

Rapid recovery of mammal fauna in the central Kimberley, northern Australia, following the removal of introduced herbivores

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Abstract Australia has lost more native mammal species than any other country in the past two centuries, and this record of loss looks likely to worsen over the next few decades. Small- to medium-sized mammals are declining in both distribution and density across large tracts of northern Australia's tropical savannas, including within protected areas. The most likely causes are a combination of changed fire patterns, the impacts of introduced herbivores and predation by feral cats. Here, in contrast to the prevailing trend across northern Australia, we report the recovery of native mammals in response to a large-scale (>40 000 ha) destocking experiment carried out at Mornington Wildlife Sanctuary in the central Kimberley, north-west Australia. Following the removal of introduced herbivores from 2004, the species richness and abundance of small native rodents and dasyurids increased significantly across all sampled habitats over the next 3 years. We discuss the implications of these results for guiding land management and applied research to help to reduce the impending risk of mammalian extinctions in northern Australia.

Key words: grazing impact, landscape experiment, mammal decline, northern Australia, tropical savannas.

INTRODUCTION

One-quarter of the world's mammal species face the risk of extinction, and over half are in decline (Schipper *et al.* 2008). Habitat loss is the single most widespread driver for this (Kingsford *et al.* 2009) and yet, despite the near-exponential increase in protected areas worldwide over the past few decades (<http://www.wdpa.org/Statistics.aspx>), species are still declining, even in protected areas (Rodrigues 2006; Brashares 2010; Karanth *et al.* 2010). Apart from examples where obvious threats like habitat loss continue unabated (e.g. Liu *et al.* 2001), the reasons for ongoing species declines within relatively intact landscapes (including protected areas) are harder to identify. To some extent, this is because species react inconsistently to particular combinations of threats (Davidson *et al.* 2009). In addition, threats combine both additively and synergistically, not only on species themselves, but also on the interactions between species (Paine *et al.* 1998; Gilman *et al.* 2010) in ways that are difficult to understand or predict.

About half of the world's mammal extinctions in the last 200 years have occurred in Australia, with 22 native species lost since European settlement (Johnson 2006; Burbidge *et al.* 2008). Additional species experienced severe declines in either distribution and/or density during this period, and some are now restricted to offshore islands (Johnson 2006; Binley *et al.* 2009). Most of the affected species occupied the arid and semi-arid zones of inland Australia which has been relatively unaffected by habitat loss (Johnson 2006; Department of the Environment and Water Resources 2007; Burbidge *et al.* 2008). Instead, native mammal losses were principally caused by introduced predators (cats and foxes), whose invasion was facilitated by the spread of introduced herbivores (especially rabbits and sheep) following European colonization (Johnson 2006). Other factors, such as changed fire regimes, interacted with the impacts of exotic animals in some areas (Burbidge *et al.* 1988).

There is accumulating evidence that Australia's modern extinction wave is now extending into the tropical savannas of northern Australia (McKenzie 1981; Sawle 1988; Woinarski 1992; Woinarski *et al.* 2001, 2007b, 2010; Start *et al.* 2007; Firth *et al.* 2010). Several species have already suffered regional extinctions. For example, the golden-backed tree-rat (*Mesembriomys macrurus*) has disappeared from the mainland

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of the Northern Territory, Australia (Palmer *et al.* 2003) and the golden bandicoot (*Isodon auratus*) has retracted to less than 10% of its former range. These declines are perplexing, because Australia's tropical landscapes are relatively unmodified (Woinarski *et al.* 2007a); the native mammal declines are clearly being driven by more complex ecological processes than simple habitat loss, but these processes remain poorly understood.

There are a number of potential threats to the ecological integrity of northern Australia. During the last 100 or so years, the region has acquired a complement of introduced species (e.g. cattle, horses, swamp buffalo, pigs), which occur at high densities (Freeland 1990), and whose impacts are manifest across all tenures, including protected areas. European red foxes (*Vulpes vulpes*) do not regularly extend into the tropics, but feral cats (*Felis catus*) are ubiquitous. Fire patterns have also shifted, usually towards a higher frequency of extensive and intense fires. This contemporary fire regime results in a complex array of changes to the structure and floristic composition of vegetation, generally with a homogenizing effect (Russell-Smith *et al.* 2002; Williams *et al.* 2003; Vigilante & Bowman 2004). Changed fire patterns and the introduction of large herbivores have both acted to reduce the productivity of entire landscapes (Burbidge & McKenzie 1989). Additional potential threats in northern Australia include the introduced cane toad (*Rhinella marina*), which is spreading rapidly from east to west and has contributed to the substantial declines in northern quolls (Shine 2010). Finally, the introduced black rat (*Rattus rattus*) may be emerging as a potent disease carrier, predator and competitor (Towns *et al.* 2006).

Research effort seeking to identify the relative importance of various threats to northern Australian native mammals has been uneven. The majority of studies have focused on the impacts of fire. These collectively (albeit somewhat noisily) suggest that most native mammal species respond negatively to fire, declining with increased fire frequency and after single extreme fire events (Woinarski *et al.* 2001, 2004, 2010; Pardon *et al.* 2003; Firth *et al.* 2006; Legge *et al.* 2008;). However, fire is not a universal explanation for the current mammal declines: some studies show inconsistent responses of species to fire, the declines do not always coincide with the timing of changed fire patterns, and native mammal declines have been documented from areas with infrequent fire (Woinarski *et al.* 2010).

There has been less research on the impacts of introduced herbivores on native fauna in northern Australia. Grazing gradient studies in blacksoil grasslands on the southern margin of the tropical savannas (Fisher 2001) showed that the abundance of one mammal species declined with increasing grazing intensity (although all mammals were sparse). Limited

sampling (single surveys at fewer than 30 sites) in two studies in Queensland tropical savannas showed that mammals were more abundant at ungrazed sites (Kutt & Woinarski 2007), and there was a significant negative relationship with increased grazing for abundance of two native mammal species (Woinarski & Ash 2002). Faunal sampling within two large-scale grazing trials (O'Reagain *et al.* 2003; Hunt *et al.* 2007) found a muted response of native mammals to variation in stocking rate or cattle exclusion (A. Fisher, unpubl. data, 2010; A. Kutt, pers. comm., 2010).

The paucity of research on grazing impacts on Australian tropical savanna fauna arises partly from lack of opportunity – large introduced herbivores are ubiquitous across the savannas of northern Australia, even in protected areas, whether as managed herds or unmanaged feral populations (Woinarski & Fisher 2003). This removes the scope for correlative studies (for an exception see Woinarski & Ash 2002). An experimental approach at the appropriate scale requires a formidable capital investment in exclusion fencing and control programmes, and an ongoing management commitment. These logistic realities have genuinely discouraged studies of introduced herbivore impacts, but it also seems likely that grazing impacts have been tacitly underestimated compared with those of extensive and intense fires, because of the disparity in visual and psychological effect (Fleischner 1994). This may be an oversight: studies from the savannas of other continents, particularly Africa and North America, demonstrate a negative relationship between the species richness and abundance of small mammals and the presence of large herbivores, both native and introduced (Keesing 1998; Eccard *et al.* 2000; Salvatori *et al.* 2001; Caro 2002). Studies of grazing impacts in Australian arid zones have also demonstrated an impact of grazing on native small mammals (Read & Cunningham 2010).

Introduced herbivores could affect native mammal communities in a number of ways. Grazing may reduce food available for herbivorous and granivorous mammals (O'Connor & Pickett 1992; Crowley & Garnett 1998, 2001; Fensham & Skull 1999; Steen *et al.* 2005). Over time, grazing can reduce the overall productivity of the landscape because of irreversible changes to vegetation dynamics and nutrient cycling (van de Koppel *et al.* 1997). Trampling by introduced herbivores can cause soil compaction which affects the habitat quality for burrowing and fossorial mammals, and grazing can also simplify vegetation structure (Smit *et al.* 2001) in a way that exposes small mammals to increased predation risk (see Fleischner 1994; Keesing 1998; and references therein).

Here, we present the results of a landscape-scale destocking experiment in the central Kimberley, north-west Australia. We measured changes in the small- to medium-sized mammal community at stan-

standard quadrats between 2004 and 2007 following the staged removal of cattle, horses and donkeys from over 40 000 ha, with control quadrats each year in adjacent areas that still carried these introduced herbivores. Against the contemporary backdrop of widespread and profound declines in northern Australia's native mammals, this experiment examined the potential for faunal recovery following the landscape-scale removal of introduced herbivores.

METHODS

Study area

The study was carried out at Mornington Wildlife Sanctuary in the central Kimberley, north-west Australia (17°30'S, 126°06'E). This 320 000 ha property is owned by the Australian Wildlife Conservancy (AWC) and has been managed primarily for conservation since 2004. Previously, Mornington had been operated as a cattle station since the 1920s, with an extensive grazing system and a standing herd of around 6000 head, which is half than the stocking rate

recommended for Mornington by the Department of Agriculture and Food, Western Australia. Cattle harvesting was centred in the current study area, which includes the majority of the more productive land systems on the property. During 2004 and 2005, a programme of strategic fencing followed by mustering and culling resulted in the removal of cattle, horses and donkeys from 40 300 ha of Mornington (Fig. 1). The destocked area lies adjacent to the King Leopold Ranges, an expansive, rugged sandstone range which supports only extremely limited numbers of feral herbivores (primarily cattle and donkeys). Therefore, the overall contiguous area that is essentially free of introduced herbivores is actually much larger than the destocked area. The destocking programme was carried out in two stages: 24 300 ha was fenced and cleared of large herbivores in 2004, and an additional 16 000 ha was cleared in 2005 (Fig. 1). Prior to 2004, the entire destocked area supported over 2000 cattle and over 200 horses and donkeys. By 2007 cattle numbered fewer than 200 and there no horses and donkeys.

Survey quadrat selection

Mornington's vegetation is comprised of various types of savanna woodlands, punctuated by riparian habitats and small

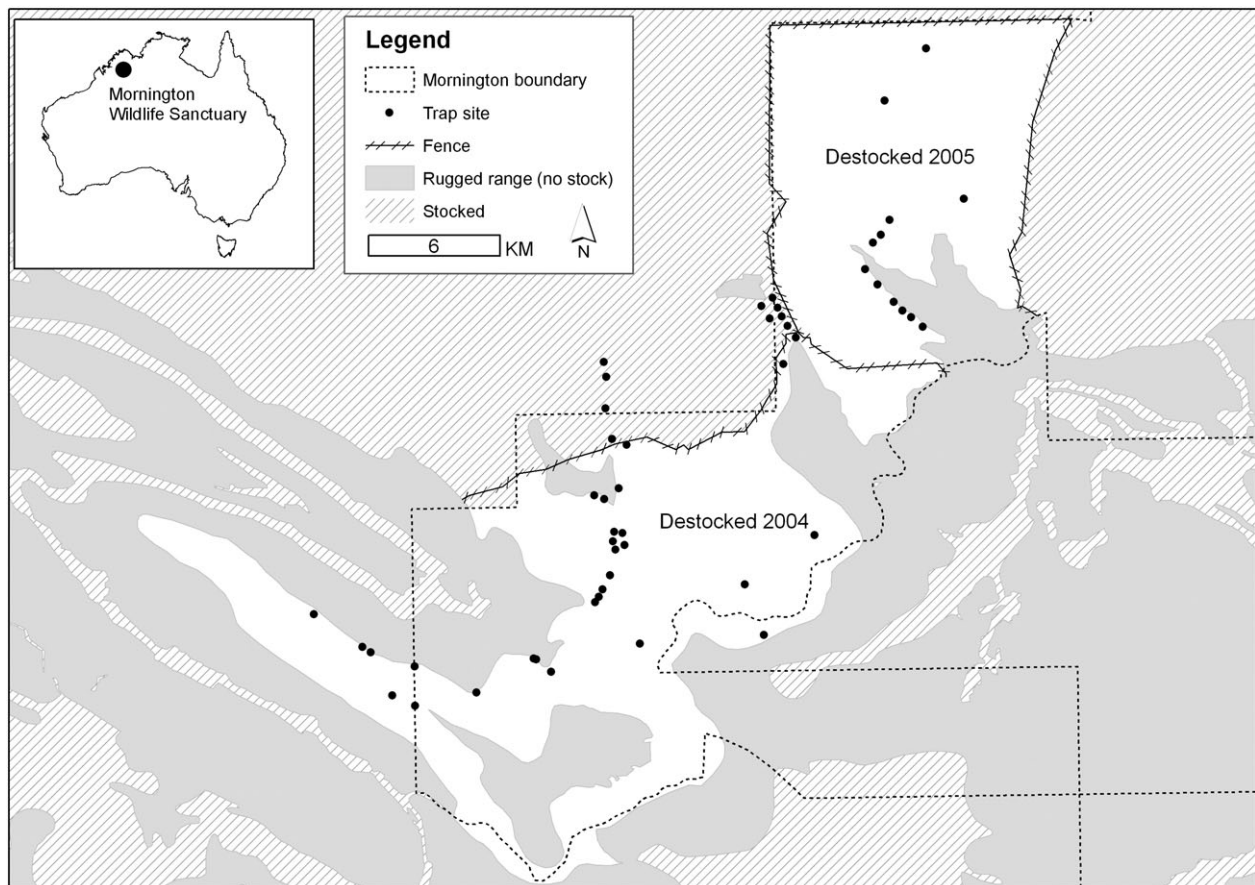


Fig. 1. The location of Mornington, in the central Kimberley and the destocked area within the sanctuary. The destocked area is in the southwest corner of Mornington, next to the King Leopold Ranges (which is virtually free of introduced herbivores). The inset shows the location of Mornington in the Kimberley.

soakage areas. We sampled four habitats that are preferred by cattle for foraging and/or resting: blacksoil grasslands, *Eucalyptus coolibah* woodlands, riparian zones and sandseeps (the moist, thickly vegetated areas at the base of sandstone ranges); a description of each habitat is given in Appendix S1.

The survey design capitalized on the staged nature of the destocking in order to introduce a control for between-year effects. In 2004, all surveyed quadrats had been exposed to stock. From 2005 on, as we progressively destocked the study area, we added extra quadrats in order to maintain a survey set that was balanced between stocked and destocked areas. Additional quadrats were selected within the same four habitats as the original set. We sampled 20 quadrats in 2004, then 42, 42, 43 quadrats in each successive year thereafter. Overall, during the 4 years of the study, we surveyed 49 discrete quadrats, between 1 and 4 times each (most were sampled 3 to 4 times). In most cases, quadrats were in the stocked area the first time they were sampled then transitioned to being in a destocked area as the programme progressed. The staged manner of the destocking meant that by 2006 and 2007, the survey was comprised of quadrats that were stocked ($n = 16$), or that had been destocked for either 1 ($n = 10$), 2 ($n = 33$) or 3 ($n = 26$) years.

Fire frequency at the study area is low. At the start of the study in 2004, none of the survey quadrats had been burnt for at least 3 years. During the course of the study, only 11 surveys (out of 147 surveys at the permanent quadrats) experienced fire in the year before sampling – all these cases were from prescribed management burns in the late wet/early dry season (i.e. the fires were small and of relatively low intensity).

Survey methods

Fauna

The survey methods broadly followed the protocols developed by the Biodiversity Unit of Northern Territory Parks and Wildlife Commission (Woinarski *et al.* 1999). Twenty aluminium box traps were set around the perimeter of a 0.25 ha quadrat and a medium-sized cage trap at each of the four corners. Eight pitfalls (15 cm diameter polyvinyl chloride pipe with end-cap; 60 cm deep) were sunk within the quadrat, arranged in pairs with 20 m of 30 cm high plastic drift-fence running through each pair. Traps were baited with a mix of oats/peanut butter/honey/vanilla essence and fish oil during the late afternoon, checked each morning and closed during the day. Pitfalls were left open continuously, and checked twice each day (in the early morning and late afternoon). Quadrats were operated for three consecutive nights. We calculated the overall abundance of each species at a quadrat by counting the number of new individuals captured during the 3-day sampling across all traps. To exclude recaptures from this figure, we clipped small areas of fur on each trapped mammal before release.

Vegetation and ground characteristics

We described the broad vegetation species composition and structure at each trapping quadrat (see Appendix S1). We

estimated the basal area of woody vegetation (using the Bitterlich method; Grosenbaugh 1952), the percentage foliage projected cover (visually) and the modal height (also visually) for each tree and shrub species in a 360 degree arc around each of two diagonal corners of the trapping quadrat, then averaged these two figures. We visually estimated the percentage of the quadrat covered by the dominant grass species.

The ground layer is likely to change more quickly in response to the removal of introduced herbivores than the basal area of woody vegetation, or the floristic composition of any strata. Ground cover was sampled by taking 100 paces through the trapping quadrat and noting whether the toe edge of each footfall touched grass or small forbs, leaf and woody litter, bare earth or rock. We estimated the amount of large woody debris by counting all logs over 5 cm diameter that crossed the perimeter of the quadrat.

Analysis

We used a statistical modelling approach in Genstat 8. Because most quadrats were sampled repeatedly over the years 2004–2007, we dealt with potential dependency by fitting linear mixed models with ‘quadrat’ specified as the random effect. Variance components were estimated using residual maximum likelihood and fixed effects using weighted least squares. The significance of fixed effects was assessed using Wald statistics. Residual and quantile diagnostic plots were used to check model assumptions.

We examined variation in the species richness and abundance of mammals by testing for relationships with habitat, year, time since destocking, and the interaction of time since destocking with habitat. We also examined whether each species responded similarly following destocking. For the seven most commonly captured species, we calculated the average number of individuals per quadrat in each year of survey. In separate species-specific models, we regressed these values against time since destocking (specified as a continuous variable) to test whether there were any significant changes in abundance with time since destocking. We also tested for significant differences in this response among species by looking at the interaction between time since destocking and species in a model that included the mean captures per quadrat from all seven species.

The proportions of grass and forbs, litter and bare soil were calculated for each quadrat. These proportions are inter-related; we picked one – the proportion of a quadrat that is covered in grass and forbs, and examined the influence of habitat, year, time since destocking, and the interaction between time since destocking and habitat. To examine changes in woody debris, we modelled the count of logs around the quadrat perimeter.

RESULTS

Trapping success

Over the 4 years of the study, we carried out 147 surveys at the permanent quadrats, equating to 14 112 trap-nights (including all box, cage and pitfall traps).

We recorded 859 mammal captures (688 individual animals) of nine native species (no introduced species were ever recorded). Trap success at quadrats ranged from 0 to 36 captures (0–37.5%), and 0 to 29 individuals (0–30.2%) over the 3 days (i.e. 96 trap-nights) that each quadrat was operated.

Western chestnut mice (*Pseudomys nanus*) and pale field rats (*Rattus tunneyi*) were the most frequently caught species (over 200 individuals each). Ningbing false antechinus (*Pseudantechinus ningbing*) and stripe-faced dunnart (*Sminthopsis macroura*) were caught least frequently (one and three individuals, respectively; Table 1). These differences in capture rates among species reflect, to some extent, the habitats sampled. This is most obvious for the ningbing false antechinus and common rock-rat (*Zyromys argurus*) which are both very common in the rocky sandstone ranges within the study area; however, this habitat was not sampled.

Habitat preferences were not a focal point of this study, but unsurprisingly, most species showed habitat preferences: long-tailed planigales (*Planigale ingrami*) and tropical short-tailed mice (*Leggadina lakedownensis*) were strongly associated with blacksoil grasslands, delicate mice (*Pseudomys delicatulus*) and common rock-rats with sandseeps, which lie at the foot of some sandstone ranges (the preferred habitat for rock rats). Pale field rats were most common in sandseeps and riparian habitats. In contrast, common planigales (*Planigale maculata*) and western chestnut mice were found in all habitats, although the latter was less common in the *E. coolibah* woodlands (Table 1).

Mammal abundance and species richness

The abundance and species richness of native mammals both increased with years since destocking, and the extent of this increase varied among habitats (Table 2). The increase in abundance was significantly

larger at quadrats in sandseeps than other habitats (Fig. 2a). The increase in species richness was largest at blacksoil quadrats (Fig. 2b). These patterns overlaid a general increase in the abundance and species richness of mammals between 2004 and 2007 (Table 2). This did not appear to be related to rainfall, as the study period included one relatively dry wet season (2004/2005 = 538 mm) followed by two average wet seasons (2005/2006 = 829 mm; 2006/2007 = 831 mm), yet the mammal abundance increased regardless of the nature of the wet season. However, the data are insufficient to test the influence of rainfall on small mammal abundance.

In separate models for each species, abundance increased with years since destocking for four species (Table 3); common rock-rats showed a non-significant increasing trend. We tested for differences in the rate of increase among species by fitting a species years since destocking interaction term; this showed that the increase was significantly more marked for pale field rats and western chestnut mice than other species ($F_{6,1029} = 8.78$; $P < 0.0001$; Fig. 3).

Table 2. Factors affecting species richness and abundance of small mammals at 147 surveys over 4 years

	d.f.	Species richness		Abundance	
		χ^2	<i>P</i>	χ^2	<i>P</i>
Year	1	26.7	<0.001	16.5	<0.001
Habitat	3	14.4	0.002	26.7	<0.001
Years since destocking	1	27.7	<0.001	5.73	<0.02
Years since destocking habitat	3	13.0	0.005	10.1	<0.02

Table shows the d.f., Wald test result and significance level for each factor tested in the mixed model.

Table 1. Numbers of individuals caught in each habitat between 2004 and 2007; from a total of 147 surveys, each with 32 box, cage and pitfall traps

Species	Blacksoil grasslands; 42 surveys	Riparian zone; 41 surveys	Coolibah woodlands; 23 surveys	Sandseep; 41 surveys	Total; 147 surveys
<i>Leggadina lakedownensis</i>	33	2	8	2	45
<i>Planigale ingrami</i>	48	0	0	2	50
<i>Planigale maculata</i>	16	10	16	14	56
<i>Pseudantechinus ningbing</i>	0	0	0	1	1
<i>Pseudomys delicatulus</i>	0	3	0	77	80
<i>Pseudomys nanus</i>	46	69	13	80	208
<i>Rattus tunneyi</i>	12	65	6	119	202
<i>Sminthopsis macroura</i>	0	1	2	0	3
<i>Zyromys argurus</i>	0	0	4	39	43
Total	155	150	49	334	688

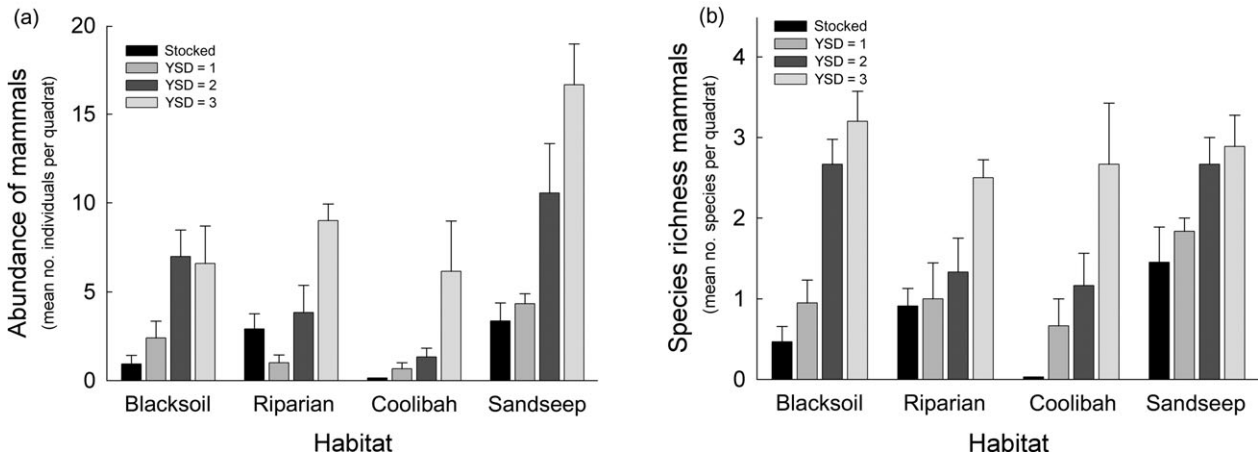


Fig. 2. Response of native small mammals to removal of introduced herbivores at permanent quadrats within Mornington. (a) Number of individual mammals per quadrat, and (b) number of mammal species per quadrat. Data show means and standard errors. Number of quadrats contributing to each mean ranges from 5 to 23, with the total sample being 147 quadrats. YSD, years since destocking.

Table 3. Results of regressions for each individual species against years since destocking

Species	Intercept and SE	Slope and SE	<i>t</i> ratio	<i>P</i>
<i>Planigale ingrami</i>	0.26 ± 0.13	0.06 ± 0.08	0.82	0.41
<i>Planigale maculata</i>	0.13 ± 0.09	0.20 ± 0.06	3.57	0.0005
<i>Leggadina lakedownensis</i>	0.06 ± 0.14	0.20 ± 0.09	2.27	0.0249
<i>Pseudomys delicatulus</i>	0.24 ± 0.29	0.25 ± 0.17	1.43	0.154
<i>Pseudomys nanus</i>	0.63 ± 0.29	0.65 ± 0.18	3.65	0.0004
<i>Rattus tunneyi</i>	-0.04 ± 0.31	1.17 ± 0.19	6.17	<0.0001
<i>Zygomys argurus</i>	0.10 ± 0.15	0.16 ± 0.09	1.67	0.097

Table shows the intercept estimate and standard error (SE), the regression slope estimate and standard error, plus the *t*-ratio and significance level for the slope. Species in bold increased significantly with years since destocking.

Ground characteristics

The proportion of a trapping quadrat that was covered by grass and forbs increased with the years since destocking ($\chi^2_1 = 24.6$; $P < 0.001$; Fig. 4). Figure 4 indicates that this effect was ‘compensated’ by a decrease in the proportion of the quadrat that was either covered with litter or bare earth. There were no significant differences among habitats, or among years. The amount of woody debris did not change with the years since destocking ($\chi^2_1 = 1.55$; $P = 0.21$).

The number of logs around the perimeter of a quadrat varied among habitats, with sandseep habitats having the highest log density, riparian second highest, followed by coolibah woodlands then blacksoil habitats ($\chi^2_3 = 8.43$; $P < 0.001$).

DISCUSSION

In contrast to the general trend of substantial declines in small- to medium-sized native mammals across the

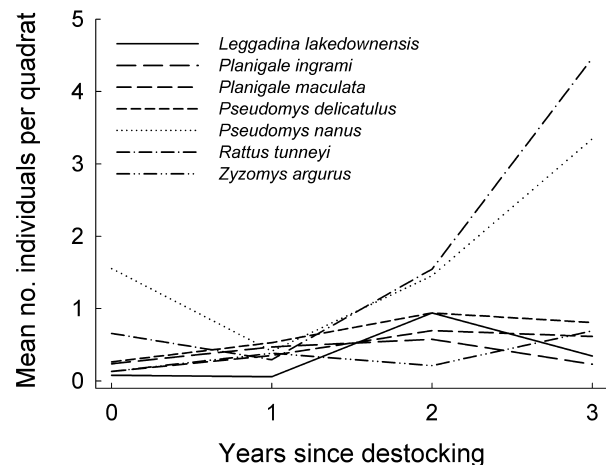


Fig. 3. Response of each of seven small mammal species to the removal of introduced herbivores. The graph shows the mean number of individuals per quadrat for each species against the year since destocking; standard errors are omitted for clarity of presentation. Sample sizes range from 26 to 54 for each year since destocking, with the total sample being 147.



Fig. 4. Changes in the ground layer within quadrats following the removal of large herbivores (mean and one standard error). Number of quadrats contributing to each mean ranges from 20 to 43, with the total sample being 147 quadrats.

tropical savannas of northern Australia, the study reported here demonstrates a rapid recovery of mammals following the removal of introduced herbivores. When the Mornington destocking experiment began, mammal captures averaged 1.1 per stocked quadrat, similar to the figure of 1.2 mammal captures per quadrat from recent surveys (using similar methods) at Kakadu National Park, Northern Territory, Australia after more than a decade of continuous decline (Woinarski *et al.* 2010). However, in the third year after destocking, mammal captures at Mornington had increased 10-fold, to 10.5 captures per quadrat. This increase was made up of two components – a general increase across all habitats and treatments over the 4 years of sampling, and an increase at destocked quadrats that was positively related to the time since destocking. By 2007, quadrats that had been destocked for 3 years had almost double the abundance and species richness (10.5 individuals and 2.8 species per quadrat) compared with quadrats sampled in the same year that still carried stock (6.5 individuals and 1.9 species per quadrat). Our results suggest that the role of introduced herbivores as contributors to the current native mammal declines in northern Australia has been underestimated as well as understudied.

The mechanism for the observed recovery is probably related to changes in ground vegetation following destocking: grass and forb cover increased, possibly providing increased food for native mammals, increased shelter from predators, or both. The two mammal species that showed the strongest increase in abundance after destocking have different diets – western chestnut mice are grass specialists, while pale field rats are more generalist, eating grass, roots and seeds. An attribute they share, however, is that they are

among the largest-bodied of the small mammal community sampled during this study. Both species are within the critical weight range (35–5500 g) of Australian mammals which have experienced the greatest incidence of extinctions since European colonization (Burbidge & McKenzie 1989). Mammals of this size are particularly vulnerable to predation from introduced European foxes and cats (Johnson 2006), and cats are now ubiquitous across northern Australia. The increase in ground cover following stock removal at Mornington may have reduced predation rates by introduced cats, as well as from native predators such as owls.

Despite the clear results from this study, removing introduced herbivores is unlikely to be the wholesale solution to northern Australia's mammal crisis. Given the geographic and taxonomic spread of the native mammal declines in northern Australia, it is unlikely that any one of the key threats of changed fire, introduced herbivores, introduced predators, disease and exotic plant species is singularly responsible. The relative contribution of each threat probably varies depending on the species and location, and the compounded consequence of all threats may be to reduce the resilience of the system to cope with any extra disturbance, even if minor (Paine *et al.* 1998; Scheffer *et al.* 2001; Brook *et al.* 2008). Finally, the threats almost certainly interact in a synergistic way (e.g. increased fire frequency and grazing both simplify vegetation structure, which may amplify the pressure from predators, including introduced cats).

A destocking experiment measures the recovery of species and ecological functions for which the grazing-induced impacts are reversible, but decades of grazing and associated land management changes may have caused some changes that are difficult or impossible to reverse (Fleischner 1994). In our case, relatively small native rodents and dasyurids responded positively, but medium-sized species known to be present on the property (e.g. northern brown bandicoots (*Isodon macrourus*), brush-tailed possums (*Trichosurus vulpecula*)) did not measurably increase. These species may naturally occur at very low densities, they may have lower tolerances for threats, or they may be suppressed by a combination of threats and their interactions of which introduced herbivores are an insignificant component.

Given the rapid nature and severity of the current native mammal declines in northern Australia and the uncertainty in our understanding of the key drivers for this process, we suggest an urgent and pragmatic combination of management and applied ecological research. Conservation management should be carried out at large scales, with an experimental approach, and integrated with monitoring programmes to measure the response of native fauna. In particular, the Mornington destocking experiment needs to be repeated at sites

with differing land management histories to test the generality of the recovery response, and to understand whether there are combinations of historical and current threats that lead to reversible or irreversible declines. Meanwhile, we need better information on the effects of each potential threat, particularly the mechanistic impacts of feral cats and disease, and how these interact with fire patterns and introduced herbivores.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Broad vegetation characteristics of the four sampled habitats.