tend to be of high intensity and low patchiness (Russell-Smith and Edwards 2006), have been implicated in the decline of small mammals in northern Australia (Kutt and Woinarski 2007; Firth *et al.* 2010; Woinarski *et al.* 2010; Radford *et al.* 2011; Woinarski *et al.* 2011). Woinarski *et al.* (2010) showed that variation amongst sampling sites in mammal decline in Kakadu National Park (KNP) over a 7-year period was correlated with fire frequency at those sites. However, a significant, unresolved question is whether large, spatially homogeneous fires (typical of late dry season wildfires), regardless of their frequency, are more detrimental than small, patchy fires (typical of early dry season prescribed fires) to biodiversity, especially small vertebrate fauna, in northern savannas (Yates *et al.* 2008; Woinarski *et al.* 2010; Radford 2012). This question is important because small patchy fires are sought by managers to reduce the likelihood of large, spatially homogenous fires. In this paper, we use a spatially extensive fauna monitoring dataset, and satellite-derived (Landsat) fire mapping, assembled as part of a long-term monitoring program in KNP, to evaluate the relative importance of the suite of fire attributes (size, frequency, seasonality, patchiness) that potentially influence small mammal status. We examine the proposition that small mammals in the tropical savannas of northern Australia

are being ‘burnt out’ of the landscape by frequent large-scale fires of low patchiness, because they typically have home ranges much smaller (e.g. 0.8 ha for the Brush-tailed rabbit-rat *Conilurus penicillatus*, to 40 ha for the Black-footed tree-rat *Mesembriomys gouldii*: Firth *et al.* 2006; Rankmore 2006) than contemporary fire sizes and cannot easily escape the effects of these large, homogeneous fires (Woinarski *et al.* 2005; Legge *et al.* 2008). Thus we predict that recent declines in small mammals in northern Australia have been exacerbated by the spatial scale of fires more so than other fire regime attributes, such as fire frequency and severity.

Methods

Study site and description of dataset

Small mammal abundance and species richness were sampled in KNP in 2001–2004 and again in 2007–2009, as part of a monitoring program assessing the effects of fire regimes on vegetation and terrestrial vertebrates (Edwards *et al.* 2003; Russell-Smith *et al.* 2009a; Woinarski *et al.* 2010). Fire frequencies in the park are high, typical of mesic savanna landscapes in northern Australia, with ~42% of the park burning in a given year (Russell-Smith *et al.* 2009a). There were no marked changes in fire management within KNP during the study period.

The mammal monitoring program is described by Woinarski *et al.* (2010). Mammals were monitored in 109 permanently marked plots distributed across the park (Fig. 1) representing the range of vegetation types (Russell-Smith *et al.* 2009a), with most plots (63%) in eucalypt woodland. It was not possible to survey all plots within any single year, so sampling was staggered over several years, but with a minimum 5-year interval between successive sampling of any single plot (of the 109 resampled plots, 39 and 20 plots were sampled at 6- and 7-year intervals, respectively). Plots were sampled in all seasons, but repeat

sampling of any plot occurred at the same time of year (± 6 weeks) as the previous sampling. We acknowledge the limited spatial and temporal replication of our monitoring data, and that there may have been significant inter-annual variation in mammal abundance, which we were unable to account for given the available data. However, we see no reason why this variation would introduce bias into our results. We note that our dataset is the best available for northern Australian savannas, where there is a dearth of vertebrate monitoring data and few Landsat fire histories. Our dataset is the same as that used in the ground-breaking paper by Woinarski *et al.* (2010), which raised the alarm in relation to the mammal declines being experienced in Kakadu National Park.

Standardised methods of sampling small mammals were applied (Woinarski *et al.* 2004). Each plot measured 50×50 m, with 20 Elliott traps ($33 \times 10 \times 9$ cm) placed equidistantly around the perimeter, a cage trap ($56 \times 20 \times 20$ cm) placed at each corner, and two 20-L pitfall traps (with 8 m of drift-line fence) placed within the plot. Traps were set over a 72-h period, with Elliott and cage traps baited with a mixture of peanut butter, honey and oats, and all traps checked within 1 h of dawn. All mammals captured were identified to species level and released at the point of capture, and not individually marked. In addition to trap captures, mammals were also recorded by two 10-min spotlight searches, and scats and other signs were searched for during daylight sampling of the plot. An abundance value for each plot was tallied for every species as the sum of all captures and all individuals recorded during timed spotlight searches. Species recorded from scats or other signs, but not trapped or observed in spotlight searches, were assigned an abundance value of one. The focus of this paper is terrestrial small mammals (< 2 kg), of which 24 species were recorded by Woinarski *et al.* (2010) (Table 1). Data relating to bats, macropods, dingoes or feral mammals (which were poorly sampled by the methodology) were not included. The decline of the Northern quoll *Dasyurus hallucatus*, is well understood to be due largely to the introduced Cane toad

Rhinella marina that colonized KNP sequentially from 2001 to ~2003 (Woinarski *et al.* 2010) and the northern quoll was not included in our analyses.

Fire regime variables

Using Kakadu's Landsat satellite-derived fire history (100-m spatial resolution), described by (Russell-Smith *et al.* 1997), we derived a range of variables to describe the fire regime for each small mammal monitoring site (Table 2). The variables relate only to fires that occurred during the monitoring period (typically 2003–2008). The variables examined were:

(1) *Fire frequency*: For each monitoring site, this variable represented point-based fire frequency, as examined by Woinarski *et al.* (2010), both overall and separately for fires in the early dry season (EDS: April–July) and late dry season (LDS: August–December), with virtually no fires occurring outside these months. *Fire frequency* was simply calculated as number of times a monitoring site was burnt, divided by the duration of the monitoring period in years.

(2) *Proportion burnt*. For each monitoring site, this variable represented the annual average proportion of the surrounding area that was burnt (Fig. 2a). For example, for a monitoring site that was first assessed on 27 February 2004 and re-assessed on 10 March 2009 (i.e. 5.0 years), we averaged the proportion burnt across the five years (2004–2009, inclusive).

(3) *Fire extent*. This index integrated both fire size and frequency. For each monitoring site, this variable represented the mean distance of each pixel in the surrounding area to the nearest unburnt vegetation at the end of each calendar year (Fig. 2b). For a calendar year, the distances to unburnt vegetation for all pixels (visible in Fig. 2b) within the area surrounding the monitoring site were averaged. An annual average was then averaged across all years in the monitoring period. Large values indicate that the surrounding area was dominated by repeated extensive, spatially homogeneous fires.

(4) *Patchiness*. For each monitoring site, this index of spatial heterogeneity represented the natural logarithm of the distance from each pixel in the surrounding area to the nearest burnt–unburnt boundary at the end of each calendar year (Fig. 2c). For a calendar year, the distances from each pixel to the nearest burnt–unburnt boundary (visible in Fig. 2c) were averaged across the area surrounding the monitoring site, and then an annual average was calculated across all years in the monitoring period. Large values indicate low patchiness, representing areas dominated by large, spatially homogeneous patches of *either* burnt or unburnt vegetation. Hence, this differs from *fire extent* which relates to the spatial extent of burnt vegetation only (i.e. distance to unburnt vegetation).

A number of the fire regime variables were not point-based, but calculated for the area surrounding each monitoring site (i.e. *Proportion burnt*, *Fire extent*, *Patchiness*). For these variables, a range of radii around each monitoring site were used: 0.1, 0.2, 0.4, 0.8, 1.6, 3.2 and 6.4 km. We considered that this spatial range amply encompassed the home ranges of all species included in the dataset, about 1–40 ha (Firth *et al.* 2006; Rankmore 2006).

Statistical analysis

We examined three response variables, all measured at the end of the monitoring period (ca. 2008): (1) species richness; (2) capture success represented as relative abundance; and (3) an approximation of the geometric mean of relative abundance (GMA). Our response variable was not change in species richness or abundance, but we included the starting value of the response, i.e. at the beginning of the monitoring period (ca. 2003), thus controlling for unexplained 'site' effects. A response variable such as proportional change in species richness or abundance could not be adequately accommodated by the error structures of standard regression models (e.g. ordinary least squares or generalized linear models), because of the excessive number of values of –1 (i.e. complete loss of species or individuals). Additionally,

a substantial proportion (30%) of the dataset had values of zero for species richness and abundance at the start of the monitoring period, and therefore proportional change cannot be calculated, so these values would have been discarded.

GMA was useful as a response variable because it integrates both species richness and abundance (Buckland *et al.* 2011), and is sensitive to trends in the abundance of a group of species as a whole (e.g. small mammals). For each monitoring site, GMA is the product of the abundances of all 23 small mammal species recorded during the monitoring period, raised to the power of 1/23, i.e.:

$$GMA = \sqrt[n]{A_1 A_2 \dots A_n},$$

where, A_n is the abundance of the n th species. However, GMA cannot be calculated if abundance values of zero are present, so we added a value of one to each abundance value prior to calculating the product:

$$\text{Approximate GMA} = \sqrt[n]{(A_1 + 1)(A_2 + 1) \dots (A_n + 1)} - 1.$$

All three response variables were zero-inflated and thus models were constructed as GLMs with a negative binomial error structure and log link function, in the program R (version 2.15.1; R Development Core Team 2014).

To account for variation in each of the three response variables, we constructed a set of 10 candidate models (Tables 2–3). Each model contained the starting value of the response variable, i.e. at the beginning of the monitoring period, thus controlling for unexplained 'site' effects. The candidate models also contained two environmental variables, representing habitat and topography, and a range of fire regime variables (Table 2). The fire regime variables *Fire frequency*, *Proportion burnt* and *Fire extent* are inherently highly correlated. Together they define the prevailing fire regime in an area. Most notably fire frequency and fire size, which are integrated in the *Fire extent* index are negatively correlated: large values for the index of fire extent indicate large fire size, which in turn is correlated with infrequent

fire. Thus, *Fire extent* emphasizes fire size while at the same time accounting for fire frequency. Nevertheless, to avoid issues of multicollinearity and to separate the relative effects of the fire variables as much as possible, we did not include more than one of them in the same statistical model.

Models were evaluated using a robust form of Akaike's Information Criterion, AIC_c , a model selection index favouring both model fit and model simplicity (Burnham & Anderson 2002). Lower values of AIC_c indicate greater support for a model relative to other models in the same candidate set. From AIC_c , Akaike weights (w_i) were calculated for each model, which are the probability of a given model being the best in the candidate set.

Some of the fire regime variables were calculated over a range of radii surrounding each monitoring site (i.e. *Proportion burnt*, *Fire extent*, *Patchiness*; Table 2). A separate set of candidate models was constructed for each search radius, and the median AIC_c value assumed for each model.

We confirmed that the residuals of the most highly ranked models were not spatially autocorrelated by inspecting correlograms (see Appendix S1, Supporting Information) based on Moran's I (Legendre and Legendre 1998).

Results

Fire regimes were the only identified correlate of species richness and abundance of small mammals at the end of the study period; environmental variables such as topography and habitat type were unimportant. The models confirmed that species richness, abundance and the geometric mean of abundance declined substantially at sites where there was a higher *Proportion burnt* and *Fire extent* (Fig. 3), while point-based *Fire frequency* had lower support (Table 3). For all three response variables, there was little difference ($<2 AIC_c$ units)

in the fit of *Fire extent* and *Proportion burnt* as predictors. There was little evidence that *Patchiness* had an effect on species richness, abundance or the geometric mean of abundance (Table 3), with this variable consistently decreasing support for the models in which it appeared.

The search radius that consistently maximized the explanatory power of *Fire extent* (i.e. the circle over which mean distance is calculated) was 1.6 km, and for *Proportion burnt* was 3.2 km (Fig. 4). *Fire extent*, assuming a 1.6 km search radius, accounted for 14%, 25% and 27% of the variation in species richness, abundance and the geometric mean of abundance, respectively. *Proportion burnt*, assuming a 3.2 km search radius, accounted for 11%, 22% and 23% of the variation in species richness, abundance and the geometric mean of abundance, respectively.

There was very little evidence of a differential effect of fire season (early versus late dry-season fire activity) on small mammal species richness and abundance. Models incorporating separate terms for early dry season and late dry season fire activity (i.e. *Proportion burnt*_{EDS} + *Proportion burnt*_{LDS}; *Fire frequency*_{EDS} + *Fire frequency*_{LDS}) performed relatively poorly (Table 3). These models generally had lower support than the simpler *Proportion burnt* and *Fire frequency* models, not incorporating season of fire.

Discussion

Increases in the frequency, intensity and spatial extent of fires in recent decades have raised concerns that fire may have a stronger role in contemporary small mammal declines than previously thought (Legge *et al.* 2008; Lindenmayer *et al.* 2008; Yates *et al.* 2008; Kelly *et al.* 2011; Andersen *et al.* 2012). We demonstrate that small mammal declines in KNP during the period 2001–2009 were associated with sites that experienced repeated large fires. Of several measures of fire, fire extent was most strongly correlated with small mammal

declines. While our index of fire extent incorporates both fire size and frequency, these parameters are negatively correlated so that large values of *Fire extent* indicate large fire size at low fire frequency. The effect of the spatial scale of fires on northern Australia's rapidly declining small mammals has not previously been quantified, although large fires have been implicated in some studies (Legge *et al.* 2008; Woinarski *et al.* 2011; Radford 2012). The greater importance of fire extent than fire frequency *per se*, demonstrated in this study, substantially advances the previous analysis of this mammal monitoring data set (Woinarski *et al.* 2010), and provides a better conceptual context for understanding how fire affects small mammals.

We hypothesize that small mammals, with small home ranges (e.g., Brush-tailed rabbit-rat, Firth *et al.* 2006; Black-footed tree-rat, Rankmore 2006) and limited capacity for dispersal, are particularly vulnerable to large fires that simplify habitats. Extensive frequent fires have also caused the decline of fire-interval sensitive, obligate seeder plant species in tropical savannas, such as the conifer *Callitris intratropica* (Yates *et al.* 2008; Russell-Smith *et al.* 2012; Lawes *et al.* 2013). If fires are so large that small mammals cannot readily disperse to unburnt areas, they will incur significant fitness costs and population decline. We argue that large fires exacerbate the decline of small mammals by increasing the spatial scale of fire effects beyond the recovery capacity of the ecosystem and its small mammal component.

In this study, small mammals appeared to be resilient to fires at a localised scale (<10 ha), but declined dramatically in abundance and species richness when the surrounding area (<3 km), was subjected to repeated large fires (Fig. 3, 4). These findings are supported by studies from other fire-prone systems in Australia. For example, in the Murray Mallee region of south-eastern Australia, characterized by far less frequent (return intervals ~ 10-20 years) but large (>100 000 ha) fires, the diversity of small mammals and birds was significantly

reduced for decades after fires (Haslem *et al.* 2011; Kelly *et al.* 2012; Taylor *et al.* 2012). In the Australian arid zone, small prescribed burns did not affect small mammal diversity, but large wildfires caused a monotonic decline in both the alpha and beta diversity of small mammals for several months after wildfire (Pastro *et al.* 2011). In the central Kimberley, north-western Australia (similar environment to KNP, with comparable fire regimes), the species richness and abundance of small mammals declined dramatically in burnt areas after an extensive ($>7000 \text{ km}^2$), late-dry-season fire, but showed no change in nearby unburnt areas (Legge *et al.* 2008). Similar findings in relation to fire were obtained from the North Kimberley region (Radford *et al.* 2011), with mammal trap success declining with increasing fire frequency within 1 km of a trapping site. Increasing mammal species richness was associated with shorter distance to large areas of low fire-frequency habitat, indicating an effect of fire extent on mammal diversity and abundance.

Changing fire regimes and the timing of small mammal decline in Kakadu

The precipitous decline of many small mammal taxa in the Kakadu region since the mid-1980s is described by several compelling studies (Braithwaite and Muller 1997; Woinarski *et al.* 2001; Woinarski *et al.* 2010). However, it is likely that small mammal decline in the region has been an ongoing, though not necessarily continuous, process during the twentieth century. For example, early naturalists commented on the regional abundance of certain taxa (*Conilurus penicillatus*, *Phascogale pirata*) which, by the 1980s, were already restricted in KNP (Woinarski *et al.* 2001). The golden-backed tree-rat *Mesembriomys macrurus* was last reported from the Kakadu region in 1969 (Woinarski *et al.* 2007). These multi-decadal patterns are also reflected in similar observations from the southern Kimberley (Kitchener 1978; McKenzie 1981).

While many researchers point to a suite of factors involved in small mammal declines

(Woinarski *et al.* 2011; Fisher *et al.* 2014), Woinarski *et al.* (2001, p. 368) surmised that, overall, “the widespread and continuing loss of traditional Aboriginal land management practice” of fine-scale, patchy landscape burning (Haynes 1985; Russell-Smith *et al.* 1997; Yibarbuk *et al.* 2001; Garde *et al.* 2009) is likely an important underlying cause of these declines. The loss of traditional Aboriginal fire management has also been implicated in the decline of other biota in northern Australia, including granivorous birds (Franklin 1999), the conifer *Callitris intratropica* (Bowman and Panton 1993) and sandstone heathland communities (Russell-Smith *et al.* 2002). Extensive fires on lowland floodplains in KNP were likely kept in check by burgeoning Asian water buffalo *Bubalus bubalis* populations until the 1980s (Petty *et al.* 2007), when buffalo were extensively culled in a bovine disease eradication program. However, in savanna habitats removed from permanent water sources, extensive late-season fires became the norm in the Kakadu region (Russell-Smith *et al.* 2009b). An assessment of recent fire patterns since 1990 on the Arnhem Plateau (contiguous with KNP, but no systematic buffalo population eradication) shows that, prior to the re-introduction of strategic early dry-season fire management from 2005, extensive late-season wildfires occurred on a boom-and-bust cycle at a periodicity of around 3 years (Russell-Smith *et al.* 2009b). Similar trends are evident also in KNP fire history data available from 1980, especially for non-floodplain fires (Russell-Smith *et al.* 1997: Fig. 4), and subsequent increasing fire patchiness observed over the ensuing 20 years (Russell-Smith *et al.* 1997: Fig. 9b; Price *et al.* 2005).

We draw two main conclusions from the above – firstly, that a regional savanna fire regime characterized by extensive, periodic late-season fires has been ongoing since the late twentieth century. And secondly, that the catastrophic decline of small mammals since the mid-1980s in the Kakadu region has occurred despite a general improvement in fire management over the same period, indicated by increasing spatial heterogeneity (Price *et al.*

2005) and the reduced prevalence of intense, late dry season wildfires (Russell-Smith *et al.* 1997).

Management implications

Our findings demonstrate that unlike other taxa, such as birds that are more responsive to the temporal dimensions of fires (Reside *et al.* 2012; Watson *et al.* 2012b), small mammal diversity and abundance in tropical savannas is largely determined by fire size. Large fires that burn at a landscape scale (>1000 ha) appear to be burning small mammals out of the landscape. Savanna fire management must seek to reduce the spatial extent of fires. Careful strategic prescribed burning in the early dry-season under fire-weather conducive to achieving fine-grained, different age-since-fire patch mosaics with an overall increase in the extent of longer-unburnt habitat is the proposed burning regime to maintain small mammal diversity in tropical savannas (Legge *et al.* 2008; Radford *et al.* 2011; Woinarski *et al.* 2011; Andersen *et al.* 2012).

Based on consideration of the home range sizes of many small vertebrates and other fauna, as well as the regeneration requirements of poorly dispersed longer-lived obligate seeder plants, fire patch sizes no larger than tens of hectares would seem appropriate in frequently burnt savanna landscapes (Woinarski *et al.* 2005; Yates *et al.* 2008). Our findings support the current attempts to implement and monitor such fine-scale patch burning at a landscape scale across much of northern Australia (Russell-Smith *et al.* 2013).

The catastrophic decline of Australia's mammal fauna appears to have few analogues globally. In Australia, a very high proportion of species have declined significantly, most dramatically in areas with little apparent habitat modification (e.g. central Australia, and to a lesser extent northern Australia). This is a starkly different pattern to the mammal declines experienced elsewhere in the world, where the drivers are typically habitat loss and

overexploitation (Schipper *et al.* 2008). However, our findings still have global relevance, by showing that extensive fires can have a severe negative affect on small mammal communities, consistent with a recent global meta-analysis (Griffiths and Brook 2014). In fire-prone landscapes, and landscapes where climate change is expected to drive increases in fire frequency and/or size, the active management of fire regimes, considering appropriate levels of spatiotemporal heterogeneity, is likely to be an important step in the effective conservation of small mammal diversity.

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Data accessibility

KNP Fire plot data – including mammal species trends and derived fire metrics: uploaded as online supporting information

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Table 1. Species recorded in 109 fauna monitoring plots in Kakadu National Park, at two sample times (ca. 2003 and 2008), and their frequency of detection in the plots. Species are listed in descending order of frequency in the first sample period.

Species name	Common name	Proportion of plots (%)	
		Sample 1 (ca. 2003)	Sample 2 (ca. 2008)
<i>Dasyurus hallucatus</i>	Northern quoll	26	2
<i>Isoodon macrourus</i>	Northern brown bandicoot	19	4
<i>Zyzomys argurus</i>	Common rock-rat	18	13
<i>Rattus tunneyi</i>	Pale field-rat	15	2
<i>Antechinus bellus</i>	Fawn antechinus	12	3
<i>Melomys burtoni</i>	Grassland melomys	9	8
<i>Planigale maculata</i>	Common planigale	8	5
<i>Pseudomys nanus</i>	Western chestnut mouse	6	2
<i>Trichosurus vulpecula</i>	Common brushtail possum	6	1
<i>Pseudantechinus bilarni</i>	Sandstone antechinus	5	8
<i>Pseudomys delicatulus</i>	Delicate mouse	4	0
<i>Rattus colletti</i>	Dusky rat	3	0
<i>Tachyglossus aculeatus</i>	Short-beaked echidna	3	1
<i>Zyzomys maini</i>	Arnhem rock-rat	3	5
<i>Petropseudes dahli</i>	Rock ringtail possum	2	3
<i>Phascogale pirata</i>	Northern brush-tailed phascogale	2	0
<i>Sminthopsis bindi</i>	Kakadu dunnart	2	0
<i>Sminthopsis virginiae</i>	Red-cheeked dunnart	2	0
<i>Hydromys chrysogaster</i>	Water rat	1	0
<i>Mesembriomys gouldii</i>	Black-footed tree-rat	1	0
<i>Pseudomys calabyi</i>	Kakadu pebble-mound mouse	1	0
<i>Conilurus penicillatus</i>	Brush-tailed rabbit-rat	0	1
<i>Leggadina lakedownensis</i>	Tropical short-tailed mouse	0	1
<i>Petaurus breviceps</i>	Sugar glider	0	1

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Table 2. Variables used in the analysis.

Variables	Definition
$S_{initial}$	Species richness at the start of the monitoring period.
$A_{initial}$	Abundance (individuals site ⁻¹) at the start of the monitoring period.
$GMA_{initial}$	Approximate geometric mean of abundance across all 23 species (individuals species ⁻¹ site ⁻¹) at the start of the monitoring period.
<i>Topography</i>	Lowland or sandstone plateau.
<i>Habitat</i>	Savanna, rainforest, heath, <i>Melaleuca</i> woodland, or open floodplain
<i>Fire frequency</i>	Point-based estimate of fire frequency (fires year ⁻¹), i.e. the number of times a site was burnt during the monitoring period, divided by the duration of the monitoring period. Derived from the Landsat satellite-record.
<i>Fire frequency</i> _{EDS}	As for <i>Fire frequency</i> , but only includes fires that occur in the early dry season (January–July).
<i>Fire frequency</i> _{LDS}	As for <i>Fire frequency</i> , but only includes fires that occur in the late dry season (August–December).
<i>Proportion burnt</i>	Proportion of the surrounding area burnt each year, averaged over the monitoring period. Calculations were made using search radii of: 0.1 km; 0.2 km; 0.4 km; 0.8 km; 1.6 km; 3.2 km; 6.4 km.
<i>Proportion burnt</i> _{EDS}	As for <i>Proportion burnt</i> , but only includes fires that occur in the early dry season (January–July).
<i>Proportion burnt</i> _{LDS}	As for <i>Proportion burnt</i> , but only includes fires that occur in the late dry season (August–December).
<i>Fire extent</i>	Distance to the <i>nearest unburnt vegetation</i> at the end of each calendar year, averaged over the surrounding area, and then averaged over the monitoring period. Calculations were made using the same search radii as described for <i>Proportion burnt</i> . Large values indicate that the search area is dominated by extensive, spatially homogeneous fires.
<i>Patchiness</i>	The natural logarithm of distance to the <i>nearest burnt–unburnt boundary</i> at the end of each calendar year, averaged over the surrounding area, and then averaged over the monitoring period. Calculations were made using the same search radii as described for <i>Proportion burnt</i> . Large values indicate low patchiness.

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596 **Table 3. Results of the model ranking procedure for negative binomial Generalized**

597 **Linear Models**

598 Variation in: (a) species richness; (b) abundance; and (c) the geometric mean of abundance of
599 small mammals at the end of the monitoring period. The models are shown ranked in ascending
600 order of the model selection criterion, AIC_c . ΔAIC_c is the difference between the model's AIC_c
601 value and the minimum AIC_c value in the candidate set. The Akaike weight (w_i) represents the
602 likelihood of the model being the best in the candidate set (Burnham and Anderson 2002). The
603 single model with a high level of empirical support (i.e. $\Delta AIC_c \leq 2$) is shown in bold.

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Model	ΔAIC_c	w_i
(a) Species richness		
$S_{initial} + Fire\ extent$	0.0	0.47
$S_{initial} + Proportion\ burnt$	1.8	0.19
$S_{initial} + Fire\ extent * Patchiness$	2.9	0.11
$S_{initial} + Fire\ frequency$	3.8	0.07
$S_{initial} + Proportion\ burnt_{EDS} + Proportion\ burnt_{LDS}$	3.9	0.07
$S_{initial} + Proportion\ burnt * Patchiness$	4.7	0.05
$S_{initial} + Fire\ frequency_{EDS} + Fire\ frequency_{LDS}$	5.5	0.03
$S_{initial} + Topography$	9.9	0.00
$S_{initial}$	10.6	0.00
$S_{initial} + Habitat$	18.1	0.00
(b) Abundance		
$A_{initial} + Fire\ extent$	0.0	0.59
$A_{initial} + Proportion\ burnt$	1.9	0.18
$A_{initial} + Fire\ extent * Patchiness$	2.4	0.18
$A_{initial} + Proportion\ burnt_{EDS} + Proportion\ burnt_{LDS}$	3.1	0.10
$A_{initial} + Proportion\ burnt * Patchiness$	4.1	0.06
$A_{initial} + Fire\ frequency$	5.2	0.10
$A_{initial} + Fire\ frequency_{EDS} + Fire\ frequency_{LDS}$	6.6	0.05
$A_{initial}$	9.8	0.00
$A_{initial} + Topography$	11.8	0.00
$A_{initial} + Habitat$	16.9	0.00
(c) Geometric mean of abundance		
$GMA_{initial} + Proportion\ burnt$	0.0	0.27
$GMA_{initial} + Proportion\ burnt_{EDS} + Proportion\ burnt_{LDS}$	0.1	0.26
$GMA_{initial} + Fire\ extent$	0.2	0.24
$GMA_{initial} + Proportion\ burnt * Patchiness$	0.8	0.18
$GMA_{initial} + Fire\ extent * Patchiness$	3.4	0.05
$GMA_{initial} + Fire\ frequency$	4.4	0.06
$GMA_{initial} + Fire\ frequency_{EDS} + Fire\ frequency_{LDS}$	4.6	0.05
$GMA_{initial}$	11.6	0.00
$GMA_{initial} + Topography$	13.5	0.00
$GMA_{initial} + Habitat$	18.5	0.00

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Figure legends

Fig. 1. Location of the 109 fauna monitoring plots used in this study, throughout Kakadu National Park (shaded grey) in northern Australia. Contour lines represent mean annual rainfall (mm).

Fig. 2. (a) A sample of the Kakadu fire history showing areas burnt at the end of 2006. Burnt area pixels are 100×100 m, derived from 30-m resolution satellite imagery. A mammal monitoring site is indicated by the red dot, and a search radius of 1.6 km is indicated by the white circle. The proportion of the surrounding area (1.6 km radius) that was burnt in 2006 is 47% (35% early and 12% late). (b) The distance to nearest unburnt vegetation at the end of the 2006 fire season, for the same sample of the Kakadu fire history shown in (a). The *Fire extent* variable simply represents the average of all the pixels within the search radius (averaged across all years in the monitoring period). Spatially extensive fires are indicated by large distances to nearest unburnt vegetation. (c) The distance to nearest burnt–unburnt boundary at the end of the 2006 fire season, for the same sample of the Kakadu fire history shown in (a). The *Patchiness* variable simply represents that average of all the pixels (natural-log transformed) within the search radius (averaged across all years in the monitoring period).

Fig. 3. Change in species richness (left-hand column), abundance (middle column) and geometric mean of abundance (right-hand column) of small mammals over the monitoring period, in relation to: (a) fire frequency; (b) the proportion of the surrounding area that was burnt (calculated within a 3.2 km radius); and (c) the mean distance to unburnt vegetation (calculated within a 1.6 km radius). Note that proportional change can only be calculated for sites where small mammals were initially present. The solid lines represent the predictions of generalized linear models of final species richness, abundance and GMA, expressed in terms

of proportional change. Predictions were made by assuming median values for initial species richness, abundance and geometric mean of abundance. Dashed lines indicate the 95% confidence intervals of the regressions.

Fig. 4. A comparison of the effectiveness of various search radii used to estimate mean distance to nearest unburnt vegetation in the surrounding area (*Fire extent*; dashed lines) and proportion of the surrounding area burnt (*Proportion burnt*; solid lines), as predictors of (a) species richness, (b) abundance and (c) geometric mean of abundance of small mammals at the end of the monitoring period. A series of generalized linear models (with negative binomial error structure) that differed only in the search radius used to calculate the spatial variables, were compared using AIC_c . Akaike weights (w_i) represent the likelihood of each model being the best in the candidate set.

Fig. 1.

(a) Sample area showing fire scars at the end of 2006 fire season

(b) Distance to nearest unburnt vegetation at the end of 2006 fire season

(c) Distance to nearest burnt–unburnt boundary at the end of 2006 fire season

Fig. 2.

(a) Point-based fire frequency (*Fire frequency*)

(b) Proportion of the surrounding area burnt (*Proportion burnt*)

(c) Mean distance to unburnt vegetation (*Fire extent*)

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648 Fig. 3.

(a) Species richness

(b) Abundance

(c) Geometric mean of abundance

Fig. 4.