

## Monitoring indicates rapid and severe decline of native small mammals in Kakadu National Park, northern Australia

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### Abstract

**Context.** Australia has a lamentable history of mammal extinctions. Until recently, the mammal fauna of northern Australia was presumed to have been spared such loss, and to be relatively intact and stable. However, several recent studies have suggested that this mammal fauna may be undergoing some decline, so a targeted monitoring program was established in northern Australia's largest and best-resourced conservation reserve.

**Aims.** The present study aims to detect change in the native small-mammal fauna of Kakadu National Park, in the monsoonal tropics of northern Australia, over the period of 1996–2009, through an extensive monitoring program, and to consider factors that may have contributed to any observed change.

**Methods.** The small-mammal fauna was sampled in a consistent manner across a set of plots established to represent the environmental variation and fire regimes of Kakadu. Fifteen plots were sampled three times, 121 plots sampled twice and 39 plots once. Resampling was typically at 5-yearly intervals. Analysis used regression (of abundance against date), and Wilcoxon matched-pairs tests to assess change. For resampled plots, change in abundance of mammals was related to fire frequency in the between-sampling period.

**Key results.** A total of 25 small mammal species was recorded. Plot-level species richness and total abundance decreased significantly, by 54% and 71%, respectively, over the course of the study. The abundance of 10 species declined significantly, whereas no species increased in abundance significantly. The number of 'empty' plots increased from 13% in 1996 to 55% in 2009. For 136 plots sampled in 2001–04 and again in 2007–09, species richness declined by 65% and the total number of individuals declined by 75%. Across plots, the extent of decline increased with increasing frequency of fire. The most marked declines were for northern quoll, *Dasyurus hallucatus*, fawn antechinus, *Antechinus bellus*, northern brown bandicoot, *Isodon macrourus*, common brushtail possum, *Trichosurus vulpecula*, and pale field-rat, *Rattus tunneyi*.

**Conclusions.** The native mammal fauna of Kakadu National Park is in rapid and severe decline. The cause(s) of this decline are not entirely clear, and may vary among species. The most plausible causes are too frequent fire, predation by feral cats and invasion by cane toads (affecting particularly one native mammal species).

**Implications.** The present study has demonstrated a major decline in a key conservation reserve, suggesting that the mammal fauna of northern Australia may now be undergoing a decline comparable to the losses previously occurring elsewhere in Australia. These results suggest that there is a major and urgent conservation imperative to more precisely identify, and more effectively manage, the threats to this mammal fauna.

### Introduction

In recent times, Australia has experienced the world's worst record of mammal extinctions (Johnson 2006; McKenzie *et al.* 2007), with the loss of 22 mammal species over the period 1850–1960, and a further eight species now extirpated from their formerly extensive mainland range but persisting still on offshore islands (Burbidge *et al.* 2008). Most of the extinctions occurred in arid, semiarid and temperate Australia. In contrast, the mammal fauna of monsoonal northern Australia has suffered

no recent extinctions (McKenzie *et al.* 2007), although a series of studies has indicated localised losses of some species, especially in its semiarid fringe (Kitchener 1978; McKenzie 1981).

However, Woinarski *et al.* (2001) demonstrated a substantial contemporary decline in the native mammal fauna in the Kapalga area of Kakadu National Park over the period of 1986–99, and collated some other evidence suggesting broader-scale decline of many small- to medium-sized (<5 kg) mammals in northern Australia. Notably, the species for which the decline was

indicated comprised largely the same groups of species as that proved extinction-prone elsewhere in Australia (bandicoots, larger dasyurids, larger rodents). Partly in response to the decline evident in the Kapalga results, we established a far more substantial fauna-monitoring program across the 20 000 km<sup>2</sup> Kakadu National Park, complemented by a similar monitoring program in Litchfield National Park (Woinarski *et al.* 2004a) and Garig Gunak Barlu National Park (Cobourg Peninsula).

In the present paper, we report results from the first 13 years (1996–2009) of the Kakadu monitoring program. The simple primary objective of the present paper is to document trends in the Kakadu mammal fauna. We then provide some consideration of factors that may have contributed to the observed results, and outline a framework for a more integrated research and management program that addresses the conservation issues evident in these results.

## Methods

The mammal monitoring program described here is a component of a broader monitoring program for terrestrial vertebrates established for a set of large conservation reserves in the monsoonal north of the Northern Territory (Russell-Smith *et al.* 2009), with this fauna monitoring program itself a component of a previously established program to assess fire regimes and their influence on vegetation (Edwards *et al.* 2003).

For Kakadu, the original fire-monitoring program comprised a set of permanently marked plots distributed broadly across the park (Fig. 1) and selected to represent relatively equitably the range of vegetation types present (Russell-Smith *et al.* 2009), with most plots (~60%) being eucalypt forest or woodland. Plots varied widely in their accessibility, with many remote from the track network and requiring helicopter access. The fire history of the plots has been shown to be representative of that of the park as a whole (Russell-Smith *et al.* 2009).

The original design of the monitoring program was to assess vegetation at every plot at 5-yearly intervals (Russell-Smith *et al.* 2009). Fauna sampling was superimposed on this design, and as a consequence of its substantially greater logistical challenge and expense, it has been implemented with less regularity and completeness. Resourcing issues dictated that it was unfeasible to undertake fauna sampling of all plots within any single year, so sampling of plots was staggered over several years, albeit with the objective of a 5-year interval between successive sampling of any single plot (although a minority of the 136 resampled plots were sampled at 6- (37 plots) or 7-year (21 plots) intervals). Plots were sampled in all seasons, but with the stipulation that repeat sampling of any plot was arranged to occur at the same time of the year ( $\pm 6$  weeks) as the previous sampling of that plot. Resourcing of the fauna-monitoring program has been discontinuous, so no sampling was undertaken in some years.

For 48 of the remote (helicopter-access) permanently marked plots, we established an additional supplementary plot sampled simultaneously and located 300–1500 m from the permanent plot. These supplementary plots were established only near the remote plots because it was cost-effective for helicopter-

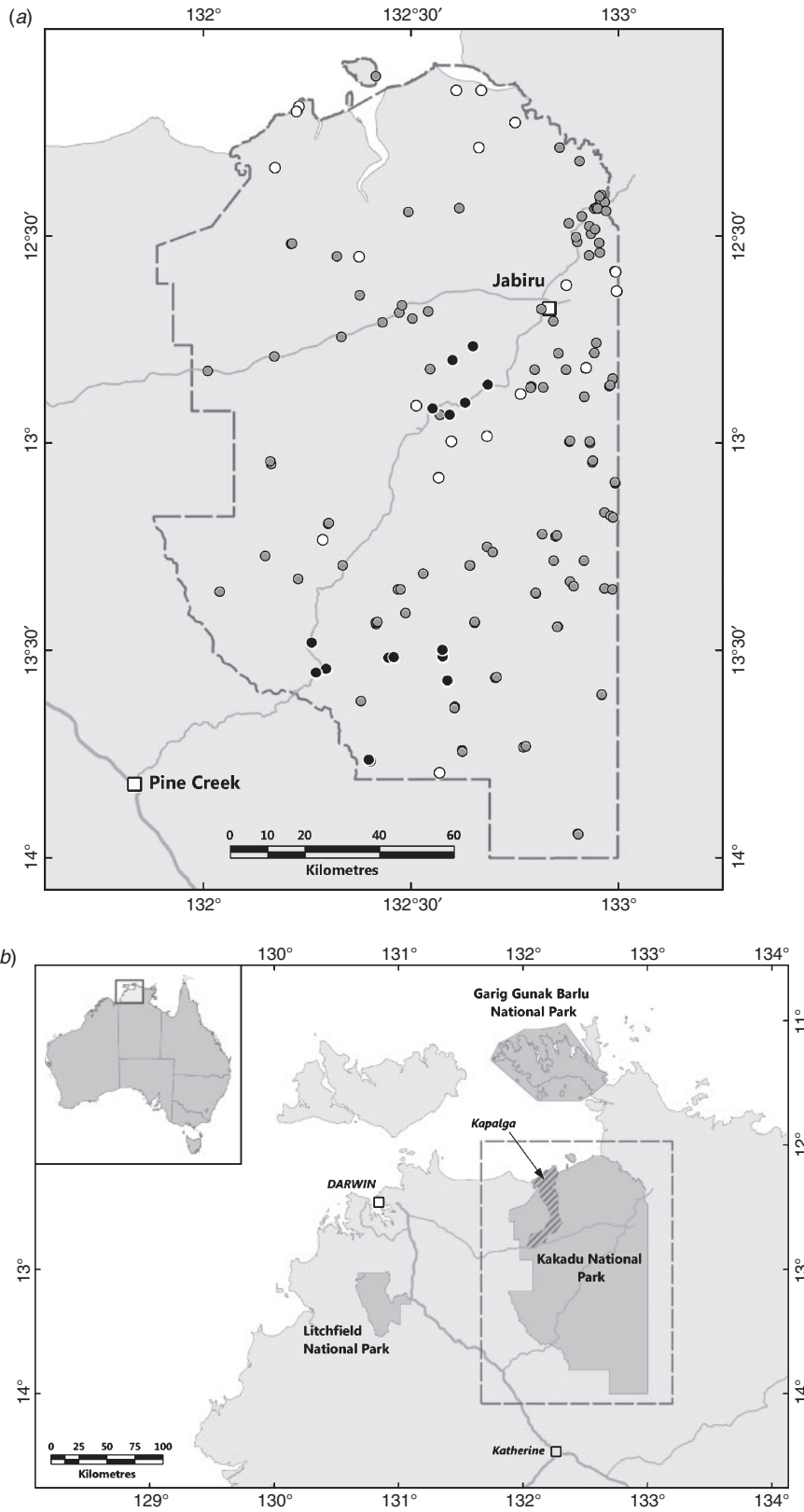
dropped groups to sample two plots (i.e. the permanently marked and supplementary) within walking distance, whereas in general with vehicle-access fixed plots, more than one permanent plot could be sampled simultaneously by driving between plots. Supplementary plots were precisely geolocated, but not permanently marked. Results from these plots are included here. In total, over the period 1996–2009, we sampled 39 plots once, 121 plots twice and 15 plots three times, for a total of 326 samples.

The procedure for sampling the mammal fauna at plots is now standard for wildlife survey and monitoring in the monsoonal tropics of the Northern Territory (e.g. Woinarski *et al.* 2004a). Each sampled plot comprised a 50 m  $\times$  50 m square, with 20 Elliott traps (33 cm  $\times$  10 cm  $\times$  9 cm) placed equidistantly around the perimeter, a cage trap (56 cm  $\times$  20 cm  $\times$  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 cage and Elliott traps baited with a mixture of peanut butter, honey and oats, and all traps checked within 1 h of dawn of each of the three sampled days. All mammals captured were identified and released at the point of capture, and not individually marked. In addition to trap captures, mammals were also recorded through two 10-min spotlight searches, and scats and other signs were searched for during daylight sampling of the plot. An abundance value 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 1. Because of differences in trappability across the different trap types, abundance values are not directly comparable across different species.

Our focus here is on terrestrial small mammals (up to the size (~2–5 kg) of common brushtail possum, *Trichosurus vulpecula*, and short-beaked echidna, *Tachyglossus aculeatus*). We do not report data on macropods, dingoes or feral mammals (other than black rat, *Rattus rattus*), and we do not report data on bats. Unless otherwise indicated, tallies of mammal species richness or the number of mammal individuals are restricted to the set of native species forming the focus of this study (i.e. echidna, all dasyurids, all rodents, all possums and gliders, and the single bandicoot species *Isodon macrourus*).

The fire history of every plot over the sampling period was described from imagery and from regular visits to all plots by Kakadu rangers, with methods detailed in Edwards *et al.* (2003) and Russell-Smith *et al.* (2009). For every plot, a sequence of fire histories was derived, with the history for each plot for each year being categorised as either unburnt, burnt in the early dry season (April–June) or burnt in the late dry season (July–November). In this region, virtually no fires occur outside these months in the wet season.

There were no marked management changes to the Kakadu area over this monitoring period. However, the entire park was colonised by cane toads, *Rhinella marina*, sequentially from 2001 to ~2003. As previous studies (Watson and Woinarski 2003) have demonstrated that this colonisation results in a rapid decline of the northern quoll, *Dasyurus hallucatus*, in particular, some of the following analyses specifically omit consideration of this species.



**Fig. 1.** (a) Map of the Kakadu area, showing location of monitoring plots. Symbols: white circle = sampled once; grey circle = sampled twice; black circle = sampled three times. (b) Map of the broader regional context, including place names referred to in text.

### Analysis

The sampling regime described here is an imperfect monitoring program, especially in its earlier years, in that not all monitoring sites have been repeatedly visited at regular intervals. We recognise this limitation by first treating all samples independently, and simply reporting on mean abundance for all species against sampling year, and testing for overall trends using Spearman rank correlation. The analysis was repeated with restriction to only those plots that were eucalypt forests or woodlands, and also with northern quoll omitted.

We then restrict the data considered to (1) only that set of 15 plots that were sampled three times (1996, 2001 and 2007) and (2) only that set of 136 sample plots that were sampled between 2001 and 2004 and again between 2007 and 2009. For these sets, we compared abundance (for individual species, total individuals and number of species recorded) between the most recent and the previous sampling of the same plot, by using Wilcoxon matched-pairs tests. For the latter set of 136 plots, the analysis was repeated with restriction to only the 77 plots sampling the most widespread vegetation type (eucalypt open forest and woodland). The analysis was also repeated for total mammal individuals and the number of species following the exclusion of the northern quoll.

For every plot in the set of 136 plots, we calculated a change in abundance by using the index  $(A_2 - A_1)/(A_2 + A_1)$ , where  $A_2$  is the abundance recorded in the most recent sampling (i.e. the period 2007–09) and  $A_1$  is the abundance recorded during the previous sampling (i.e. 2001–04), with this change index varying from  $-1$  (if now absent but previously present) through  $0$  (if present at the same abundance in both sampling periods) to  $+1$  (if now present but absent at the previous sampling). Across plots, we compared this index with the fire history (the proportion of years for which fire was recorded in the period between samples, and the proportion of years for which late dry season fire was recorded), using Spearman rank correlation. Again, this analysis was repeated for the mammal dataset considering only eucalypt forest and woodland plots, and also for the set of all native mammals excluding the northern quoll.

### Results

In these samples, we recorded a total of 25 small mammal species, including one non-native species, *Rattus rattus* (Table 1).

Overall, the number of individual mammals and the number of species reported per plot decreased significantly ( $r_s = -0.42$ ,  $P < 0.001$ , for number of individuals, and  $r_s = -0.40$ ,  $P < 0.001$ , for number of species) over the 13-year sampling period (Fig. 2), by 71% for total number of individuals and 54% for number of species per plot. The proportion of plots that had no mammals increased from 13% in 1996 to 55% in 2009. Of 19 native species recorded from three or more samples, 10 species showed significant decline over this period, nine species showed no significant change, and no species showed significant increase (Table 1). Declines were most marked for northern quoll, *Dasyurus hallucatus*, fawn antechinus, *Antechinus bellus*, northern brown bandicoot, *Isodon macrourus*, common brushtail possum and pale field-rat, *Rattus tunneyi*. The pattern of decline across years was broadly similar when analysis was restricted to only the set of

194 eucalypt forest and woodland samples ( $r_s = -0.49$ ,  $P < 0.001$ , for number of individuals, and  $r_s = -0.47$ ,  $P < 0.001$ , for number of species), and when northern quolls were excluded from the tallies of individuals and species per plot ( $r_s = -0.37$ ,  $P < 0.001$ , for number of individuals, and  $r_s = -0.33$ ,  $P < 0.001$ , for number of species).

Mean species richness and the total number of individuals declined over the sampling period for the set of 15 plots sampled three times (Fig. 3), with this decline most severe in the period 2001–07 (Table 2).

For the larger set of plots sampled in 2001–04 and again in 2007–09, there was a highly significant ( $P < 0.001$ ) decline in the total number of mammal individuals (a 75% decline) and species (65% decline) (Table 1). Of 15 species reported in at least three of these samples, seven showed significant decline, eight showed no significant change, and none showed significant increase (Table 1). With analysis restricted to only eucalypt forest and woodland plots sampled in both 2001–04 and 2007–09, there remained a highly significant ( $P < 0.001$ ) decline of all mammal individuals and the number of species (Table 1). With analysis excluding northern quolls, there remained a highly significant decline in all mammal individuals and in the number of species for plots sampled in both 2001–04 and 2007–09 (Table 1).

For this set of repeat-sampled plots, the extent of change in the number of mammal individuals and native species over the period between samples was significantly negatively related to the percentage of years in which the plot was burned in that between-sample period ( $r_s = -0.25$ ,  $P < 0.01$ , for both the number of individuals and the number of species) (Fig. 4). Neither change in the number of native mammal individuals ( $r_s = 0.03$ ) nor species ( $r_s = 0.01$ ) was related significantly to the proportion of years in the between-sample period with late dry season fires ( $r_s = 0.03$  and  $0.01$ , respectively). These results were similar when the dataset was restricted to only the set of eucalypt forest and woodland plots. For this set, change in the number of mammal species and individuals per plot was significantly correlated with the percentage of years in which the plot was burnt ( $r_s = -0.29$ ,  $P < 0.01$ , for both species richness and number of individuals), but not with the percentage of years in which the plot was burnt by late dry season fires ( $r_s = 0.06$ ,  $P > 0.05$ , for both species richness and number of individuals). The relationships were also similar when northern quolls were excluded from the dataset: change in the remaining number of individual mammals and the remaining number of mammal species was negatively correlated with the percentage of years in which the plot burned ( $r_s = -0.25$ ,  $P < 0.01$ , for number of individuals, and  $r_s = -0.24$ ,  $P < 0.01$ , for number of species), and there was no significant relationship with the proportion of years with late fires ( $r_s = -0.02$ ,  $P > 0.05$ , and  $r_s = 0.01$ ,  $P > 0.05$ , respectively).

### Discussion

This analysis documents a collapse of the native small mammal fauna of Kakadu National Park over the course of this monitoring study, with decline particularly in the period of most substantial sampling, 2001–09. Severe decline has occurred across many species, across a broad taxonomic range and with contrasting ecologies. The pattern of decline may be

**Table 1. Summary table, showing changes in abundance of mammal species over the course of the monitoring program**

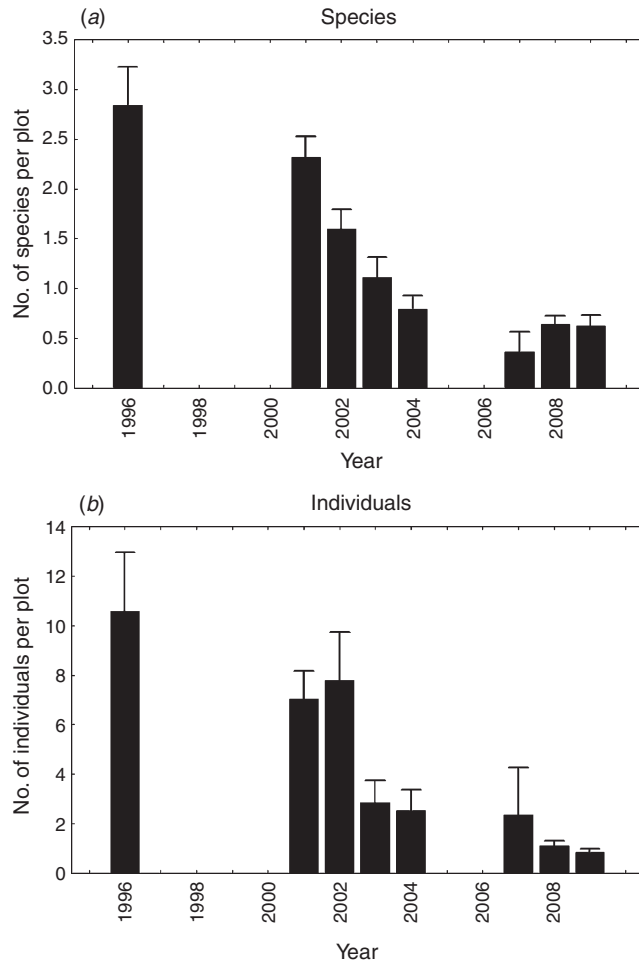
N1 refers to the total number of samples from which reported (of a maximum possible of 327 samples); N2 is the total number of samples from which recorded in either years 2001–04 or 2007–09 samples (of a maximum possible of 136 paired samples);  $r$  is the Spearman correlation coefficient of abundance against sampling year; abundance is the mean (s.e. in parentheses) for the 136 plots sampled in both periods 2001–04 and 2007–09, and  $Z$  is the  $z$ -score from Wilcoxon matched-pairs test. n.s. = not significant, \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$

Species name	Common name	N1	N2	$r$	Abundance 2001–04	Abundance 2007–09	$Z$
<i>Tachyglossus aculeatus</i>	Short-beaked echidna	9	8	0.07n.s.	0.04 (0.02)	0.02 (0.01)	0.63n.s.
<i>Antechinus bellus</i>	Fawn antechinus	26	16	-0.30***	0.40 (0.13)	0.04 (0.02)	2.92**
<i>Dasyurus hallucatus</i>	Northern quoll	37	29	-0.46***	0.49 (0.11)	0.02 (0.02)	4.27***
<i>Phascogale pirata</i>	Northern brush-tailed phascogale	2	2	-0.17**	0.02 (0.02)	0	–
<i>Planigale maculata</i>	Common planigale	17	13	-0.07n.s.	0.12 (0.05)	0.04 (0.02)	1.26n.s.
<i>Pseudantechinus bilarni</i>	Sandstone antechinus	18	16	0.09n.s.	0.10 (0.05)	0.13 (0.05)	0.57n.s.
<i>Sminthopsis bindi</i>	Kakadu dunnart	3	2	-0.11*	0.01 (0.01)	0	–
<i>Sminthopsis virginiae</i>	Red-cheeked dunnart	2	2	-0.09n.s.	0.04 (0.04)	0	–
<i>Isodon macrourus</i>	Northern brown bandicoot	34	23	-0.37***	0.34 (0.09)	0.04 (0.03)	3.39***
<i>Trichosurus vulpecula</i>	Common brushtail possum	8	6	-0.15**	0.07 (0.03)	0.01 (0.01)	2.20*
<i>Petaurus breviceps</i>	Sugar glider	2	2	0.04n.s.	0	0.01 (0.01)	–
<i>Petropseudes dahli</i>	Rock ringtail possum	8	7	0.11n.s.	0.02 (0.01)	0.04 (0.02)	0.73n.s.
<i>Conilurus penicillatus</i>	Brush-tailed rabbit-rat	1	1	0.03n.s.	0	0.01 (0.01)	–
<i>Hydromys chrysogaster</i>	Water rat	1	1	-0.08n.s.	0.01 (0.01)	0	–
<i>Leggadina lakedownensis</i>	Tropical short-tailed mouse	1	1	0.03n.s.	0	0.01 (0.01)	–
<i>Melomys burtonis</i>	Grassland melomys	26	18	0.01n.s.	0.32 (0.13)	0.40 (0.17)	0.47n.s.
<i>Mesembriomys gouldii</i>	Black-footed tree-rat	6	1	-0.25***	0.01 (0.01)	0	–
<i>Pseudomys calabyi</i>	Kakadu pebble-mound mouse	1	1	-0.08n.s.	0.02 (0.02)	0	–
<i>Pseudomys delicatulus</i>	Delicate mouse	6	5	-0.17**	0.04 (0.02)	0	2.02*
<i>Pseudomys nanus</i>	Western chestnut mouse	10	9	-0.05n.s.	0.07 (0.03)	0.02 (0.02)	1.30n.s.
<i>Rattus colletti</i>	Dusky rat	5	3	-0.12*	0.84 (0.48)	0	1.60n.s.
<i>Rattus rattus</i>	Black rat	3	2	0.06n.s.	0	0.02 (0.02)	–
<i>Rattus tunneyi</i>	Pale field-rat	32	22	-0.34***	0.70 (0.19)	0.04 (0.02)	3.62***
<i>Zyzomys argurus</i>	Common rock-rat	58	40	-0.01n.s.	0.82 (0.22)	0.24 (0.06)	2.92**
<i>Zyzomys maini</i>	Arnhem rock-rat	16	12	0.10n.s.	0.19 (0.13)	0.09 (0.03)	0.04n.s.
Total individuals (of native species)				-0.43***	4.68 (0.69)	1.17 (0.22)	6.14***
Native species richness				-0.41***	1.34 (0.11)	0.61 (0.07)	5.37***
Total individuals (of native species) (eucalypt plots only)					4.44 (0.75)	1.00 (0.31)	5.15***
Native species richness (eucalypt plots only)					1.44 (0.15)	0.53 (0.10)	4.98***
Total individuals (of native species) (excluding quolls)					4.18 (0.68)	1.15 (0.22)	5.37***
Native species richness (excluding quolls)					1.14 (0.09)	0.61 (0.07)	4.37***

even more marked than evident in the results here, as a range of other evidence suggests decline also for some species that were insufficiently recorded in the present study, most notably including brush-tailed rabbit-rat, *Conilurus penicillatus*, and northern brush-tailed phascogale, *Phascogale tapoatafa* (Firth *et al.* 2006a). These are disconcerting results given that this is one of Australia's largest and best-resourced National Parks, located within an ostensibly largely unmodified region. It is also disconcerting in that many of the declining species are closely related in ecology or taxonomy to the mammal species that became extinct elsewhere in Australia over the period of ~1860–1960.

These results should be viewed within a broader temporal and spatial context. Decline was previously reported over the period 1986–99 for the mammal fauna of the Kapalga area of Kakadu (Braithwaite and Griffiths 1996; Braithwaite and Muller 1997; Woinarski *et al.* 2001), with this decline particularly evident for many of the species showing most marked decline for the period reported here; that is, to some degree the results reported here are a continuation or amplification of previously apparent trends.

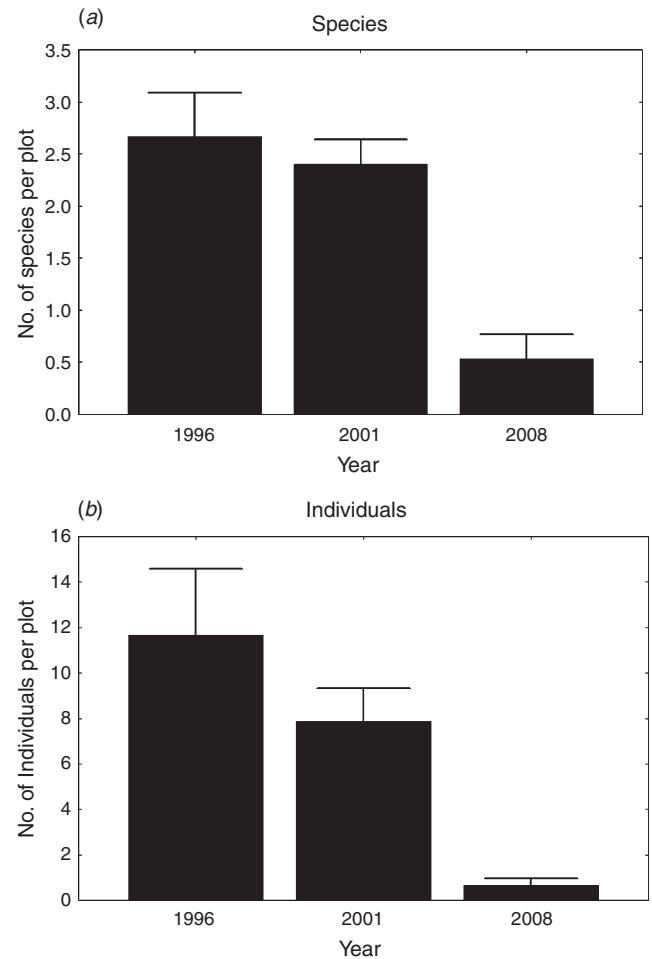
A pattern of decline in the mammal fauna has also been reported from a range of other sites in northern Australia, although the timing of such decline has previously been



**Fig. 2.** Change over the course of the monitoring period in (a) the number of native mammal species and (b) the number of individual native mammals recorded per plot. Columns show the mean, and whiskers the standard error. Sample sizes: 15 plots (1996), 22 plots (2001), 37 plots (2002), 57 plots (2004), 11 plots (2007), 101 plots (2008) and 56 plots (2009).

difficult to discern because of the sparseness of the historical information base (Kitchener 1978; McKenzie 1981; Braithwaite and Griffiths 1994). The Kakadu monitoring program provides for far more precision in defining the timing and patterning of decline.

We have two comparable monitoring programs (using the same standard sampling methodology) in other conservation reserves in the Top End region of the Northern Territory, at Litchfield National Park and Garig Gunak Barlu National Park (Cobourg Peninsula). Woinarski *et al.* (2004a) reported a slight increase in the mammal fauna at Litchfield over the period from 1995/96 to 2001/02, on the basis of repeat sampling of 47 plots. Thirty-nine of these plots have now been sampled three times, with the most recent sampling now indicating a significant decline (Fig. 5a:  $r = -0.20$ ,  $P < 0.05$ , across the three sampling periods). At Garig Gunak Barlu National Park, a set of 30 plots has now been sampled four times during the period 2004–09. These data also indicate a significant decline in the native



**Fig. 3.** Change over time in (a) the number of native mammal species and (b) the number of individual mammals for the 15 plots sampled three times. Columns show the mean, and whiskers the standard error.

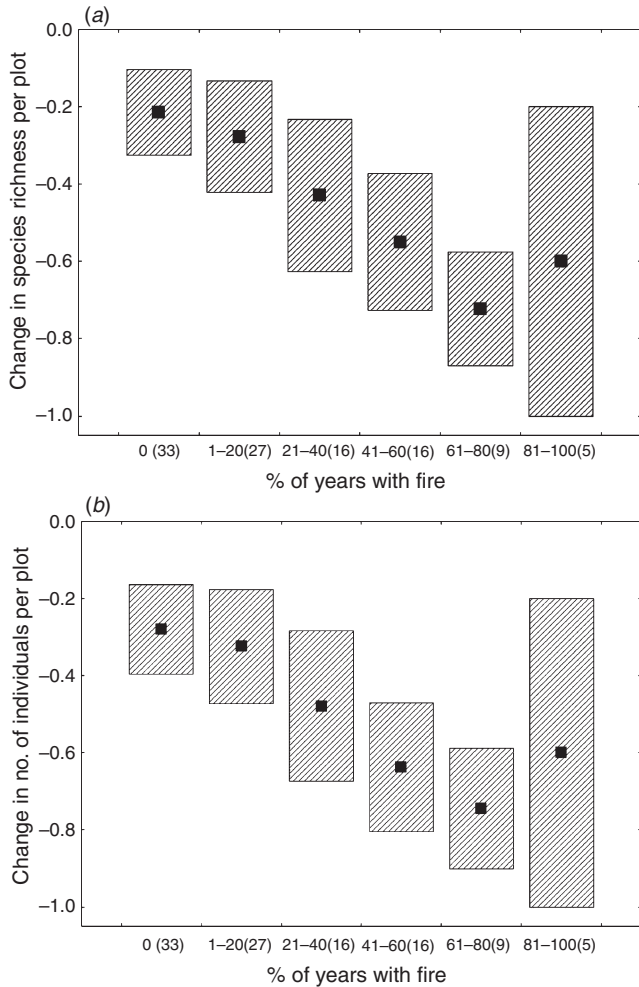
**Table 2.** Significance of change in the number of individuals and the number of species per plot, for the 15 plots sampled three times (1996, 2001, 2008) (see Fig. 3)

Values in the body of table show z-score (from Wilcoxon matched-pairs test). n.s., not significant; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$

No. of individuals			No. of species		
1996/2001	1996/2008	2001/2008	1996/2001	1996/2008	2001/2008
0.80n.s.	3.18**	3.52***	0.31n.s.	2.93**	3.27***

mammal fauna (Fig. 5b:  $r = -0.27$ ,  $P < 0.01$ ). However, in neither case has the decline been as severe as for Kakadu.

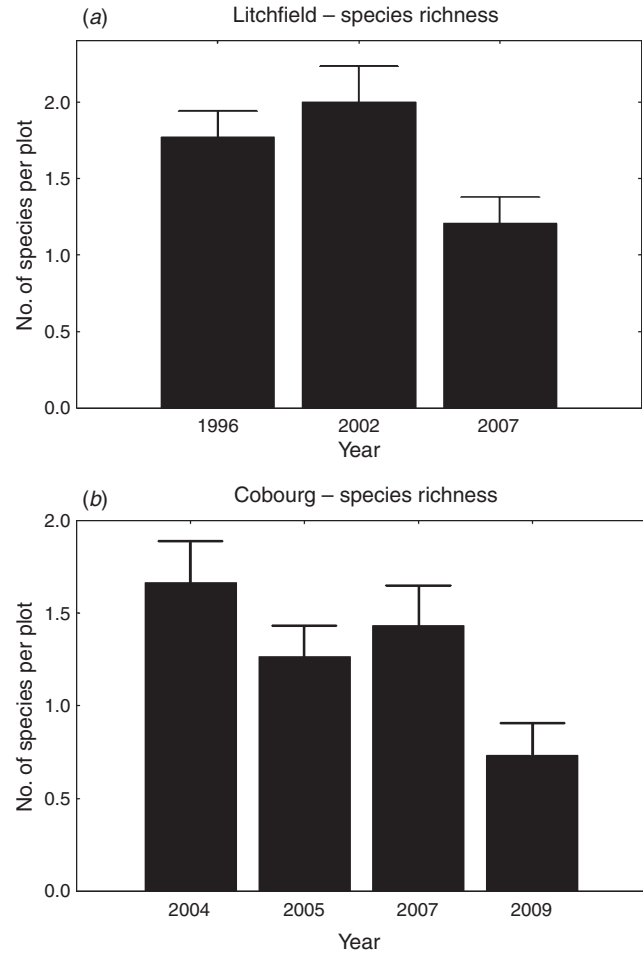
Another context for considering these results is the patterning and causes of decline and extinction of mammals elsewhere in Australia. Most such declines and extinctions have not occurred because of marked changes in land use. Rather, the most compelling evidence suggests extinctions have been primarily driven by exotic predators, European red fox, *Vulpes vulpes*, and cat, *Felis catus* (Johnson 2006), in some cases with contributions from vegetation changes due to grazing by non-



**Fig. 4.** Relationship between the extent of change in (a) the number of native mammal species within a plot and the fire history of that plot, for only those plots sampled in 2001–04 and again in 2007–09, and (b) the number of native mammal individuals. Small black squares indicate the means, larger boxes with diagonal striping indicate standard errors. Values in parentheses on the fire axis indicate the number of plots with that fire history.

native mammals or due to altered fire regimes (Morton 1990). Disease may have contributed to some declines, although, with the current notable exception of devil facial tumour disease in the Tasmanian devil, *Sarcophilus harrisii* (Hawkins *et al.* 2006), the evidence remains somewhat meagre. One characteristic of the Australian mammal declines has been the ‘saving’ of some formerly widespread species on ‘lifebuoy’ islands, a characteristic supporting the role of either feral predators or disease rather than habitat change as primary causal agent (Short and Turner 1994). To some extent, a comparable pattern of greater chance of persistence on islands may also be occurring in the mammal fauna of northern Australia (Southgate *et al.* 1996; Firth *et al.* 2006b).

For the decline in the mammal fauna of Kakadu National Park, we consider possible causes to be inappropriate fire regimes, predation by feral cats, poisoning by cane toads, disease, environmental change due to invasion by weeds and/



**Fig. 5.** Change in the number of mammal species per plot for resampled plots with comparable monitoring programs and identical sampling protocols at (a) Litchfield National Park (39 plots) and (b) Garig Gunak Barlu National Park (Cobourg: 30 plots).

or impacts of non-native herbivores, a combination of these factors, or to be not universal but rather species-specific and idiosyncratic. These alternatives are considered in turn below.

Fire is a pervasive factor in monsoonal northern Australia, and its influence on the abundance of small native mammals has been somewhat contested. Woinarski *et al.* (2004b) demonstrated a marked change in the mammal assemblage in a cross-fence comparison between a frequently burnt site and a site for which fire had been excluded for 23 years, and noted that such long-unburnt sites were abnormal. Far less substantial differences were evident in the mammal fauna in the Kapalga experiment, where large areas were exposed to four contrasting fire regimes (annual early dry season fire, annual late dry season fire, unburnt, and annual burns throughout the year) over a 5-year period (Corbett *et al.* 2003). However, a subset of those data were more substantially analysed and modelled for one species, *Isoodon macrourus*, by Pardon *et al.* (2003) who demonstrated a marked decline under all fire regimes, and particularly that of annual late dry season fires, and argued that these results indicated that this species required a patchy and variable fire regime.

Detailed autecological studies of *Trichosurus vulpecula* (Kerle 1985), *Conilurus penicillatus* (Firth *et al.* 2006a), *Antechinus bellus* (Friend 1985) and *Mesembriomys gouldii* (Friend 1987; Rankmore 2006) in this region have all indicated that habitat suitability is generally reduced under frequent fire regimes, particularly where these result in simplification of the forest structure and a reduction in understorey shrubs and hollow logs. Marked responses of mammal species to a single (intense) fire were reported for the Kakadu sandstone highlands (Begg *et al.* 1981), and in a comparable lowland environment in the central Kimberley (Legge *et al.* 2008). The current monitoring study (Fig. 4) suggests that there is a substantial influence of fire on the abundance of mammals in Kakadu; under all fire regimes, plots experienced decline in mammal richness and number of individuals, and this decline was markedly greater with increasing fire frequency. If the current fire regime is driving the decline of mammals in Kakadu, this mirrors a broadly contemporaneous and extensive decline in some 'fire-sensitive' plants in Kakadu and elsewhere in northern Australia, under some current fire regimes (e.g. Bowman and Panton 1993; Russell-Smith *et al.* 1998, 2002; Bowman *et al.* 2001; Prior *et al.* 2007).

However, fire alone cannot explain the pattern of rapid decline reported here, because there has been no substantial change in the fire regime of Kakadu that coincides directly with this most recent precipitous decline. Frequent fire has been a characteristic of this park for at least 30–50 years (Press 1988; Gill *et al.* 2000; Edwards *et al.* 2003; Russell-Smith *et al.* 2009), and over the monitoring period of this study, the fire regime may have become slightly more benign, with some increase in the extent of early dry season fires leading to some decrease in the extent of more intense late dry season fires. Even though this shift in timing of fires is a management objective, the data reported here suggest that decline of mammal fauna is more related to fire frequency in total rather than to the occurrence of late dry season fires.

There is little direct evidence of the role of predation by cats in the decline reported here. Incidental results from telemetry studies in Kakadu, examining the ecology of *Dasyurus hallucatus* (Oakwood 2000) and the small arboreal monitors *Varanus tristis* and *V. scalaris* (Sweet 2007) have demonstrated that predation by feral cats may be a substantial contributor to mortality for these species, and hence perhaps many others. However, there is little information on the abundance, diet and ecology of feral cats in this region. Feral cats have probably been present in the area for at least a century (Short and Calaby 2001; Abbott 2002), so it is difficult to tie predation by feral cats directly to the recent rapid decline of this mammal fauna. Nonetheless, O'Neill (2002) suggested that feral cat numbers may have increased recently, at least in the Kapalga area, as a consequence of decline in the dingo population, citing Corbett (1995) 'heartworm virtually eliminated dingoes at Kapalga (Kakadu National Park) in the 1980s'.

Cane toads invaded Kakadu National Park in 2000/01 and spread throughout over the next 2–3 years. They were undoubtedly responsible, through poisoning in predation attempts, for the extirpation reported here of *Dasyurus hallucatus* across most of Kakadu (and elsewhere in the monsoonal tropics of the Northern Territory), and this rapid

loss of a formerly common native mammal species is a substantial component of the reduction reported here in the number of native mammal species and individuals per plot. The colonisation of Kakadu by cane toads may have also affected other native mammals, both positively and negatively. The loss or marked reduction in the abundance over large areas of many terrestrial predators (quolls, large goannas, snakes) because of toads (Phillips *et al.* 2003; Doody *et al.* 2006; Griffiths and McKay 2007) should have benefited many native mammal species that were presumably formerly major prey items for these predators. No such increase is evident in our monitoring data. Conversely, some other carnivorous mammal species may have suffered declines because of cane toad poisoning. This may be a plausible cause for the decline reported here for *Phascogale pirata*, *Antechinus bellus* and *Sminthopsis bindi*. More conjecturally, some more largely omnivorous or herbivorous species (such as *Isoodon macrourus*, *Trichosurus vulpecula*, *Rattus tunneyi* and *Mesembriomys gouldii*) may also have declined because of mortalities associated with predation attempts on toads. However, although toads have clearly contributed to the observed changes in status, the Kakadu mammal fauna (explicitly including *Dasyurus hallucatus*) was in decline before the arrival of toads (Woinarski *et al.* 2001).

There is no direct evidence for a role of disease in the decline reported here, but such evidence may be difficult to detect without a specific focussed study. The broad taxonomic and ecological range spanned by the declining species argues somewhat against a simple disease explanation (Johnson 2006). However, in a review of fragmentary historical sources, Abbott (2006) noted that a wide range of native mammal species declined sharply across large areas of Western Australia because of a presumed novel disease over the period 1875–1925. In considering the possibility of disease as a causal factor in the decline observed in the Kakadu mammal fauna, we note the increase in reporting of *Rattus rattus* in our inventory studies across the monsoonal tropics of the Northern Territory (J. Woinarski, unpubl. data), including in Kakadu and other areas remote from infrastructure or other substantial disturbance. Studies elsewhere have shown that parasites carried by this species have spread to native rodents (e.g. Smith and Carpenter 2006), and diseases carried by this species have led to a rapid decline and extinction of two island endemic *Rattus* species (e.g. Wyatt *et al.* 2008).

There is little evidence for the decline being caused by environmental change owing to spread of weeds and/or impacts of feral herbivores. Although there are some major concerns about weeds in Kakadu (Cowie and Werner 1993), most of the ecosystem-transforming weed species (such as mimosa, *Mimosa pigra*, gamba grass, *Andropogon gayanus*, perennial mission grass, *Pennisetum polystachion*) are relatively localised and controlled, and most of the sampled plots had no non-native plant species (Edwards *et al.* 2003). Kakadu has populations of feral Asian water buffalo, *Bubalus bubalis*, cattle, *Bos indicus*, donkey, *Equus asinus*, horse, *E. caballus*, and pig, *Sus scrofa* (Bradshaw *et al.* 2007), with at least some consequential localised environmental damage. However, for most of these species, numbers have probably been greater in the past (when the area was managed as a set of pastoral properties) and far higher densities of feral buffalo

were present before a major eradication program in the period 1980–89 (Skeat *et al.* 1996). Historically, changes in the abundance of feral herbivores (particularly buffalo and cattle) have led to wide-ranging changes in vegetation patterning in the Kakadu area, although these are relatively subtle for non-wetland vegetation (Petty *et al.* 2007; Bowman *et al.* 2008; Lehmann *et al.* 2008); however, the timing and magnitude of such changes does not appear to coincide with that of the decline of mammals. There has been some other vegetation change in Kakadu, notably some expansion over the last 50 or so years in monsoon rainforests, probably attributable to increased atmospheric CO<sub>2</sub> (Banfai and Bowman 2006), and some upriver expansion of mangroves (Finlayson *et al.* 2006); however, these gradual and relatively localised changes also do not coincide with the rapidity and extent of mammal decline.

On the basis of the discussion above, we do not believe that the observed decline can be satisfactorily explained by a single factor alone. Rather, several factors may be operating in a compound manner. Especially noting Fig. 4, one of these factors appears to be the high frequency of fires. Predation by cats is likely to be more substantial in extensively burnt areas (which provide fewer shelter sites for small mammals) (Oakwood 2000). Cane toads are probably also favoured by, although more likely to be encountered by predatory small mammals in, areas with little undergrowth, such as burnt areas (Lever 2001).

One other explanation is that there is not one explanation. Rather, there are different primary causal factors for different species. This *Anna Karenina* hypothesis ('All happy families are alike; each unhappy family is unhappy in its own way': Tolstoy 1877) may be realistic, given the taxonomic and ecological range of species involved, and the clear evidence of the tight linkage between the marked very recent decline of *Dasyurus hallucatus*, but less so other species, and the colonisation of the area by cane toads.

The rapid and severe decline reported here calls for an urgent management response, not least because the World Heritage qualification case for Kakadu National Park emphasised its value as a secure area for threatened species. Until now, the form of this management response has been obscured by uncertainty about the primary cause, or relative contribution of different causes, and by practical difficulties of implementing effective threat-management responses. The data reported here indicate that frequent fire is a contributor to mammal decline, and hence managers should aim to reduce substantially the extent and frequency of fire. The greater the reduction achieved, the more likely it should be to retain the mammal fauna. On the basis of the evidence here, we suggest a nominal target of no more than 20–25% of the area burnt per year (appreciably less than the current 40–50%). We recognise substantial practical management difficulties in such a target.

The present study has demonstrated the marked value of monitoring programs in detecting trends in biodiversity, and in providing some inference about the drivers of those trends. However, monitoring programs have some limitations, and complementary experimental studies may be better suited for providing more precise and timely information on the relative impacts of a range of threatening factors, or the relative success of a range of possible management responses. The key

information gap identified here is the relative contribution of predation by cats, poisoning by toads and disease in the observed overall mammal decline, or the decline of any species (except for toads and *D. hallucatus*). We propose adaptive management trials based on enclosure fencing for determining the impacts of cats and toads. We also propose a systematic assessment of the disease status of native mammals and *Rattus rattus*, with this assessment particularly comparing the disease status in native mammals at sites recently colonised by *R. rattus* and at sites with no such colonisation. Such research must be embedded within an adaptive management framework, to ensure rapid identification and implementation of priority management responses.

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