

# Experimental evidence that feral cats cause local extirpation of small mammals in Australia's tropical savannas

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## Summary

1. Small mammal species are declining across northern Australia. Predation by feral cats *Felis sylvestris catus* is one hypothesised cause. Most evidence of cat impacts on native prey comes from islands, where cat densities are often high, but cats typically occur at low densities on mainland Australia.

2. We conducted a field experiment to measure the effect of predation by low-density cat populations on the demography of a native small mammal. We established two 12.5-ha enclosures in tropical savanna in the Northern Territory. Each enclosure was divided in half, with cats allowed access to one half but not the other. We introduced about 20 individuals of a native rodent, *Rattus villosissimus*, into each of the four compartments (two enclosures × two predator-access treatments). We monitored rat demography by mark-recapture analysis and radiotracking, and predator incursions by camera surveillance and track and scat searches.

3. Rat populations persisted over the duration of the study (18 months) in the predator-proof treatment, where we detected no predator incursions, but declined to extinction in both predator-accessible compartments. In one case, cat incursions were frequently detected and the rat population was rapidly extirpated (<3 months); in the other, cat incursions were infrequent, and the population declined more gradually (c. 16 months) due to low recruitment. We detected no incursions by dingoes *Canis dingo*, the other mammalian predator in the area.

4. *Synthesis and applications.* This is the first study to provide direct evidence that cats are capable of extirpating small mammals in a continental setting, in spite of their low population densities. This finding supports the hypothesis that predation by feral cats is contributing to declines of small mammals in northern Australia. The conservation management of native small mammals in northern Australia may require intensive control of cat populations, including large cat-free enclosures.

**Key-words:** manipulative experiment, mark-recapture, predator–prey interactions, predator-proof fences, reintroduction, small-mammal extinction, survival

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## Introduction

Almost a quarter of the world's terrestrial mammal species are threatened with extinction (Hoffmann *et al.* 2011; Di Marco *et al.* 2012), mainly due to habitat loss, habitat degradation and overhunting (Schipper *et al.* 2008). Small- and medium-sized invasive predators, notably feral cats *Felis sylvestris catus* and black rats *Rattus rattus*, have caused declines in small-mammal populations, but so far this has mostly been documented on small islands (Nogales *et al.* 2004; Bonnaud *et al.* 2011). The powerful effect of predators on island faunas may be explained by several factors: (1) small-to-medium-sized introduced predators often occur at high densities on islands; (2) native animals on islands may be naïve to predators, and (3) native species may have low total population sizes; and (4) larger mammalian predators, which can reduce the impact of small- to medium-sized predators (Ritchie & Johnson 2009), are absent from many islands. Additionally, the date of arrival of non-native predators is often better documented on islands, allowing for more accurate documentation of causes and responses than on the mainland.

Cats have been spread world-wide by people (Denny & Dickman 2010), and while it is clear they have caused extinction of many vertebrate species on islands (Dickman 1992; Bonnaud *et al.* 2011; Medina *et al.* 2011; Loss, Will & Marra 2013), there is much less evidence for impact on continental faunas (Woods, McDonald & Harris 2003; Loss, Will & Marra 2013). A recent study by Loss, Will & Marra (2013) in the United States showed that the impact of free-ranging cats is likely to be much higher than previously thought, with more than 20 billion mammals killed by cats each year in the United States alone. Translated to Australia, this implies a potentially significant impact of cats on currently widespread small-mammal species.

Since the 15th century, Australia has lost more mammal species (at least 23) than any other continent, accounting for approximately one-third of all recent global extinctions of mammals (Johnson 2006). Many of these extinctions have been attributed to invasive predators, especially the red fox *Vulpes vulpes* (Johnson 2006). Although Australia's Commonwealth Threat Abatement Plan for predation by feral cats (2008) lists 36 mammals as threatened by cats, evidence linking feral cats to past mammalian extinctions is equivocal (Denny & Dickman 2010), except in a few instances on Australian islands (Dickman 1992).

Until recently, the tropical savannas of northern Australia seemed to be unaffected by the declines and extinctions that occurred among mammals of the central arid zone and southern Australia (Woinarski *et al.* 2007). This was attributed primarily to the absence there of foxes. However, small mammals are currently declining across much of northern Australia (Woinarski *et al.* 2011a; Fisher *et al.* 2013). Six species are at imminent risk of extinction, and more than 20 species (of c. 40 species in

the small-to-medium body size range) have suffered severe reductions in geographic range (Fitzsimons *et al.* 2010). There are indications that feral cats may be at least partly responsible for these declines (Fisher *et al.* 2013). For example, the species declining most severely are in the preferred prey-size range of feral cats (<1500 g) and occupy relatively open habitats where exposure to predation is likely to be high (Fisher *et al.* 2013). Species that are declining across the mainland of northern Australia mostly have stable populations on cat-free islands, but have declined on islands where cats have recently been introduced (Dickman 1992; Woinarski *et al.* 2011b). This evidence of the effect of cat predation is countered by the fact that cats have been present in northern Australia for at least 100 years, and a view that the abundance of feral cats in Australia's tropical savannas is generally too low to account for major declines affecting many species simultaneously over large areas (Bradshaw *et al.* 2007).

Here, we provide the first experimental test of the effect of cat predation on demography of small mammals in northern Australia. We used a replicated experiment to directly measure the impact of feral cats on the survival and population growth rates of a small-mammal species, while accounting for the potential effects of the other mammalian predator in the area, the dingo *Canis dingo*, using cameras to monitor predator activity. The experimental enclosures were located in tropical savanna typical of environments that have recently experienced small-mammal declines (Woinarski *et al.* 2011a), and in which small-mammal abundance is now very low (Sarah Legge, unpublished data). Previous monitoring in the area suggested that cat density was typical of the low-density populations that occur elsewhere in northern Australia (<0.03 km<sup>2</sup>, Ridpath 1990; Katherine Tuft & Sarah Legge, unpublished data). We monitored the fate of small-mammal populations that had been introduced into two paired (12.5 ha) enclosures in natural landscapes that were either exposed to or protected from cats, testing the prediction that population growth rates and survival would be significantly lower in the predator-accessible than the predator-inaccessible treatments.

## Materials and methods

### STUDY SITE

This study was conducted at Wongalara Wildlife Sanctuary (14°08'S, 134°28'E), a 192 200 ha reserve in the Northern Territory (NT), Australia. Wongalara was a pastoral property grazed at low intensity by cattle *Bos taurus x indicus*, buffalo *Bubalus bubalis*, horses *Equus caballus* and donkeys *Equus asinus*, until it was acquired by the Australian Wildlife Conservancy (AWC) in 2006. Management has since focussed on removal of grazing ungulates, and fire management designed to reduce the size, intensity and frequency of fires. The only mammalian predator apart from the feral cat currently present is the dingo *Canis dingo*; dingoes were suppressed by poison baiting before the property was acquired by the AWC, but are now uncontrolled.

Wongalara experiences a monsoonal climate with a pronounced wet season from December to April, a dry season from May to September, and the 'build-up' to the wet season in October and November. Mean annual rainfall is ~900 mm, and daily temperatures range from 11.2 °C (mean minimum) in June to 31.3 °C (mean maximum) in January. The dominant vegetation is low open savanna woodland.

#### EXPERIMENTAL DESIGN

We constructed two 12.5-ha rat-proof enclosures, each divided in half, one half allowing cats and dingoes access (the fence was low enough at 0.9 m that cats could easily jump over) and the other half surrounded by a taller (2 m) (Medina *et al.* 2011) electrified floppy-top fence (Robley *et al.* 2007) (see Fig. S1, Supporting information) to exclude mammalian predators. We refer to these as 'low-fence' and 'high-fence' treatments. To prevent small mammals from moving in or out of these treatments, a strip of smooth poly belt, 40 cm high was attached to the inside lower section of all fences (Fig. S2, Supporting information).

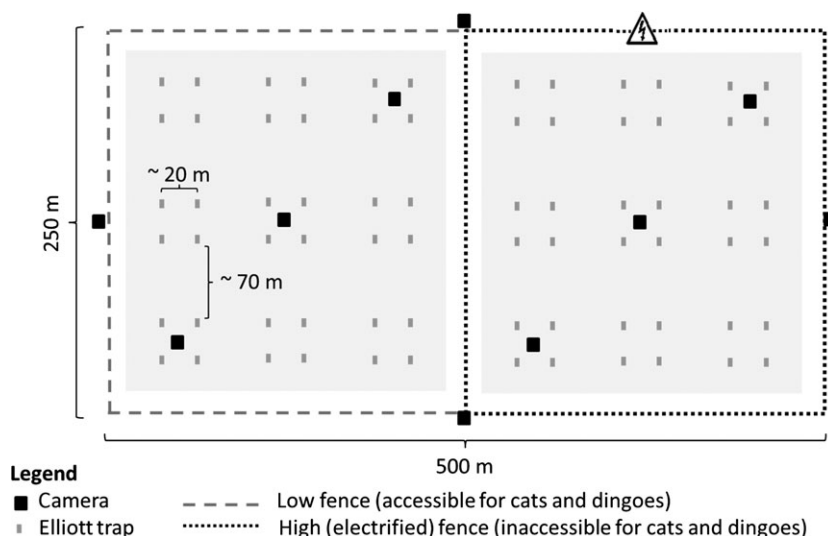
The two enclosures were *c.* 13 km apart. Enclosure I was in low (*c.* 10 m high) open woodland co-dominated by mixed *Eucalyptus* spp. and *Terminalia* spp., over a mixed *Triodia* spp. hummock grassland and mixed shrub understorey on sandy soils. Enclosure II was in similar low open woodland, but tree cover comprised *Eucalyptus* spp. and Cooktown Ironwood *Erythrophleum chlorostachys*, over a tussock grassland dominated by *Chrysopogon* spp., on sandy/lateritic soils. Mean percentage vegetation cover at rat height (10 cm above ground) was higher in Enclosure I than Enclosure II, but similar between the low- and high-fence treatments within each enclosure (Table S1, Supporting information).

We surveyed resident small mammals in both enclosures over three trapping sessions (June 2011, October 2011 and April 2012). In Enclosure I, we caught three *Rattus villosissimus* from 1728 trap nights, and in Enclosure II, we caught one *Pseudomys delicatulus* from 1152 trap nights. None of these animals was ever recaptured. Due to this very low current abundance of small mammals, which we interpret as being the result of recent declines as observed elsewhere in the northern savannas, we introduced populations of the long-haired rat *Rattus villosissimus* (Status 'Least Concern', IUCN 2013), to all enclosure compartments for the purpose of this

experiment. *Rattus villosissimus* weighs up to 280 g; females are sexually mature at *c.* 2 months, have a gestation period of *c.* 20 days, produce litters of up to nine young and wean pups at *c.* 21 days old (Breed & Ford 2007). It is a gregarious species and can live at high density under favourable conditions (Greenville, Wardle & Dickman 2013). We collected 20 free-ranging *R. villosissimus* from Quoin Island about 530 km west of Wongalara (14°87'S, 126°56'E, 219 ha), NT, in April 2011. To provide the numbers needed for introductions, these rats were initially housed and captive-bred, with handling kept to a minimum, at the Territory Wildlife Park before each release.

In April 2012, we released 46 captive-bred rats – as many as available – into Enclosure I: 13 females and 10 males in the low-fence treatment and 11 females and 12 males in the high-fence treatment, with similar age composition in each group. In October 2011, we released 31 rats into Enclosure II, five rats (three females and two males) originating from Quoin Island, and the rest bred in captivity. Seven females and nine males were released into the low-fence treatment and nine females and six males into the high-fence treatment. All were at least 1.5 months old and fully weaned; most (66%) were adults (>60 g). All were marked with passive integrated transponder (PIT) tags. Rats of sufficient size (*c.* 100 g) were fitted with radiocollars (*c.* 4 g). In Enclosure I, seven rats (five males and two females) were radiocollared at release in each treatment. In Enclosure II, 10 rats (five males and five females) were radiocollared at release in each treatment. All radiocollared rats were tracked weekly until the end of the study at June 2013. We used the time of last recorded change of location to fix the latest date on which a rat was known to be alive. Where corpses were located, we sought to identify cause of death.

The fate of released rats was also monitored using live-trapping at intervals of *c.* 2 months (see Table S1, Supporting information). Thirty-six aluminium box traps (Elliott design) were arranged in a uniform pattern in 0.4-ha grids in each of the four enclosure halves (Fig. 1). Traps were baited with a mixture of rolled oats and peanut butter, set in the late afternoon and checked at first light on the following day. Due to logistical constraints, the number of trapping sessions and their duration (number of nights) differed between enclosure sites, but not between the paired compartments (low fence and high fence) of each enclosure (Table S2, Supporting information). In Enclosure



**Fig. 1.** Camera and Elliott trap layout for an enclosure pair. Up to 13 cameras (one in each Elliott trap quadrat and another one in the middle of the inside periphery facing towards the fence) were located inside each enclosure half between October 2011 and April 2013. Note that objects are not drawn to scale.

I, trapping commenced 2 months after release of rats. Seven trapping sessions of between two and four consecutive trap nights were carried out (24 trap nights in total). In Enclosure II, trapping commenced 6 months after the release of rats because of limited access during the wet season. In this enclosure, nine trapping sessions of between two and four consecutive nights occurred (29 nights in total; Table S1, Supporting information).

At each capture, individuals were identified, weighed and sexed. Body condition was scored using the method of Ullmann-Culleré & Foltz (1999), from category 1 = emaciated to 5 = obese. Recruits (i.e. individuals trapped in the enclosures that were not part of the initial release) were PIT-tagged at first capture. Any uncollared rats larger than 100 g were radiocollared, resulting in 49 rats (Enclosure I – low: 7, high: 13; Enclosure II – low: 13, high: 16) being radiocollared and tracked over the course of the study.

#### DETECTION OF PREDATORS

We used heat-in-motion cameras (Reconyx PC800 Hyperfire, Holmen, WI, USA) and weekly visual inspections for tracks and scats in the soft soil around the inside and outside of the perimeter fences to detect predators. At least three cameras (but up to 13 and always the same number of cameras at a time) were placed inside each half of the enclosure, and one camera was installed at each side on the outside of the fences of each enclosure (Fig. 1). Cameras were unbaited, to avoid attracting predators.

#### ANALYSIS

To estimate population size and individual survival of rats, capture–recapture data were analysed using Pollock's robust survey design (Pollock *et al.* 1990). Trapping data were used to create individual encounter histories for each rat indicating capture (1) or non-capture (0) during each sampling occasion. Data were analysed using a Huggins model with a robust design in program MARK v7.1 (White & Burnham 1999) and plotted using R v3.0.3 (<http://cran.r-project.org>). There are multiple primary sampling periods (i.e. repeated nights of sampling during a trapping episode) in Pollock's robust survey design, which are separated by longer periods of time during which the population is open to gains (births and immigration) and losses (deaths and emigration). Data in each primary period are pooled to estimate survival probability  $S$ , between primary sampling periods. Within each primary sampling period, there are several secondary sampling periods separated by a short period during which the population is assumed closed. Data from each secondary sampling period were used to estimate the probability of first capture  $p$  and recapture  $c$ . Although robust design models can be used to estimate probabilities of migration into and out of the study area, here we fixed the migration parameters to zero. This was due to the presence of a fence that precluded animal movement (i.e. probability of emigration,  $\gamma'$ , and probability of remaining away from the study area if the individual had previously emigrated,  $\gamma''$ ). To ensure parameter identification, we assumed the probability of first capture  $p$  and probability of recapture  $c$  were constant (.) within each trapping session.

Forward model selection was used, whereby the simplest null model was fitted (i.e.  $S(.)$   $p(.) = c(.)$ ), representing constant survival  $S(.)$ , constant probability of capture  $p(.)$  and constant probability of recapture  $c(.)$ , as well as no behavioural effect on

the capture process, that is, chance of first capture is the same as chance of recapture ( $p \neq c$ ). Model complexity was introduced by first investigating whether there was a behavioural effect in the capture process (i.e.  $p \neq c$ ) or a seasonal effect (i.e.  $p(\text{session})$ ,  $c(\text{session})$  model), and then whether covariates influenced survival (i.e. the group to which the individual belonged, either released or recruited on site, a session effect, sex, and whether it was in the low- or high-fence treatment of the enclosure). Model selection used Akaike's information criterion adjusted for small sample size (AICc). Models were assumed equivalent if the AICc value differed by less than 2 from the model with the lowest AICc (Burnham & Anderson 2002). To describe factors affecting survival, 15 candidate models were chosen *a priori* and fitted separately for Enclosure I and Enclosure II (Table S2, Supporting information).

Survival of radiocollared rats was analysed as mean number of months tracked while known to be alive (indicated by last location change), and this was compared between compartments for each enclosure using two-tailed  $t$ -tests in Microsoft Excel 2010. Homogeneity of variance was tested using an  $F$ -test. Body condition and reproductive status were compared between treatments by comparing weight changes between the release and first trapping session, also using two-tailed  $t$ -tests.

Using camera trap data, we calculated an activity index in R v3.0.3 for mammalian predators by dividing the number of encounters by the number of cameras to account for malfunctioning cameras. This index was calculated for each night, then averaged monthly and reported with *c.* 95% binomial confidence intervals. We also recorded all instances of predator occurrences inside the enclosures and averaged how regularly these occurred.

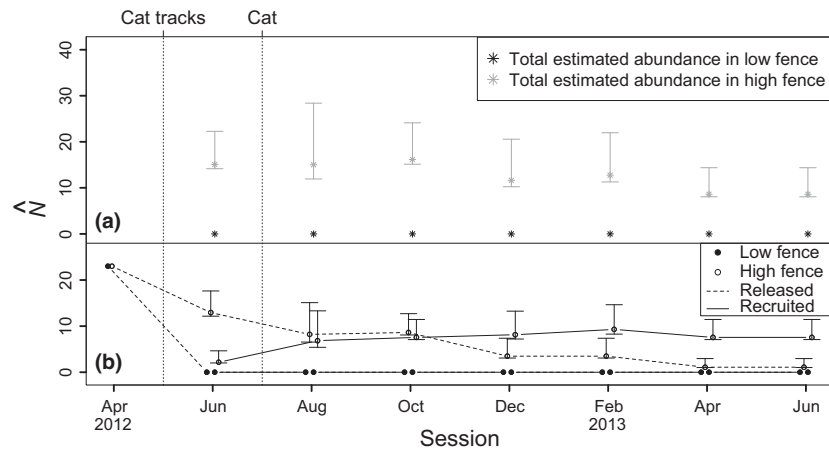
## Results

#### PREDATOR ACTIVITY AND INCURSIONS

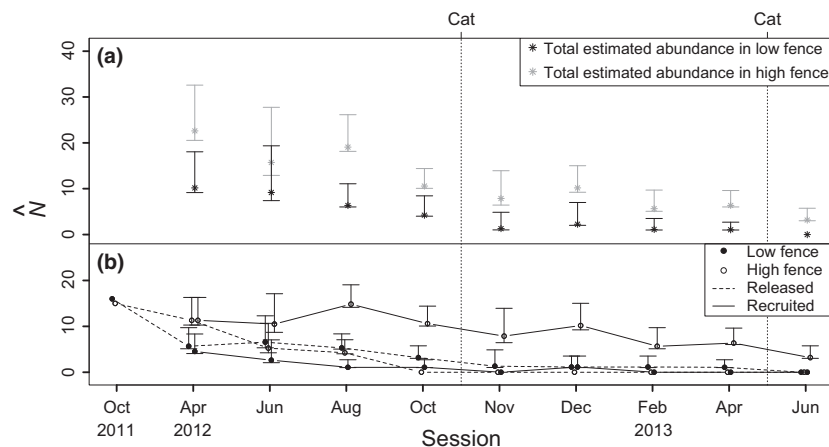
Cats or signs of cats were never detected inside the high-fence treatment of either enclosure. However, cat tracks were detected inside the low-fence treatment of Enclosure I less than 1 month after rats were released (Fig. 2). At least two individual cats were detected on camera at that site 4 weeks later (Fig. 2). Thereafter, cat detections recurred, on average, every week (June–October 2012: 7.9 day intervals; October 2012–April 2013: 6.0 day intervals) in the low-fence treatment of Enclosure I until the end of the study. There was a longer delay of nearly 1 year before cats were first detected inside the low-fence treatment of Enclosure II (Fig. 3); during the entire survey period, there were only two cat-detection events of two different individuals inside this treatment. Dingoes or signs of dingoes were never recorded inside either Enclosure I or II in either treatment.

Camera traps on the outside of the enclosures indicated that in general, dingo activity was similar to cat activity outside Enclosure I (Fig. S2a, Supporting information), while outside Enclosure II, dingo activity was variable and greater than cat activity for the duration of the study (Fig. S2b, Supporting information). Cat activity was similar around Enclosure I (Fig. S2a, Supporting information) and Enclosure II (Fig. S2b, Supporting information).





**Fig. 2.** Estimated abundance of rats at Enclosure I, from the release date (Session = 1), to the end of the survey period (Session = 8). The first point at which cat tracks were first detected inside the low-fence treatment and the first time a cat was detected on camera inside the low-fence treatment are shown as dotted lines. Cat incursions on camera after the initial detection occurred for the remainder of the study period on average once per week. There was no evidence of cats on cameras or from tracks inside the high-fence treatment and no evidence of dingoes inside either treatment of the enclosure. Panel (a) Total estimated abundance of rats in the low (black asterisk) and high (grey asterisk) fences. Panel (b) Estimated abundance of rats in the low and high fences separated according to whether rats were released (solid line) or recruited (dashed line).



**Fig. 3.** Estimated abundance of rats at Enclosure II, from the release date (Session = 1), to the end of the survey period (Session = 10). The time intervals between sessions were not equal. The point at which a cat was first detected on camera inside the enclosure is shown as a dotted line. There was no evidence of cats on cameras or from tracks inside the high-fence treatment and no evidence of dingoes inside either treatment of the enclosure. Panel (a) Total estimated abundance of rats in the low (black asterisk) and high (grey asterisk) fences. Panel (b) Estimated abundance of rats in the low and high fences separated according to whether rats were released (solid line) or recruited (dashed line).

Dingoes were frequently detected in groups of two to four individuals and sequentially on multiple cameras as they patrolled the outside periphery of the enclosures while cats always occurred solitarily. We found no evidence of snakes or goannas preying on the rats. However, a camera recorded one instance of an owl preying on a rat in the high-fence treatment of Enclosure II. In addition, a collar with a rat skull was found outside the high-fence treatment of Enclosure I, probably representing another victim of an aerial predator.

#### RAT DEMOGRAPHY

For the Enclosure I data, the selected model indicated an effect of fence height on survival and a behavioural effect

of trapping on capture probability (i.e. model  $S(\text{low-fence}) p(.) c(.))$ . The model with the next lowest AIC had substantially less support (i.e.  $\Delta\text{AIC} = 8.32$ , Table 1) and was not considered further (Burnham & Anderson 2002). For Enclosure II, there were two models with a  $\Delta\text{AIC} < 2$ , suggesting some model selection uncertainty. Nonetheless, both of these models suggested a strong seasonal effect on survival (Table 1). Whether trapping influenced capture probability was uncertain (i.e. the  $\Delta\text{AIC}$  between the model  $S(\text{session}) p(.) = c(.)$  and  $S(\text{session}) p(.) c(.)$  was 0.22; Table 1). There was no detectable effect of fence height (i.e. predation) on rat survival in Enclosure II (Table S2, Supporting information).

At Enclosure I, recruitment of rats increased steadily in the high-fence treatment, with 16 wild-born individuals

**Table 1.** Model selection results for the top three fitted models (according to AIC) to Enclosure I and Enclosure II data (full results are available in Table S2, Supporting Information). Four covariates were investigated: the treatment (*lowf* = low-fence), a session effect (*sess*, i.e. time between primary occasions), whether the animals belonged to the captive-bred or recruited group (*rec*) and sex of the rat (*sex*). Chance of capture was assumed equal to the chance of recapture and both were assumed to be constant (.). Migration ( $\gamma'$  and  $\gamma''$ ) was assumed to be zero

Model	AICc	dAICc	No. Par.	Deviance
Enclosure I				
S( <i>lowf</i> ) $p(.) = c(.)$	514.75	0	3	508.65
S( <i>lowf</i> ) $p(sess) = c(sess)$	523.29	8.53	9	504.45
S( <i>lowf</i> ) $p(.) = c(.)$	523.64	8.89	3	517.53
Enclosure II				
S( <i>sess</i> ) $p(.) = c(.)$	732.93	0	10	712.00
S( <i>sess</i> ) $p(.) = c(.)$	733.15	0.22	11	710.03
S( <i>rec</i> ) $p(.) = c(.)$	742.58	9.65	3	736.48

recorded by the end of the study period, while little recruitment was recorded in the low-fence treatment (Fig. 2). Similarly, captures of recruited rats at Enclosure II were always much higher in the high-fence compared to the low-fence treatment, with a total of 39 compared to six wild-born individuals, respectively (Fig. 3).

We estimated the abundance of each group of rats (i.e. released or recruited) for each treatment from each enclosure using the model with the lowest AIC. For all rats at Enclosure I (Fig. 2), abundance in the low-fence treatment was estimated as zero from the first sampling period (2 months after release) until our study ceased. The abundance of all released rats in the high-fence treatment of Enclosure I declined slowly over the 12 months following their release (Fig. 2). The abundance of rats at Enclosure II declined more rapidly in the low-fence than in the high-fence treatment (Fig. 3). Three of the four radio-tracked females in the low-fence treatment were dead within 2 months of their release, and neither of the uncollared rats was ever recaptured. After the first sighting of cats in the low-fence treatment, about 1 year after the rats were released, the last released female rat was missing and the population abundance declined by 75%. After the second cat detection, no rats were recorded in the low-fence treatment (Fig. 3).

Radiocollared rats were never recorded moving outside the enclosures. While we occasionally found rat tracks along the periphery of the enclosures, we recorded no evidence of rats trying to exit the enclosure. In Enclosure I, there was a significant difference ( $t = 5.14$ , d.f. = 13,  $P < 0.001$ ) in the known minimum survival time of radiocollared adult rats in the low-fence treatment ( $1.1 \pm \text{SE } 0.26$  months) compared to the high-fence treatment ( $3.8 \pm \text{SE } 0.34$  months). For Enclosure II, there was no detected difference in the known minimum survival time ( $t = 1.25$ , d.f. = 18,  $P = 0.23$ ) between the low-fence ( $3.8 \pm \text{SE } 1.2$  months) and high-fence ( $6.0 \pm \text{SE } 0.9$  months) treatment (Fig. S4, Supporting information). Of the radiocollared rats assumed or known to be dead at

the end of the study, the corpses of only 50% (three out of six) were recovered from the high-fence treatment and 43% (three out of seven) from the low-fence treatment of Enclosure I, and 55% (five out of nine) in the high-fence treatment and 25% (three out of 12) in the low-fence treatment of Enclosure II.

On average, the body condition of rats in the enclosures was 'well conditioned' (category BC3; Ullmann-Culleré & Foltz 1999). Weights of released recaptured rats in Enclosure I increased *c.* 26% during the 2 months before the first trapping session in the high-fence treatment (Fig. S4, Supporting information); weight changes in the low-fence treatment of Enclosure I could not be assessed as rats were not recaptured after release. Over the 6 months between the release and the first trapping session in Enclosure II, the mean weights of released recaptured rats increased by 71% in the low-fence treatment and 40% in the high-fence treatment. The mean weights of rats in the two halves of the enclosure did not differ significantly ( $t = 1.42$ , d.f. = 12,  $P = 0.18$ ). Survivorship of the five wild-born rats was similar to the first-generation animals bred in captivity (three of the five wild rats died within a month of release, one died within six, and the last wild rat died within 8 months of release).

## Discussion

We found a marked difference in the survival and population growth rate of rats between the low- and high-fence treatments. This was evidently due to predation by cats. Population declines were closely related to incursions by cats. There was no evidence that dingoes ever entered any enclosure, and avian and reptilian predators (snakes and goannas) would have been equally likely to enter all compartments. Rats in our experimental enclosures maintained good body condition throughout the study period. Therefore, differences in survival were not related to food limitation or stress from the indirect effects of predation.

In both replicates, rats were extirpated from low-fence (hereafter called 'cat-accessible') but not high-fence (hereafter called 'cat-inaccessible') treatments. However, the demographic mechanisms leading to extirpation differed in our two replicates. In Enclosure I, reduced survival in the cat-accessible treatment caused rapid extirpation within 2 months of releasing the rats; in Enclosure II, lower levels of cat predation and a low recruitment rate by the rats in the cat-accessible treatment caused a more gradual decline in the rat population over 1.5 years. Although we were unable to determine cause of death of individuals, it was highly likely that cats were the cause of their ultimate extirpation. Although the rat populations were confined to fenced areas, our enclosures were large relative to the home range size of individual rats (as indicated from our radiotracking results) and offered sufficient space for rats to shelter in dense vegetation, logs and hollow trees. Thus, even though cats occur at low population densities in tropical savannas of northern

Australia, they can exert sufficient predation pressure to drive local populations of small mammals to extinction, by concentrating their hunting activity in a small part of their home range (typically for males: 837 ha  $\pm$  SE 86,  $n = 26$ ; for females: 393 ha  $\pm$  SE 161,  $n = 7$ , Hugh McGregor, personal communication) that harbours a locally highly abundant and attractive food source.

The more gradual decline of the rat population in the cat-accessible treatment of Enclosure II compared with the cat-accessible treatment of Enclosure I was associated with both lower rates of recruitment by rats and lower rates of detected incursions by cats. Because we used a passive surveillance system to monitor predator activity in and around the enclosures, some cat incursions may well have gone undetected, especially those of short duration and confined to only a small part of the enclosure. Such brief incursions might have resulted in the death of some rats, even if they did not cause the catastrophic declines observed in Enclosure I. Brief visits may have forced the cats to concentrate their hunting activities on the more vulnerable stages of the population, such as juveniles that are more naïve and easier prey to handle (Childs 1986), and females that often move less than males and leave higher concentrations of odoriferous waste attractive to predators (Banks, Norrdahl & Korpimäki 2002) or which could be more susceptible to predation because oestrous odours can attract predators (Cushing 1985). Targeted predation on either juveniles or adult females may explain the lack of recruitment in this population.

Although our analysis did not show a significant effect of cats on rat survival in Enclosure II, it is notable that the final and rapid demise of the rat population – the loss of all remaining animals bar a single large male – coincided with the first record on camera of a cat inside that enclosure. This happened at a time when dingo activity outside the enclosure was particularly low. Higher dingo activity at Enclosure II also coincided with lower rates of detection of cats. Dingoes can cause feral cats to alter their behaviour and activity patterns (Brook, Johnson & Ritchie 2012; Kennedy *et al.* 2012). In our case, when dingo activity was high, cats probably made shorter visits to the enclosure and spent less time hunting within it. Dingoes often make use of roads (Read & Eldridge 2010) and their frequent presence around Enclosure II could be because one edge of this enclosure was within less than 10 m of a road, whereas Enclosure I was 250 m away from that same road.

This research provides the first experimental evidence that feral cats can extirpate local populations of small native mammals in continental situations. This happened even in a situation where low grazing pressure by ungulates and conservative fire management resulted in a dense and diverse vegetation cover that ought to have provided good habitat. While our results do not demonstrate that cat predation alone might have caused the decline of initially abundant and widespread populations to the state of extreme rarity that currently prevails at Wongalara, they do make it clear that sustained predation pressure

from cats is capable of preventing localised recovery of small-mammal populations from these low levels. Our results complement other evidence that suggests that cat predation has been a contributing factor, at least, to the recent decline of many species of small mammals from high to low abundance across large areas of northern Australia (Fisher *et al.* 2013). To protect native mammals, and to recover populations that have been driven to very low densities by invasive predators, it will be necessary to control and/or eliminate feral cats.

Cats are difficult to control using traditional means such as poison baiting, trapping and shooting (Denny & Dickman 2010). The scale of the problem of accomplishing levels of control needed to allow small-mammal recovery is shown by the fact that in our study, even one or two individual cats were sufficient to extirpate local populations of small mammals. The presence of dingoes may help to reduce the impacts of cats (Ritchie & Johnson 2009; Brook, Johnson & Ritchie 2012), and managing fire and grazing to manipulate vegetation structure could also mitigate predation pressure by feral cats (Sutherland & Predavec 1999; Stokes *et al.* 2004; Denny & Dickman 2010; Puan *et al.* 2011). However, these approaches alone are unlikely to allow recovery of small mammals from low abundance provided cats are present. Cat-free refuges are required, both on islands and in predator-proof enclosures ('mainland islands'). In addition, alternative methods for controlling cats over large landscapes (including disease and cat-specific baiting) need to be developed.

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## Data accessibility

Rat-release and trapping data: doi: 10.4227/05/53BB83CABCFFF.

Rat radiotracking data: doi: 10.4227/05/53C7655E08FF0.

Cat and dingo camera data: doi: 10.4227/05/53C76F01766C2.

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## Supporting Information

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

**Fig. S1.** The fence design in Enclosure I and Enclosure II.

**Fig. S2.** Dingo and cat activity surrounding Enclosure I and Enclosure II.

**Fig. S3.** Mean vegetation cover in percent at 10 cm above ground.

**Fig. S4.** Survival of radio-collared released rats.

**Fig. S5.** Weight changes of all rats between their release and the first trapping session.

**Table S1.** Summary of release information and trapping occasions.

**Table S2.** Results of all selected models.