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Declines in the mammal assemblage of a rugged sandstone environment in Kakadu National Park, Northern Territory, Australia.

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Abstract. There has been marked recent decline in the terrestrial mammal fauna across much of northern Australia, with most documentation of such decline for lowland areas. Here we report changes in the assemblage of small mammals in a rugged sandstone environment (Nawurlandja, in Kakadu National Park) over intermittent sampling between 1977 and 2002. Four native mammal species were commonly recorded in the original sampling: sandstone antechinus (*Pseudantechinus bilarni*), northern quoll (*Dasyurus hallucatus*), Arnhem rock-rat (*Zyzomys maini*) and common rock-rat (*Z. argurus*). Trap success rates declined significantly for the northern quoll, Arnhem rock-rat and all species combined, but increased for the common rock-rat. Despite being recorded commonly in the initial (1977-79) study, no Arnhem rock-rats were recorded in the most recent (2002) sampling. Trap success rates for northern quoll declined by ca. 90% from 1977-79 to 2002. The reasons for change are not clear-cut. Notably, all sampling occurred prior to the arrival of cane toads (*Rhinella marina*), a factor that has caused severe decline in northern quolls elsewhere. Fire was more frequent in the sampling area in the period preceding the 2002 sampling than it was in the period preceding the initial (1977-79) sampling, and this may have contributed to change in mammal abundance.

Running head: Mammal decline at a sandstone site

Additional keywords: monitoring, rock-rat, northern quoll, sandstone antechinus, fire.

Introduction

Several studies have suggested a pattern of recent broad-scale decline in components of the terrestrial mammal fauna of northern Australia (Kitchener 1978; McKenzie 1981; Braithwaite and Muller 1997; Oakwood 2000; Woinarski *et al.* 2001; Pardon *et al.* 2003; Firth *et al.* 2010; Woinarski *et al.* 2010, 2011a, 2011b; Ziembicki *et al.* 2013, 2015; Davies *et al.* 2017). These studies have mostly been conducted in the extensive *Eucalyptus*-dominated lowland savannas. Many intensive demographic studies undertaken in the 1980s and 1990s of individual mammal species or mammal assemblages in lowland environments (e.g. Friend 1985; Friend and Taylor 1985; Friend 1987; Friend 1990; Braithwaite and Brady 1993; Braithwaite and Griffiths 1994, 1996; Braithwaite and Muller 1997) provided a foundation against which more recent studies can be compared to provide an assessment of the timing and extent of subsequent mammal decline.

Far less attention has been paid to the rugged sandstone ranges that contrast sharply with the relatively featureless lowlands, although some monitoring data indicate declines of some mammal species in these environments, albeit less drastic than for lowland sites (Woinarski *et al.* 2004, 2010). These sandstone areas support a diverse set of mammal species, many of which are endemic to them (Woinarski *et al.* 2009); and their topographic complexity has been presumed to offer refuge from some threatening processes that may pervade the lowland environments (Freeland *et al.* 1988; Radford *et al.* 2014; Hohnen *et al.* 2016b). For example, whereas vegetation change due to extensive pastoralism has been posited as a possible contributory agent for faunal change in the lowlands (Woinarski *et al.* 2001; Woinarski and Ash 2002; Woinarski and Fisher 2003; Legge *et al.* 2011), cattle and feral livestock generally are largely absent from more rocky and rugged areas, and hence this factor would be unlikely to be involved in any change in the fauna of the sandstone uplands.

Detection of a consistent pattern of change in the sandstone mammal fauna is constrained by the relatively sparse set of quantitative studies that may serve as foundations for monitoring. Some such foundation and subsequent monitoring has been reported for rugged areas of the Kimberley (Start *et al.* 2007, 2012), but there have been few relevant studies in the upland areas of monsoonal Northern Territory. In this region, the first and most substantial mammal demographic study was from 1977 to 1980 at one sandstone site (Little Nourlangie Rock, now called Nawurlandja) within what is now Kakadu National Park (Begg 1981a, 1981b, 1981c; Begg *et al.* 1981; Dunlop and Begg 1981b). This set of studies focused particularly on the four small to medium-sized mammal species that were commonly caught at the site: northern quoll (*Dasyurus hallucatus*) (weight *ca*. 600 g), sandstone antechinus (*Pseudantechinus bilarni*) (weight *ca*. 25 g) (with name given as *Antechinus bilarni* in Begg's papers), Arnhem rock-rat (*Zyzomys maini*) (weight *ca*. 120 g) (with name given as *Z. woodwardi* in Begg's papers) and common rock-rat (*Z. argurus*) (weight *ca*. 50 g). A few other terrestrial small to medium-sized mammals were reported rarely and incidentally in this initial study (Dunlop and Begg 1981b), and that study did not consider macropods or bats.

Our paper reports on a re-sampling of this site in 1994 and in 2002 and assesses change in these four mammal species since Begg's original study. There are two main constraints in the interpretation of any such comparison. First, we provide only three points in a temporal pattern, and as such we cannot readily disentangle monotonic longer-term trends from oscillations without long-term trends. Second, this single site may not be representative of the status of sandstone environments (and of their mammal fauna) across the broader region. Such interpretive limitations could feasibly be resolved through meta-analyses of results from a series of re-samplings of historic studies (although we note that there are few such foundation studies) and/or through broader-based long-term monitoring program: such a program has now been established for this region (Russell-Smith *et al.* 2014).

Begg *et al.* (1981) provided one interpretive key to the population status of the complement of mammals in his studies. Following his initial autecological studies from 1977 to 1979, he burnt the study site and then assessed short-term (to 13 months post-fire) responses of the four mammal species, reporting population declines especially for the Arnhem rock-rat. In recognition of the possible influence of fire on the mammal fauna considered in this study, we assessed the fire history of the site in the seven years preceding our 2002 sampling. Unfortunately, this was the only potential threat that was considered in the initial and subsequent sampling: other potential factors (such as feral cats *Felis catus*) were not monitored. However, notably the 1977-79 and our re-sampling of the study site occurred prior to the 2003 invasion of this area by the cane toad (*Rhinella marina*), demonstrated to have caused severe decline in northern quolls elsewhere (Burnett 1997; Oakwood 2004; Oakwood and Foster 2008; O'Donnell *et al.* 2010).

The objective of this study is to extend and complement the previous substantial studies of recent change in the lowland mammal fauna of northern Australia, through re-sampling the upland sandstone site with the most substantial historical information, and in doing so contribute towards further clarification of information on the timing, extent and potential causality of mammal decline in the region. We assess the extent and pattern of change in the assemblage of small mammals at this rugged site over a period of ca. 25 years, and provide some inferences on factors that may have contributed to any observed change.

Methods

Study Site

The study was undertaken at Nawurlandja (12°51'S, 132°47'E) in Kakadu National Park (although the initial sampling commenced before the Park's declaration). This sandstone block occupies 2 km^2, and is an outlier of the sandstone massif of the Western Arnhem Land Plateau. Nawurlandja rises about 100 m from the surrounding plain, which isolates it (by about 500 m) from the much larger (30 km^2) Nourlangie Rock (Burrunggui), itself about 10 km from the main massif.

The study area has a strongly seasonal monsoonal climate, with ca. 90% of the annual rainfall of ca. 1500 mm occurring during the December-March wet season. Numerous small streams flow down the eastern face of Nawurlandja into an adjacent billabong. Because of the rocky nature of the site it remains largely undisturbed by feral pigs (*Sus scrofa*), cattle (*Bos taurus*), water buffalo (*Bubalus bubalis*) and horses (*Equus caballus*) that occur (sometimes in high numbers) in the surrounding lowland habitats (Dunlop and Begg 1981b; Bradshaw *et al.* 2007). There is also little disturbance from weeds.

In the original study, Dunlop and Begg (1981b) defined, described and mapped four distinct habitats for the study site (Rocky Crevices, Closed Forest, Rocky Slopes and Scree Slopes), with these habitats differentiated mostly on vegetation structure, cover and floristic composition, and geomorphology.

Although Dunlop and Begg (1981a) provided a list of plant species recorded at the site at the time of the 1977-79 sampling, the non-quantitative nature of this description prohibited an assessment of vegetation change over the subsequent 23 years to our 2002 re-sample.

1977-79 mammal sampling

The Begg study provides a good foundation for comparison with subsequent sampling because of its highly explicit sampling protocol and the extent to which the data were reported. The original trapping methodology was described in Begg (1981b) and is summarised here. In each sampling period, 100 Elliott traps were set in each of the four habitats, in two fixed transect lines of 50 traps. Traps were baited with peanut butter, oats, mixed fruit and sardines. Traps were placed approximately 10 m apart and the two lines were separated by 20-40 m, depending on the terrain. The traps were set for three consecutive nights around the middle of every month from February 1977 to June 1979. Sampling effort totalled 34,800 trap-nights, with 300 trap-nights per month in each of the four habitats. Using the same procedure and monthly sampling effort, Begg extended the original study to August 1980 to examine the response of the mammal fauna to his imposition of an experimental fire (in July 1979) (Begg *et al.* 1981).

Re-sampling

Since the location of the original trapping transects was not documented nor presented in published maps it was impossible to relocate the 1977-79 study's transects precisely. However, the four habitats identified in the original study were mapped in Dunlop and Begg (1981b), were still easily identifiable on ground and provide only limited possible options for transects of the dimensions described. As such the locations of transects in the repeat sampling were assumed to be largely consistent with that of the original study. Repeat sampling was conducted in 1994 (by MO) and 2002 (by MI) using methodology that largely replicated the original design (with variations as described below).

The 1994 re-sample comprised one trapping session only, in mid-June. Because the focus of this re-sampling was an assessment of the status of northern quoll, trapping was carried out only at the two habitats deemed to be most relevant for this species – Rocky Slopes and Rocky Crevices. One hundred Elliott traps were set in two lines in each of the two habitats, following the spacing used by Begg, for three consecutive nights. The total trapping effort was 600 trap-nights.

Re-sampling in 2002 comprised two trapping sessions, in April and July. In the April 2002 re-survey, 200 Elliott traps were laid out in two lines in each of the four habitats. This effectively doubled the trapping effort of any one trapping episode in the original survey, giving a total of 600 trap-nights in each habitat. In the July 2002 re-survey, 100 Elliott traps were laid out in every habitat, equalling the trapping effort of one episode in the original survey. The total trapping effort in 2002 was 3600 trap-nights.

Fire history

For at least several years prior to the 1977-79 study, and during that study, fire had largely been excluded from the study site, except for two relatively small individual fires in 1973 and 1976 that affected less than 25% of the study area (Dunlop and Begg 1981b). As a result, Begg's study (Begg 1981a, 1981b, 1981c) mostly occurred in areas that had been unburnt for at least 4-6 years. However, in July 1979, after the completion of the initial sampling, the study area was deliberately burnt. Fires were ignited using a combination of incendiaries dropped from a helicopter and ground-based drip torches that were used to burn areas that remained unburnt after the aerial burning (Begg *et al.* 1981). After the application of this fire, the populations of small mammals were monitored for a further 12 months. As reported by Begg *et al.* (1981), overall trapping rates declined over this period, although changes were inconsistent between species, habitats and seasonal comparisons (Table 1).

We derived fire histories for the study area for the six years preceding (and the year of) our 2002 re-survey. The locations of trapping transects used in 2002 were overlaid on Landsat TM satellite imagery using ArcView 3.2a software (ESRI 2002), then, for each transect, we counted the number of pixels burnt in each year from 1996-2002 and thence calculated the percentage of each transect burnt annually.

Analysis

The 1977-79 study reported percentage trap success for each of the four species in each of the four habitats, for each of four seasons (March-May, June-August, September-November and December-February) (Begg 1981a, 1981b, 1981c). Trap success rates for our two 2002 re-samples (April, July) were compared with means for the 1977-1979 sample years for March-May and June-August respectively, in all cases with results from all four habitats combined. We also compare our results with Begg's post-fire results of June-August 1980 and March-May 1980. The analysis we used is a z-ratio test of proportions, testing whether the earlier trap success rate is the same as or different to that of our 2002 re-sampling. Tests were performed for each of the four species, and for all species combined. Given that this analysis involves 20 separate comparisons (i.e. four species and all mammal species combined, with two seasonal comparisons, and with 2002 results compared with both 1977-79 and 1980 results), probability thresholds were adjusted by Bonferroni correction. Our analyses are based on trap success rates, in part because the initial (1977-79) study design did not allow for estimates of detectability or density. Trap success rates generally provide a reasonable index of relative abundance or population size for individual species, but (because of varying trappability between species) do not provide a good indicator of relative abundance among different species (Slade and Blair 2000; Hopkins and Kennedy 2004).

We also present results from our June 1994 sampling of two habitats relative to those of sampling of the same two habitats in June-August 1977-79, June-August 1980 and July 2002, but, given the smaller sample sizes involved, we do not test statistically for differences among these samples.

Patterns in small mammal community composition were also examined using multi-dimensional scaling in the program PRIMER (Clarke and Gorley 2001). Untransformed abundance (trap success rate) data for all four species were included in the ordination, with compositional similarity of paired cases (unique combinations of habitat, sampling season and sampling year) assessed using the Bray-Curtis similarity index. The influence of sampling year (four levels: Begg's 1977-79 study, the 1980 post-fire sampling, 1994 and 2002), habitat, and sampling season (March to May *cf.* June to August) on this pair-wise similarity was examined using ANOSIM (Clarke and Gorley 2001) with the significance of the resultant global R-statistic tested by comparison with 1000 random configurations.

Results

Trap success rates in April 2002 were lower for Arnhem rock-rat (decline of 100%), and significantly lower for northern quoll (decline of 95%) and sandstone antechinus (decline of 96%) and for total mammals (decline of 73%) than in March-May 1977-1979 (Table 1a). In contrast, trap success rate was significantly greater for common rock-rat in April 2002 than in March-May 1977-1979 (increase of 126%). These trends were generally consistent when our re-sampling was compared with results from March-May 1980 (Table 1), 8-10 months after Begg's extensive experimental fire, notwithstanding an overall decrease in capture rate from pre-fire (1977-79) to post-fire (1980) (Begg *et al.* 1981).

Trap success rates in July 2002 were lower for northern quoll (88% decline) than in June-August 1977-79 and significantly lower for Arnhem rock-rat (100% decline) (Table 1b). Capture rates in July 2002 for sandstone antechinus were lower (by 24%) than in June-August 1977-79, but significantly higher than for the June-August 1980 post-fire sampling. Capture rates in July 2002 were significantly higher for common rock-rats compared to the June-August 1977-79 sampling (increase of 102%) but not significantly different to rates in June-August 1980 post-fire sampling.

No Arnhem rock-rats were caught in either of the two 2002 re-sample periods, whereas 30 captures would have been expected based on their 1977-1979 capture rates and the trap effort in 2002. Only two northern quolls were captured during the 2002 re-samples, whereas the 1977-1979 capture rates would have predicted a tally of 28 given the trap effort in 2002. The expected tally for sandstone antechinus was 139 (whereas 41 were caught), and for common rock-rat was 33 (whereas 63 were caught).

Trap success results for northern quoll and Arnhem rock-rat from the more limited 1994 sampling of two habitats were intermediate between the earlier (1977-79, 1980) and later (2002) sampling, indicating decline for these species probably substantially preceded our 2002 sampling.

Variation in mammal species composition was significantly related to sampling period ($R=0.47$, $p=0.001$), with significant variation between the 1977-79 and 1979-80 periods ($R=0.17$, $p<0.05$), 1977-79 and 1994 periods ($R=0.85$, $p<0.05$), 1977-79 and 2002 periods ($R=0.60$, $p<0.001$), 1979-80 and 1994 periods ($R=0.57$, $p<0.05$), and 1979-80 and 2002 periods ($R=0.68$, $p<0.001$), but not between the 1994 and 2002 periods ($R=0.03$, $p>0.05$). In contrast to the strong influence of sampling period, variation in mammal species composition was unrelated to either habitat ($R=0.058$, $p>0.05$) or sampling season ($R=0.045$, $p>0.05$).

Fire history

The study area was burnt in 5 of the 7 years preceding the 2002 sampling, with an average of 17% burnt per year: 1996 (fires burnt 17% of the study area), 1997 (17%), 2000 (24%), 2001 (31%) and 2002 (31%),

Discussion

This study considers only one site, Nawurlandja, and provides only a limited number of points in a temporal sequence. Furthermore, we recognise that this site, due to its small size and isolation, may be unrepresentative of rugged upland areas more broadly: for example its isolation may reduce the likelihood of re-colonisation, following local population decline or extirpation, from a larger population base in more extensive sandstone environments.

The terrestrial small mammal assemblage of Nawurlandja is simple, with four species comprising >99% of all captures (in every episode of sampling). Of these four species, two (Arnhem rock-rat and northern quoll) unequivocally declined from 1977-79 to 2002, and the absence of records of Arnhem rock-rats in 1994 and 2002 suggests that it may have become extirpated at this site. Both of these species are now recognised as threatened nationally. In contrast, the common rock-rat increased, and the trends for sandstone antechinus were inconsistent. These results may represent long-term monotonic trends or they may simply be part of a dynamic system whose pattern of oscillations cannot be interpreted from so few samples. There is some evidence for short-term dynamism in this assemblage, most notably in the six-fold increase in trap success for sandstone antechinus from April 2002 to July 2002 (possibly associated with changes in activity and dispersion during the mating season), and to some fluctuations in populations across the three years of the intensive initial study (Begg 1981a, 1981b, 1981c). But the influence of such seasonal dynamism is dampened in our assessment, as our comparisons between the initial sampling and re-sampling were restricted to comparable seasons.

A case can be made for the results reported here being representative of long-term trends, and to be indicative of the status of mammal assemblages in sandstone environments more broadly. First, trends in abundance for northern quoll and Arnhem rock-rat from the initial sampling to the 1994 re-sampling are broadly consistent with, and intermediate to, trends from the 1977-79 results to the 2002 re-sampling, suggesting a directional change. Second, while recognising that this mammal assemblage is very simple, there is some consistency in the pattern of change with that reported for recent changes in the lowland mammals of northern Australia (Woinarski *et al.* 2001): declines occurred mostly in the larger (and/or more specialised) dasyurids and rodents, with increase or relative stability in the smaller (and/or more disturbance favoured) dasyurids and rodents. Third, a broader monitoring program in Kakadu (incorporating lowland and sandstone upland sites), and other nearby reserves, also demonstrated significant declines for northern quoll over the period spanned in this study, and subsequently (Woinarski *et al.* 2010; Russell-Smith *et al.* 2014). However other trends from this monitoring were less consistent with the results reported here: the broader Kakadu monitoring program reported no overall change for Arnhem rock-rat and some decrease for common rock-rat over the period 2001 to 2009, and comparable sampling at nearby Litchfield National Park reported no change in abundance for northern quoll over the period 1995 to 2002 (Woinarski *et al.* 2010; Russell-Smith *et al.* 2014).

This study offers some useful perspective in relation to the role of some factors considered as possible causative agents in the decline of components of the mammal fauna of northern Australia (Woinarski *et al.* 2011a). First, our re-sampling showed a substantial decline (88-95%) for the northern quoll over a period immediately preceding the arrival of cane toads, so demonstrates that toads alone are not responsible for the full extent of recent declines in this species. Second, given that feral stock were largely absent from the study area throughout the period spanned by this study, the decline we report for northern quoll and Arnhem rock-rat is also likely to be unrelated to habitat degradation due to introduced herbivores.

The study provides some, albeit weak, evidence that fire is implicated in the decline in this mammal fauna. Fire is a pivotal factor in the ecology of these sandstone environments. A series of studies has shown that recent regimes of frequent and extensive fires are detrimentally affecting sandstone plant communities, most notably heathlands (Russell-Smith *et al.* 1998, 2002) and monsoon rainforests (Russell-Smith *et al.* 1993), and causing regional declines in fire-sensitive plant species, such as *Callitris intratropica* (Trauernicht *et al.* 2013; Bowman *et al.* 2014), although intensive management may have improved this regime in some sandstone areas of Kakadu subsequent to our 2002 sampling (Murphy *et al.* 2015). Fire regimes that degrade sandstone rainforests in particular, and less so sandstone heathlands, may be disadvantageous for the Arnhem rock-rat, as this species is strongly associated with sandstone rainforests and a substantial component of its diet comprises fleshy fruits from savanna and rainforest plant species, such as *Owenia vernicosa*, *Canarium australianum* and *Terminalia carpentariae* (Begg and Dunlop 1980, 1985), whose abundance, stature and fruit productivity is likely to be reduced by frequent fire (Russell-Smith *et al*. 2014).

In the Kakadu region generally, the mammal fauna at re-sampled sites has been shown to have a greater rate of decline when those sites are burnt more frequently or extensively (Griffiths and Brook 2015; Griffiths *et al.* 2015; Lawes *et al.* 2015), although studies in other sandstone regions have not reported such relationships (Radford 2012).

At Nawurlandja, trap success was significantly higher in 1977-79 (when the study area had been largely unburnt for at least 3-5 years) than in our 2002 re-sampling (when the study area had experienced more frequent and pervasive fire in the preceding years). Begg's experimental fire also demonstrated that these mammal assemblages respond strongly to fire, reporting decline in the abundance of most species and some changes in habitat use following the imposition of an extensive fire (Begg *et al.* 1981). Other studies have also shown that populations of northern quoll (Oakwood 2000) and Arnhem rock-rat (Kerle and Burgman 1984) are adversely affected by extensive and/or frequent fire.

Fire may be a direct cause of changes in mammal abundance (e.g. by causing a reduction in food availability for some mammal species), or it may work indirectly or in concert with other factors. Recent studies in the Kimberley region of northern

Australia have demonstrated that feral cats are attracted to recently burnt areas and that their impacts on native mammal species are more intense in such areas, especially where fires leave few unburnt patches (McGregor *et al.* 2014, 2016; Leahy *et al.* 2015). This compounding interaction of two threat factors may be responsible for the decline that we report for this study area, however the incidence of cats, and change in this incidence over time, was not evaluated in our study. There is some evidence from other regions that cat densities may be lower, and/or their predation impacts may be less, in rugged areas than nearby lowland areas (Hohnen *et al.* 2016b; Legge *et al.* 2017).

Much of the recent decline in the mammal fauna of northern Australia has occurred in relatively featureless lowland areas (Woinarski *et al.* 2001), with the fauna of more rugged sandstone areas showing more resilience (Hohnen *et al.* 2016a). This has led to some speculation that these rugged areas may provide a robust refuge from those threat factors that operate almost pervasively in lowland areas (Woinarski *et al.* 2009; Start *et al.* 2012; Hohnen *et al.* 2016b;). Our results suggests that this hopeful assumption may be valid only in part, and that at least some of the influential threat factors operating in lowland areas are also affecting the mammal fauna of rugged upland areas.

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Conflicts of Interest

The 2002 study formed part of a consultancy for Parks Australia to the Tropical Savannas Cooperative Research Centre.

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Table 1a. April 2002 sampling results compared with March-May 1977-79 and March-May 1980 results. Values in body of table are % trap-success (per 100 trapnights), with z-ratio score (for comparison with 2002 results) and Bonferroni-adjusted probability in brackets: * p<0.0025; ** p<0.0005; *** p<0.00025.

Species	1977-79	1980	2002
trap-nights	*10,800*	*3600*	*2400*
sandstone antechinus	3.68 (z=9.18, ***)	1.83 (z=6.08, ***)	0.13
northern quoll	0.82 (z=4.21, ***)	0.85 (z=4.27, ***)	0.04
Arnhem rock-rat	0.36 (z=2.95, ns)	0.80 (z=4.41, ***)	0
common rock-rat	0.57 (z=3.80, **)	0.33 (z=4.31, ***)	1.29
all species	5.43 (z=8.32, ***)	3.83 (z=5.84, ***)	1.46

Table 1b. July 2002 sampling results compared with June-August 1977-79 and June-August 1980 results. Conventions as for Table 1a.

Species	1977-79	1980	2002
trap-nights	*8400*	*3600*	*1200*
sandstone antechinus	4.27 (z=1.66, ns)	1.70 (z=3.27, *)	3.25
northern quoll	0.69 (z=2.52, ns)	0.67 (z=2.43, ns)	0.08
Arnhem rock-rat	1.77 (z=4.65, ***)	1.31 (z=3.98, ***)	0
common rock-rat	1.57 (z=3.92, ***)	2.25 (z=1.77, ns)	3.17
all species	8.31 (z=2.15, ns)	5.91 (z=0.73, ns)	6.50