Declining populations in one of the last refuges for threatened mammal species in northern Australia

Hugh F. Davies[A], Michael A. McCarthy[A], Ronald S. C. Firth[B, C], John C.Z. Woinarski[D,E], Graeme R. Gillespie[E,F], Alan N. Andersen[D], Willie Rioli[G], José Puruntatameri[G], Willie Roberts[G], Colin Kerinaiua[G], Vivian Kerinauia[G], Kim Brooks *Womatakimi* [G] and Brett P. Murphy[D]

[A] Quantitative and Applied Ecology Group, The University of Melbourne, Parkville, Victoria, 3010, Australia.
[B] Research Institute for the Environment and Livelihoods, Charles Darwin University, Casuarina, Northern Territory, 0909, Australia.
[C] 360 Environmental, West Leederville, Western Australia, 6007, Australia.
[D] NESP Threatened Species Recovery Hub, Research Institute for the Environment and Livelihoods, Charles Darwin University, Casuarina, Northern Territory, 0909, Australia.
[E] Flora and Fauna Division, Department of Environment and Natural Resources, Berrimah, Northern Territory, 0820, Australia.
[F] School of BioSciences, The University of Melbourne, Victoria, 3010, Australia.
[G] Tiwi Land Council, Winnellie, Northern Territory, 0821, Australia.

Corresponding author details: Hugh Davies, hdavies1@student.unimelb.edu.au, 0417 828 202.

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MR. HUGH DAVIES (Orcid ID : 0000-0002-8473-4540)

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[B] Research Institute for the Environment and Livelihoods, Charles Darwin University, Casuarina, Northern Territory, 0909, Australia.
[C] Strategen Environmental, Subiaco, Western Australia, 6008, Australia.
[D] NESP Threatened Species Recovery Hub, Research Institute for the Environment and Livelihoods, Charles Darwin University, Casuarina, Northern Territory, 0909, Australia.
[E] Flora and Fauna Division, Department of Environment and Natural Resources, Berrimah, Northern Territory, 0820, Australia.
[F] School of BioSciences, The University of Melbourne, Victoria, 3010, Australia.
[G] Tiwi Land Council, Winnellie, Northern Territory, 0821, Australia.

Abstract:

Australia has contributed a disproportionate number of the world’s mammal extinctions over the past 200 years, with the greatest loss of species occurring through the continent’s southern and central arid regions. Many taxonomically and ecologically similar species are now undergoing widespread decline across the northern Australian mainland, possibly driven by predation by feral cats and changed fire regimes. Here we report marked recent declines of native mammal species in one of Australia’s few remaining areas that support an intact mammal assemblage, Melville Island, the largest island off the northern Australian coast. We have previously reported a marked decline on Melville Island of the threatened brush-tailed rabbit rat (Conilurus penicillatus) over the period 2000 to 2015, linked to predation by feral cats. We now report a 62% reduction in small mammal trap-success and a 36% reduction in site-level species richness over this period. There was a decrease in trap-success of 90% for the northern brown bandicoot (Isoodon macrourus), 64% for the brush-tailed rabbit-rat and 63% for the black-footed tree-rat (Mesembriomys gouldii), but no decline for the common brushtail possum (Trichosurus vulpecula). These results suggest that populations of native mammals on Melville Island are exhibiting similar patterns of decline to those recorded in Kakadu National Park two decades earlier, and across the northern Australian mainland more generally. Without the implementation of effective management actions, these species are likely to be lost from one of their last remaining strongholds, threatening to increase Australia's already disproportionate contribution to global mammal extinctions.

Keywords: Threatened mammals, extinction, refuge, northern Australia

Introduction:

Australia has experienced the highest number and proportion of mammal extinctions of any continent over the past two centuries (IUCN, 1996), having lost around 10% of its native mammal species (Short et al., 2002, Woinarski et al., 2014). While most of these mammal extinctions occurred from the mid 19th to early 20th Centuries and were concentrated in the southern and arid parts of Australia, over the past three decades severe declines have occurred further north in the monsoonal tropics (Woinarski et al., 2001, Woinarski et al., 2010). Given that the current decline of mammals in northern Australia is most evident in taxa similar to those driven to extinction and severe decline elsewhere in Australia (e.g. bandicoots, large rodents and dasyurids in the 'critical weight range' (CWR) of 35–5500 g) (Burbidge and McKenzie, 1989, Woinarski et al., 2010, Murphy and Davies, 2014), similar factors may be responsible. There is compelling evidence that predation by the introduced red fox (Vulpes vulpes) and feral cat (Felis catus) was the driver of decline and extinction of many mammal species in temperate, arid and semi-arid Australia (Johnson, 2006, Hardman et al., 2016, Short, 2016). Red foxes do not occur in monsoonal Australia, but the feral cat has been present across the northern Australian mainland since the 19th Century (Abbott, 2002, Abbott, 2008).

There is accumulating evidence that predation by feral cats is a key factor in the current declines across northern Australia. Recent studies have demonstrated extirpations of some native mammal species on islands recently colonised by cats, but persistence on islands without cats, with this pattern especially strong for mammal species that have declined extensively across mainland areas (Southgate et al., 1996, Woinarski et al., 1999, Woinarski et al., 2011b). An experimental reintroduction of the long-haired rat (Rattus villosissimus) on the northern Australian mainland failed outside predator exclosure areas, due primarily to predation by feral cats (Frank et al., 2014). At another mainland site, Leahy et al. (2016) demonstrated that predation by feral cats and dingoes (Canis dingo) was the primary cause of local population declines of two native mammal species over the 12-month study period. Fire was also a significant factor, but its influence was not through direct fire-related mortality, nor fire-induced reductions in food availability or reproductive success, or emigration. Rather, the influence of fire was related to cat predation, the effects of which were most severe in areas subject to high-intensity fire that removed a greater proportion of vegetation cover (Leahy et al., 2016). The synergistic relationship between fire and predation was further supported by McGregor et al. (2016), who demonstrated that feral cats concentrated their hunting activity to areas recently burnt by high-intensity fires.

Despite the accumulating evidence that predation by feral cats is a key factor in the current declines across northern Australia, the apparent asynchrony between the establishment of the feral cat in monsoonal northern Australia and the late 20th Century mammal declines, suggests other factors may be involved. Frequent, high-intensity fires, such as those characterising the fire regime across northern Australia since the breakdown of traditional Aboriginal burning practices, significantly alter the availability of critical resources, including fleshy-fruit bearing shrubs, logs and tree hollows (Russell-Smith et al., 2003b, Vigilante and Bowman, 2004, Firth et al., 2006b, Woinarski and Westaway, 2008). Any species with a strong reliance on such resources may be strongly disadvantaged by current northern Australian fire regimes, even in the absence of predation. However, species that are both dependent on these fire-mediated resources and also susceptible to predation are likely to be particularly threatened, and expected to be the first to exhibit decline and range contraction.

Predation by feral cats and frequent high-intensity fire both occur throughout far northern Australia, and therefore are potential threats to areas that currently still retain their full mammalian fauna. One such area is Australia's second-largest island, Melville Island, where the threatened brush-tailed rabbit-rat (Conilurus penicillatus) has recently contracted to areas where feral cats were rarely detected and shrub density was high (Davies et al. 2016). Here we build on that study by investigating changes in the broader mammal assemblage on Melville Island, which includes many species that have declined extensively across mainland northern Australia (Firth et al., 2006a, Woinarski et al., 2010, Firth et al., 2010) and several endemic subspecies. We predict that: (1) a range of native mammals on Melville Island, and not just the brush-tailed rabbit-rat, will be in decline; (2) declines will be most evident in those species that have declined most dramatically on the mainland; (3) the current distribution of small mammals on Melville Island will be inversely related to the presence of feral cats and frequent fire.

Methods:

Study site:

Melville Island (5788 km^2) is the larger of the two main Tiwi Islands, located ~20 km off the coast of Australia's Northern Territory (Figure 1). The Tiwi Islands became separated from mainland Australia relatively recently (between 12,000 and 8,000 years ago) (Woodroffe et al., 1992), and hence have an environment and a mammal assemblage largely comparable to the mainland (with the notable absence of the northern quoll (*Dasyurus hallucatus*). The islands are of low relief (≤ 103 m above sea level) and experience a tropical monsoonal climate with an intense wet season (November–April) in which over 90% of the annual rainfall occurs. There is a substantial rainfall gradient on Melville Island, from 1400 mm in the east, to 2000 mm in the northwest. The major vegetation types are savanna woodlands and open forests dominated by *Eucalyptus miniata*, *E. tetrodonta* and *Corymbia nesophila*, with a predominantly grassy understorey. Shrub density is highly variable, and studies on the mainland have shown that it is negatively affected by frequent, high-intensity fires (Russell-Smith et al., 2003a, Woinarski et al., 2004). Fire mapping of the Tiwi Islands, has shown that an average of 54% of the savannas were burnt each year from 2000-2013, with 65% of this area burning in the late dry season (Richards et al., 2015).

There is currently no evidence to suggest any recent change in fire intensity or frequency, feral animal densities or invasive weeds on the Tiwi Islands (see Woinarski et al. (2001) for further details on introduced species). Over the past two decades, the expansion of the forestry industry across the western half of Melville Island, has seen the replacement of around 30,000 ha of eucalypt tall open forest with short-rotation plantations of exotic *Acacia mangium* (Woinarski and Tiwi Land Council, 2001). Due to a lack of historical records (Abbott and Burbidge, 1995), the timing of the arrival of feral cats on Melville Island is unknown. While cats could have arrived as far back as the establishment of a British military outpost at Fort Dundas in 1824 (Brocklehurst, 1998), they also could have arrived appreciably later than in other parts of northern Australia (Davies et al. 2016).

Data collection:

From 2000–2002, small to medium-sized, non-flying mammals were sampled systematically at 351 sites as part of a general wildlife survey of the Tiwi Islands. These surveys involved a 50 × 50 m quadrat with 20 Elliott traps (33 × 10 × 9 cm) spaced equidistantly around the perimeter with one cage trap (56 × 20 × 20 cm) located on each of the four corners. Traps were baited with a mixture of peanut butter, oats and honey, and set for three consecutive nights. Four pitfall traps (two 20 L and two 10 L plastic buckets, each with 10 m of 30 cm high drift-line fence) were also used at each site over the 3-day sampling period. Additionally, five 10-minute searches (two at night using spotlights and three during daylight hours) were conducted at each site.

Between April and December 2015, 88 of the original 351 sites were revisited (Davies et al. 2016), all located in the savanna woodland and open forests of Melville Island (Figure 1). These 88 sites were chosen to capture the large variation in both annual rainfall and fire history on Melville Island. Eighty-two of these sites were surveyed using both live-trapping and camera-trapping, with the remaining six sites being surveyed using only camera-trapping. Live-trapping followed the 2000–2002 protocol but was conducted over four consecutive nights instead of three, and used eight cage traps and 16 Elliott traps. To avoid bias relating to possible seasonal differences in trap-success, re-visited sites were trapped at a comparable time of year to when they were originally surveyed. In 2015, no pitfall traps were used or site searches undertaken. Camera-trapping involved five horizontally facing motion-sensor cameras left continuously recording (24-hours per day) for a minimum 35 consecutive day period that overlapped with each site's live-trapping survey. Camera traps were baited with a mixture of peanut butter, oats and honey. To ensure maximum likelihood of being triggered, each camera was carefully positioned to ensure the bait was in the centre of the field of view (Gillespie et al., 2015).Vegetation within each camera's field of view was cleared to reduce the chance of false triggers and to reduce the risk posed by fire. Of the five cameras deployed at each site, two were Reconyx^{TM} HC550 Hyperfire white flash cameras (Reconyx Inc., Holmen, USA), while the remaining three were Reconyx^{TM} PC800 Hyperfire Professional infra-red flash cameras. All cameras were set to take three image bursts per trigger, with a 1-second delay between images. The sensitivity of each camera was set to high, with cameras re-arming instantly after being triggered.

To allow for direct comparison of the live-trapping results, we excluded captures from the original surveys arising from methods not repeated in 2015 (i.e. pitfall traps and site searches). We acknowledge here a potential source of bias arising from the exclusion of the pitfall records. On any given night, a particular animal caught in a pitfall trap is no longer able to be trapped in an Elliott or cage trap. Therefore the number of animals caught in pitfall traps could have influenced the 2000-2002 trap-success. We highlight that this source of bias relates only to those species small enough to be caught in pitfall traps (i.e. mice and dunnarts), and note that the number of mammals caught in pitfall traps in 2000-2002 was low and therefore not a large source of bias. As trap-success and species richness do not increase linearly with the number of nights that traps are deployed, we also excluded all captures recorded on the fourth night of live-trapping in 2015. The initial sampling derived an abundance measure from the number of captures and noted the possibility that multiple captures could include the same individual. For consistency we derived trap success the same way.

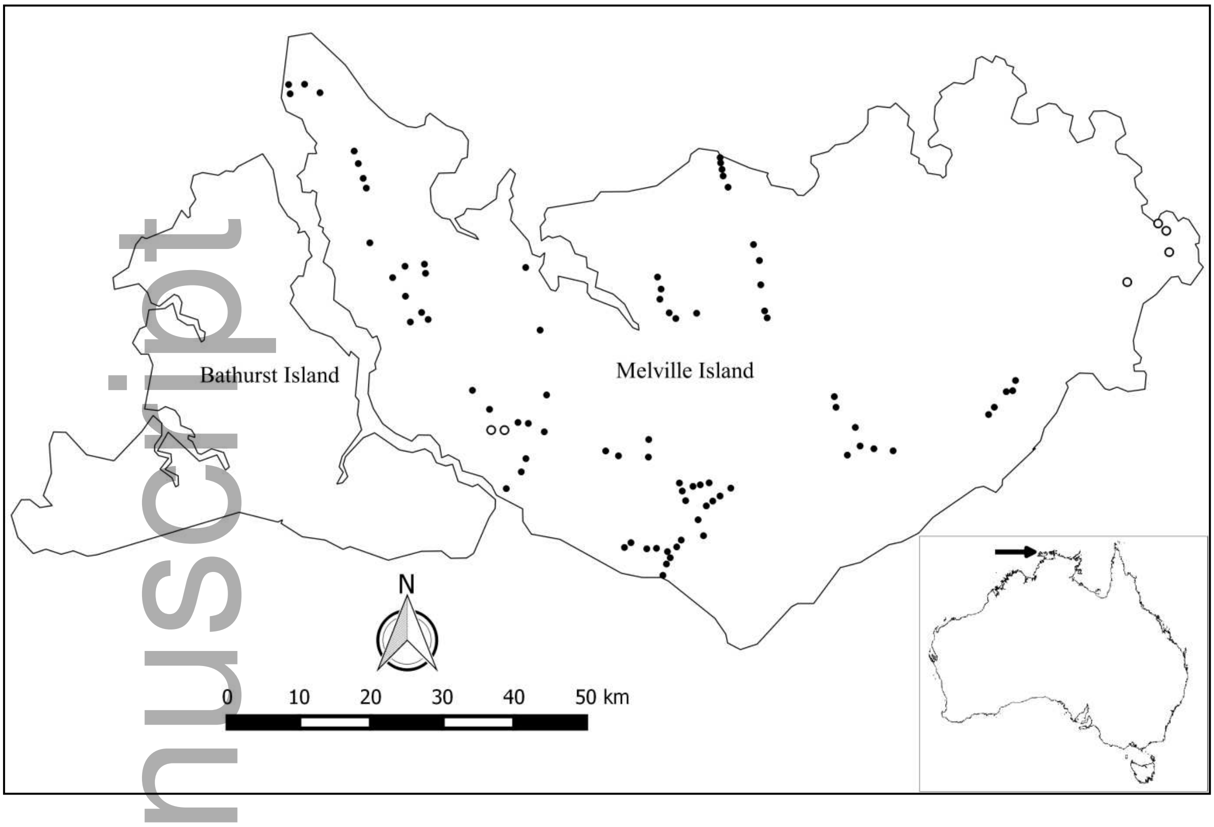


Figure 1: Location of the 88 sites surveyed for CWR mammals in 2015 on Melville Island. Filled circles represent the 82 sites where both camera-trapping and live-trapping were conducted, and open circles represent the six sites where only camera-trapping was conducted. The location of Melville Island relative to mainland Australia is shown in the inset.

Table 1: Description and justification of the variables used in analyses to assess the correlates of Melville Island mammal distribution in 2015.

Explanatory variable	**Description and justification for inclusion**	**Variable used in analyses to predict:**
Fire activity	Following Lawes et al. (2015), a remote-sensed fire variable derived from fine-scale (30 × 30 m) LANDSAT satellite imagery, representing the proportion of the area surrounding each site that was burnt in each year, averaged over the five years preceding mammal sampling. Calculations were made using an area with a radius of 3.2 km as shown by Lawes et al. (2015) to have the strongest influence on mammal populations.	• Feral cat activity • Mammal occupancy and detectability
Rainfall	Mean annual rainfall (Australian Bureau of Meteorology	• Feral cat

	2015). Throughout Australia, feral cat densities tend to be lower in areas of high rainfall (Legge et al., 2016) and mammal species in areas of high rainfall have declined the least (Fisher et al., 2013).	activity • Mammal occupancy and detectability
Basal area	Calculated as the sum of the basal area (m^2/ha) of 50 trees (with a diameter at breast height greater than 5 cm) measured within a quadrat 5 m wide with a length equal to the distance to the 50th measured tree or a maximum of 200 m. Firth et al. 2006a demonstrated the influence of basal area on the occurrence of mammals.	• Mammal occupancy and detectability
Dingo activity	The proportion of nights that dingos were recorded on camera at each site. This was taken as an approximation of dingo activity at each site. Included in analyses to investigate the potential negative influence of dingos on feral cats and potential benefits for mammal populations (Johnson, 2006, Kennedy et al., 2012).	• Feral cat activity • Mammal occupancy and detectability
Shrub density	A count of the number of shrubs in a 1 × 100 m quadrat at each site. Shrubs were defined as anything greater than 20 cm in height with a diameter at breast height of less than 5 cm. Shrubs with multiple stems were counted as a single individual. Vegetation structure has been demonstrated to reduce feral cat hunting success, and therefore influence the distribution of feral cats as well as the occupancy and detectability of mammals (McGregor et al., 2015).	• Feral cat activity • Mammal occupancy and detectability
Distance to water	A remote-sensed variable measuring the distance (m) from each site to the closest permanent water body. The distance to water was demonstrated by Firth et al. (2006a) to strongly influence a number of mammals on Melville Island.	• Mammal occupancy and detectability
Coarse woody debris (CWD)	A count of the number of logs with a diameter of greater than 5 cm that crossed a 200 m transect at each site. Included in analyses due to Firth et al. (2006b) demonstrating the reliance of some mammals on fallen logs as den sites.	• Mammal occupancy and detectability

Feral cat activity	As an index of feral cat activity, we used the predicted probability of detecting feral cats at each site, derived from spatially explicit generalised linear models (Murphy et al., 2010). The probability of feral cat detection was included in the analyses as cats have been implicated as a major factor in the northern mammal decline (Woinarski et al., 2011a, Ziembicki et al., 2014). SeeDavies et al. (2016).	• Mammal occupancy and detectability
Julian day	The Julian day of the calendar year that sampling started at each site. Recent work by Geyle (2015) demonstrated that the detectability of the brush-tailed rabbit-rat (Conilurus penicillatus) increases throughout the dry season (May – November).	• Mammal detectability
Number of cameras operating	An observation level covariate to account for the variation in detectability arising from uneven numbers of cameras operating at different sites due to camera malfunction and destruction.	• Mammal detectability

Data analysis:

1) Trends in trap-success

Mammal species >200 g, such as northern brown bandicoot (Isoodon macrourus), common brushtail possum (Trichosurus vulpecula) and black-footed tree-rat (Mesembriomys gouldii), were caught almost exclusively in cage traps, whereas smaller species such as the delicate mouse were exclusively caught in Elliott traps (See Table S1 in supplementary material). Therefore, prior to investigating changes in trap-success, we first had to account for the different ratio of cage traps to Elliott traps used at each site between sampling years, as this would strongly influence the recorded trap-success in each year. To account for this bias, we derived a species-specific effective trap-success based on the relative effectiveness of each trap type (cage vs. Elliott). This was done for each species that showed a strong bias for either trap type (See Table S2 in supplementary material). These scaling factors could only be determined from the 2015 live-trapping data as the original data did not consistently record the trap type. For example, although the trap effort for Elliott traps was twice that of cage traps in 2015, Elliott traps accounted for only 2.7% of black-footed tree-rat captures. Therefore the effective trap-success in each year for this species was calculated as:

Effective trap-success = number of captures ÷ (number of cage trap nights + 0.027*number of Elliott trap nights) * 100

Wilcoxon matched-pairs tests were used to investigate changes in trap-success (calculated as the sum of all species' effective trap-success at each site), site-level species richness and species-specific effective trap-success at the 82 sites where live-trapping was conducted in both 2000–2002 and 2015.

2) Correlates of mammal distribution in 2015

Davies et al. (2016) investigated a range of environmental correlates of the distribution of the brush-tailed rabbit-rat on Melville Island. Here we use the same approach to investigate the 2015 distribution of three other mammal species that were detected by camera traps sufficiently to permit occupancy modelling: the northern brown bandicoot, black-footed tree-rat and common brushtail possum. Single-season occupancy models were used to investigate how each predictor variable (Table 1) influenced site occupancy. For comparison, we also present results published by Davies et al. (2016) for the brush-tailed rabbit-rat. Occupancy modelling was conducted using only the 2015 camera trapping data (88 sites) in the package "unmarked" in R (Fiske and Chandler, 2011). Explanatory variables were centred and standardised prior to analysis.

Due to the many variables and therefore the large number of possible models, occupancy modelling was applied in a two-step process. First we determined which variables best explained the detectability of each species by running all combinations (512 models) of the nine variables we hypothesised might influence the detectability of small mammals. This was done with occupancy constrained to a saturated model of the seven variables we hypothesised might influence site occupancy for the mammal species. Model selection based on AIC was then used to select the most parsimonious model in the candidate set. The second step involved running all possible combinations of the seven occupancy variables (128 models) with detectability constrained to the most important variables identified in step one. Model selection based on AIC was then used for the second time to determine the best model in the candidate set. Where no single model was clearly superior at explaining the distribution of a species (i.e. ΔAIC <4), we used model averaging to obtain parameter estimates (Burnham and Anderson, 2002).

Once the most parsimonious model with only the main effects was identified, we investigated the possible effect of an interaction between the feral cat activity and both fire and shrubs. This was done because processes that simplify vegetation structure (such as frequent fire) might amplify the impact of feral cats. We also tested whether the inclusion of tree basal area increased the model fit.

Accounting for imperfect detection provides more realistic, but less precise, estimates of occupancy (Guillera-Arroita et al., 2014). To gauge how accounting for detectability influenced our occupancy estimates and hence the confidence in our conclusions drawn from these models, we also ran all combinations of the occupancy variables but assuming constant detectability.

We assessed the fit of the most saturated model for each mammal species with three goodness-of-fit tests based on parametric bootstrapping: Pearson's chi-square statistic, the sum of squared errors and the Freeman-Tukey chi-square statistic. These methods repeatedly simulate datasets based on a fitted model, and then evaluate the probability that the observed history of outcomes has a reasonable chance of happening if the model assessed is assumed to be correct (MacKenzie and Bailey, 2004).

Results:

1) Trends in trap-success

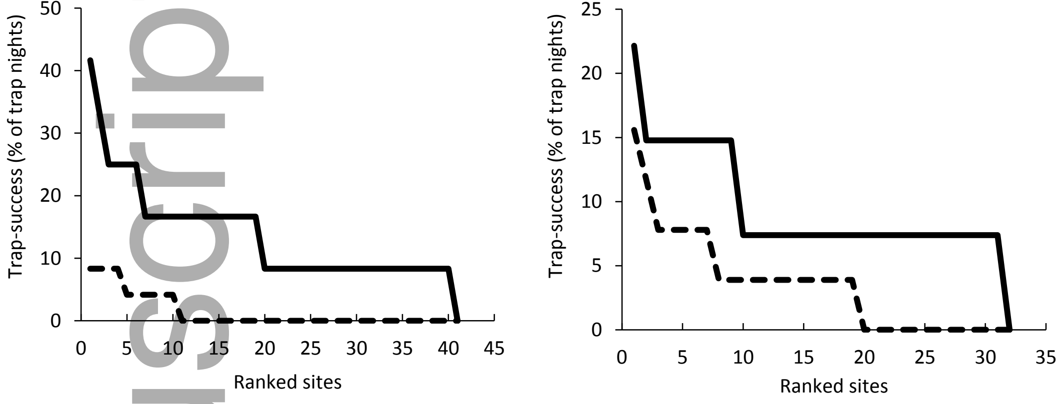
A total of twelve mammal species were recorded, two of which do not have a mean body size within the CWR: delicate mouse and Butler's dunnart. Overall trap-success was 62% lower in 2015 (6.1 ± 0.8) than in 2000–02 (16.1 ± 1.5; $Z = 5.6$, $p < 0.001$). Three of the five species recorded from at least ten sites across the sampling periods, exhibited a significant decrease in trap-success, with northern brown bandicoot decreasing by 90% ($Z = 5.42$, $p < 0.001$), brush-tailed rabbit-rat by 64% ($Z = 1.97$, $p < 0.05$) and black-footed tree-rat by 63% ($Z = 3.33$, $p < 0.001$) (Figure 2). The remaining five species (mostly reported from few sites) showed no significant change (Table 2).

Site-level species richness decreased by 36% between 2000-02 (1.6 ± 0.1) and 2015 (1.0 ± 0.1; $Z = 3.82$, $p < 0.001$). The proportion of sites where no native mammals were trapped doubled from 13% to 26%. Six species exhibited a large decrease in naïve occupancy (39 – 80%), while the common brushtail possum and delicate mouse were recorded at 29% more sites in 2015 than in 2000-02 (Table 2).

2) Correlates of mammal distribution in 2015

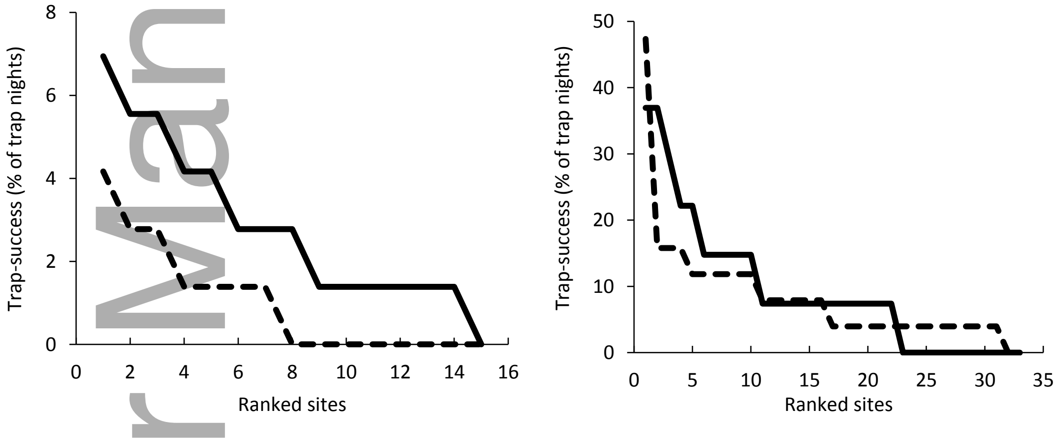
Given the overall high detectability for all species, the estimated rate of occupancy by the respective best model for each species was very similar to the naïve and null model estimates (See Table S2 in supplementary material). As such, the effect of each covariate on site-occupancy was similar regardless of whether the models included effects of covariates on detectability or not.

Shrub density was a (borderline) significant predictor of site-occupancy by the black-footed tree-rat, as it was for the brush-tailed rabbit-rat, but not for the northern brown bandicoot or common brushtail possum (Figure 3). Unlike the situation for the brush-tailed rabbit rat, feral cat detection was not a significant predictor variable for any of the other species (Figure 3). Fire was not a significant predictor for any species, and neither the inclusion of neither tree-basal area nor an interaction between fire and shrubs with feral cat activity improved the model fit for any species.



a) Northern brown bandicoot*

b) Black-footed tree-rat*



c) Brush-tailed rabbit-rat*

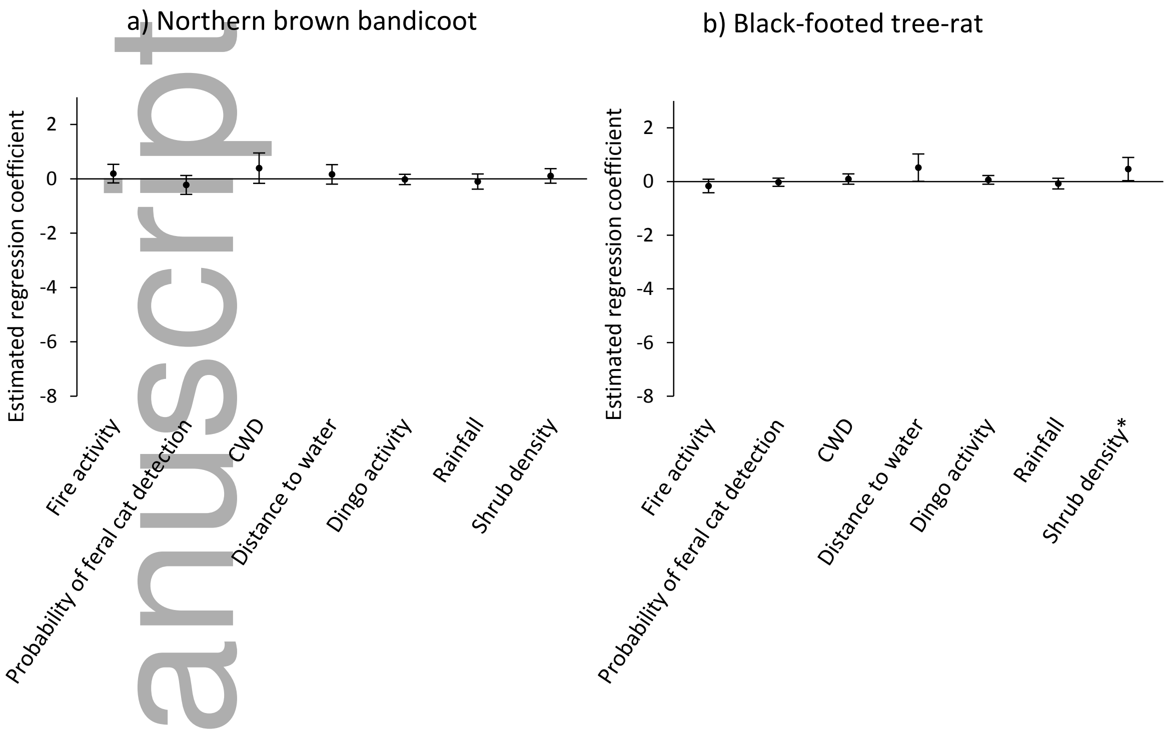
d) Common brushtail possum

Figure 2: The difference in live trap-success in 2000-02 (solid line) and 2015 (dashed line) for a) northern brown bandicoot b) black-footed tree-rat c) brush-tailed rabbit-rat and d) common brushtail possum. Asterisks indicate a statistically significant ($p < 0.05$) change in trap-success.

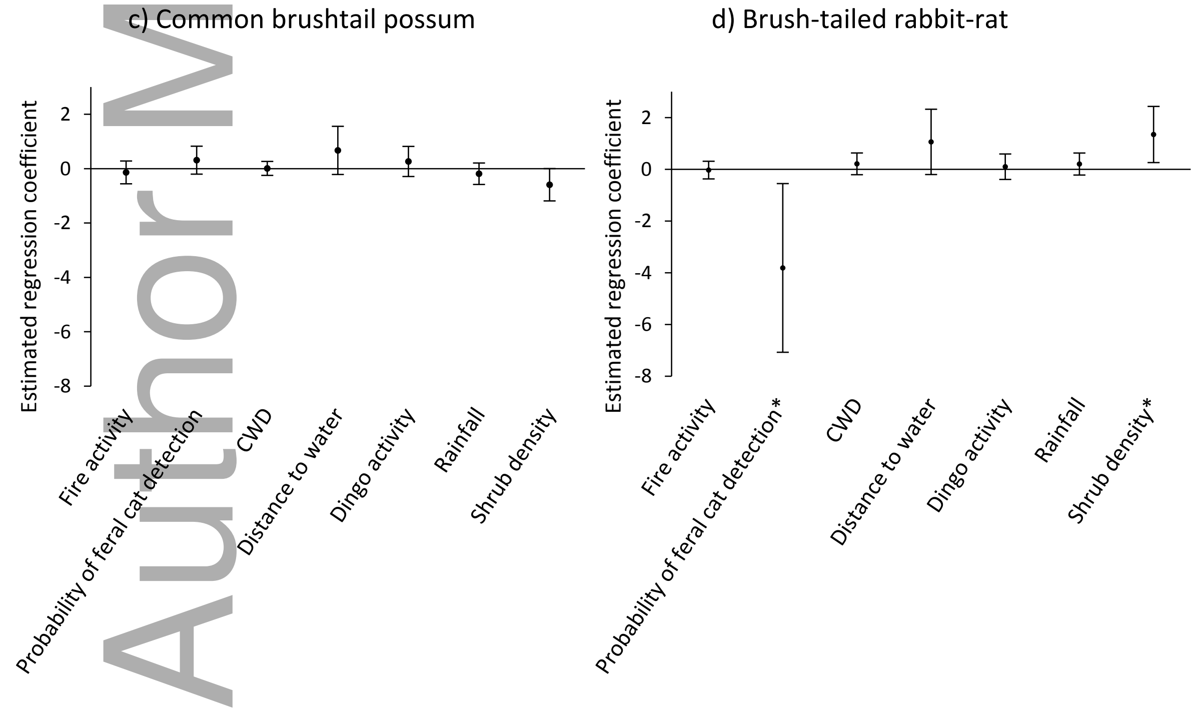
Table 2: Summary of the changes in the native mammal populations of Melville Island recorded with live-trapping between 2000–02 and 2015. Naïve occupancy was calculated as the percentage of the 82 live-trapped sites where a species was detected. * = $p < 0.05$, *** = $p < 0.001$. Decreases denoted by -, increases denoted by +. Species in bold indicate a body-size outside the critical weight range. Dashes indicate species for which a proportional change in trap-success could not be calculated.

Species	Naïve occupancy 2000-02 (%)	Naïve occupancy 2015 (%)	Change in naïve occupancy (%)	Trap-success 2000-02 (%) (±SE)	Trap-success 2015 (%) (±SE)	Change in trap-success (%)
Northern brown bandicoot (Isoodon macrourus)	49	12	- 75	6.91 (0.99)	0.71 (0.23)	- 90***
Black-footed tree-rat (Mesembriomys gouldii)	38	23	- 39	3.69 (0.59)	1.38 (0.33)	- 63***
Common brushtail possum (Trichosurus vulpecula)	27	38	+ 29	3.78 (0.88)	3.32 (0.73)	- 12
Brush-tailed rabbit-rat (Conilurus penicillatus)	17	9	- 50	0.53 (0.15)	0.19 (0.08)	- 64*
Grassland melomys (Melomys burtoni)	7	4	- 50	0.69 (0.31)	0.10 (0.06)	- 88
Delicate mouse (Pseudomys delicatulus)	7	12	+ 29	0.20 (0.09)	0.30 (0.10)	+ 33
Pale field-rat (Rattus tunneyi)	6	1	- 80	0.10 (0.05)	0.02 (0.02)	- 80
Red-cheeked dunnart (Sminthopsis virginiae)	5	1	- 75	0.10 (0.06)	0.03 (0.03)	- 70
Northern sugar glider (Petaurus breviceps)	2	0	-	0.03 (0.02)	0	-
Northern brush-tailed phascogale (Phascogale pirata)	2	0	-	0.03 (0.02)	0	-
Butler's dunnart (Sminthopsis butleri)	1	0	-	0.03 (0.02)	0	-

Western chestnut mouse (Pseudomys nanus)	0	2	-	0	0.03 (0.02)	-


a) Northern brown bandicoot

b) Black-footed tree-rat


c) Common brushtail possum

d) Brush-tailed rabbit-rat

Figure 3: Model averaged regression coefficient estimates for a) the northern brown bandicoot, b) the black-footed tree-rat, c) the common brushtail possum and d) the brush-tailed rabbit-rat (first published in Davies et al. (2016)). Error bars indicate 95% confidence intervals; asterisks indicate

where they do not overlap zero, i.e. a statistically significant effect. Data sourced from 2015 camera-trapping.

Discussion:

Many native mammal species have recently experienced severe range contractions across northern Australia, and Melville Island is one of the few remaining areas to have retained an intact mammal fauna (Woinarski et al. 2010, Ziembicki et al. 2014). However, Davies et al. (2016) demonstrated that the Melville Island population of the brush-tailed rabbit-rat had retracted to areas where feral cats were rarely detected and shrub density was high. Here we build on that study to report evidence of broader decline in the mammal assemblage of Melville Island. We found that trap-success and species richness at the site-level decreased by 62% and 36% respectively from 2000-02 to 2015. As predicted, declines were most evident for three species that have suffered considerable declines on mainland northern Australia: northern brown bandicoot (90% decrease in trap-success), brush-tailed rabbit-rat (64%) and black-footed tree-rat (63%). These severe declines are particularly notable because the local subspecies of black-footed tree-rat (M. gouldii melvillensis) is endemic to the island, and the local subspecies of brush-tailed rabbit-rat (C. penicillatus melibius) is endemic to Melville Island and the adjacent Bathurst Island. However, inconsistent with our prediction, there was no such decline for the common brushtail possum, a comparably-sized species that has also exhibited marked decline on the northern Australian mainland (Woinarski et al., 2010).

We acknowledge the limitations associated with inferring mammal decline with only two data points spaced 15 years apart. However, the pattern of decline observed on Melville Island is very similar to that recorded in Kakadu National Park between 2001 and 2009. Over this period in Kakadu, the brush-tailed rabbit-rat and black-footed tree-rat were not recorded frequently enough to permit statistical analysis (despite both species being common 30–40 years previously) (Woinarski et al., 2010), and the abundance of the northern brown bandicoot and common brushtail possum decreased by 88 and 86% respectively (Woinarski et al., 2010). This suggests that in Kakadu, the brush-tailed rabbit-rat and black-footed tree-rat were among the first mammal species to decline. It is therefore plausible that Melville Island is currently experiencing the pattern of decline that occurred in Kakadu National Park over a decade earlier.

Unlike the brush-tailed rabbit-rat (Davies et al. 2016) and despite substantial decreases in trap-success, neither the northern brown bandicoot nor black-footed tree rat appear to have suffered marked range contractions on Melville Island. This suggests that their declines have not yet progressed to the point of influencing their distribution. The lack of change in the occurrence of these species (as opposed to abundance) can explain why we failed to detect relationships between environmental variables, including the presence of feral cats or frequent fire, and site occupancy.

There are a number of potential explanations for why small mammal declines on Melville Island have not progressed to the same extent as on mainland northern Australia. First, Melville Island is a highly productive area of monsoonal northern Australia (Richards et al., 2012), and receives the highest annual rainfall in the Northern Territory. This productivity likely results in high resource availability and high rates of survival and reproduction. As such, mammal populations on Melville Island might not only be more resilient than those on the mainland, but initial population sizes on Melville Island may have been higher. Either of these possibilities may result in a longer period of time being required to cause widespread contractions of species distributions.

Second, and also related to the higher rainfall, much of Melville Island has a particularly dense understorey and midstorey of shrubs and small trees (Richards et al., 2012, Davies et al., 2016). As a result, the predation pressure imposed on mammal populations, particularly by feral cats, may be lower on Melville Island compared with the mainland (McGregor et al., 2015, Hohnen et al., 2016, Leahy et al., 2016). This is supported by evidence that site occupancy by the brush-tailed rabbit-rat and the black-footed tree-rat on Melville Island is positively related to shrub density (Davies et al., 2016).

Third, it is possible that fire intensity is generally lower on Melville Island than on the mainland. Melville Island has a longer wet season and experiences a greater amount of dry-season rain than is the case for the mainland, and so dry fuel for fire is available for a shorter period of time. The amount of flammable grass-layer fuel loads may also be lower on Melville Island due to a higher density of trees and shrubs. As such, any fire-related depletion of resources on Melville Island may not have occurred to the same extent. If the decline of common brushtail possum populations on mainland northern Australia has been primarily driven by fire-driven resource depletion (especially tree hollows)(Woinarski and Westaway, 2008), the apparent stability of this species on Melville Island may be related to a more benign fire regime. There is currently no direct evidence demonstrating that fire regimes have been more benign on Melville Island than other areas. Addressing this knowledge gap should be the focus of future research.

Finally, it is likely that cats have not been on Melville Island for as long as they have on the mainland (Abbott and Burbidge, 1995, Abbott, 2002, Abbott, 2008), and although there have been some anecdotal reports that cats were introduced to Tiwi islands only within the past few decades (Firth, 2010), definitive evidence of an introduction date is not available. It is also plausible that feral cat populations (and their impact on native mammals) on Melville Island have been suppressed by high dingo densities (Kennedy et al., 2012).

Unfortunately, the validity of the above explanations are difficult to evaluate given a lack of relevant information on changes in native mammal populations, feral cat and dingo densities, as well as any changes in fire regimes. However, our finding of widespread declines in an area recently thought to be a refuge for mammals highlights the importance of differentiating between true refuges, where threatening processes are either absent or effectively mitigated, and areas that appear intact simply because declines have been delayed or have occurred relative to a higher initial density level. The latter appears to be the case on Melville Island. This distinction may help prioritise management actions and facilitate timely intervention. These results also have important implications for conservation management. Davies et al. (2016) suggested that fire management that enhances the density of the shrub layer could be a feasible management option to reduce the impact of feral cats on the threatened brush-tailed rabbit-rat. Here, we have also demonstrated a weak but significant, positive association between the density of shrubs and the probability of site-occupancy by the black-footed tree-rat. While this association might be due to increased food availability rather than shelter from predation (Friend, 1987), it appears that fire management that maintains a dense understorey could also benefit this species. Small mammal populations have been shown to respond positively to strategic fire management in the Kimberley region of Western Australia (Legge et al., 2011), and a similar approach to fire management could prove beneficial for Melville Island biodiversity.

In conclusion, we have shown that the severe population declines that have been documented for small mammals across mainland northern Australia appear to be underway on Melville Island. On the basis of current evidence, we cannot distinguish between a series of potential primary causal mechanisms, and hence cannot yet provide a tight focus for remedial management response. We recommend the following explicit research actions to tease apart the relative impacts of these putative causal factors: (1) quantify the availability of critical small mammal resources across Melville Island and determine how fire frequency and intensity influences their rate of depletion (2) determine how (and why) the density of mammalian predators varies across Melville Island (3) quantify the response of small mammal populations to a range of experimentally manipulated combinations of predation pressure (using fenced exclosures) and fire frequency. In 2001, Woinarski et al. (2001) warned that the mammal fauna of northern Australia may suffer the same fate as the decimated central Australian mammal fauna. Unfortunately, this appears to be coming to fruition, with many species suffering widespread contraction across mainland northern Australia (Woinarski et al. 2010). Here we reiterate this warning with increased urgency and highlight that the consequences of losing these species go beyond the ecological. Traditional food sources (including small mammals) are an important part of the Tiwi diet and provide vital healthy food options for communities. Hunting activities reinforce traditional authority structures, are an important way of passing on traditional knowledge, and form the basis for cultural land management. If Tiwi small mammal populations continue to decline, there will be significant impacts on the expression of Tiwi culture. As such, there is a a critical need to improve our understanding of the factors driving these declines, and to implement management actions before these species are lost from one of the last remaining areas in Australia with an intact small mammal fauna.

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Table 1: Description and justification of the variables used in analyses to assess the correlates of Melville Island mammal distribution in 2015.

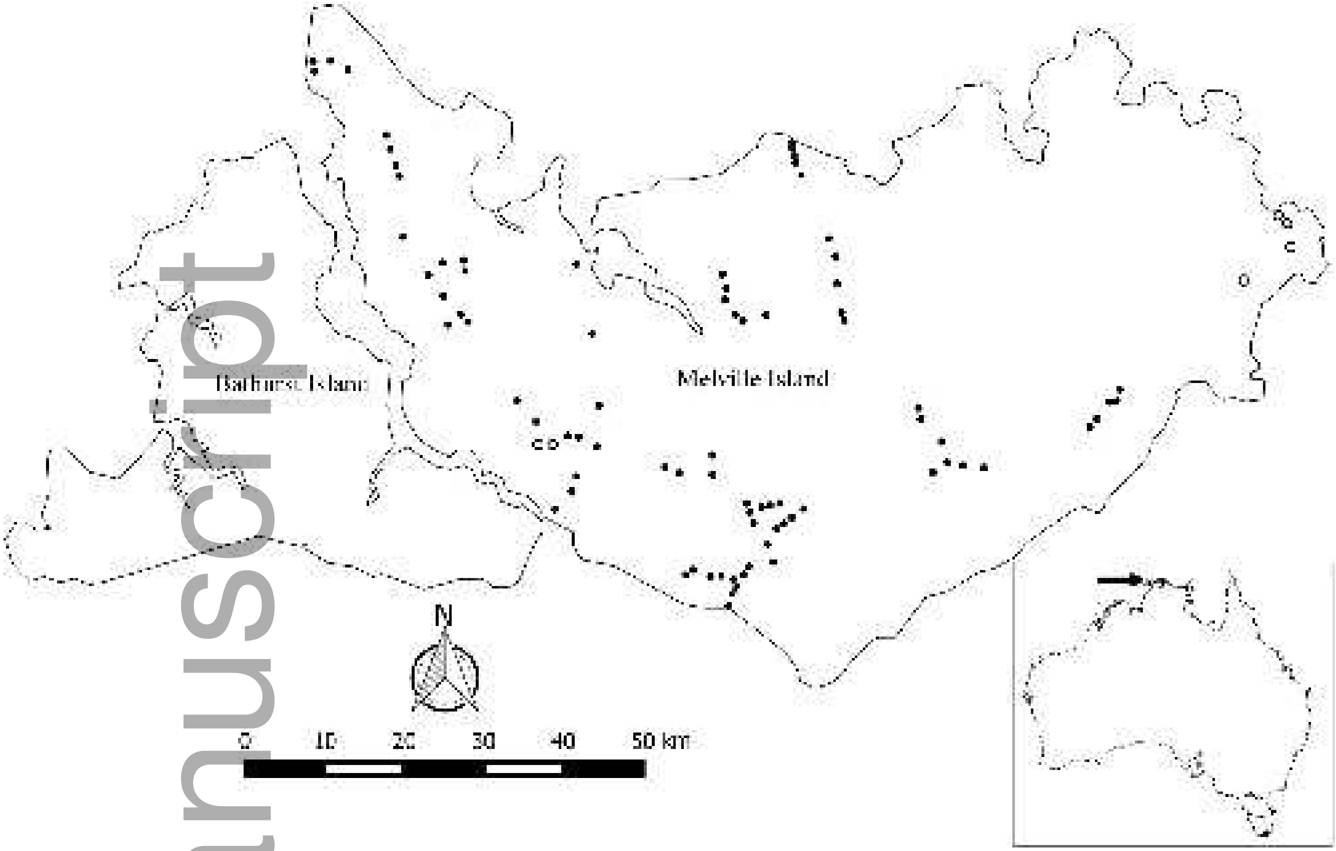
Explanatory variable	Description and justification for inclusion	Variable used in analyses to predict:
Fire activity	Following Lawes et al. (2015), a remote-sensed fire variable derived from fine-scale (30 × 30 m) LANDSAT satellite imagery, representing the proportion of the area surrounding each site that was burnt in each year, averaged over the five years preceding mammal sampling. Calculations were made using an area with a radius of 3.2 km as shown by Lawes et al. (2015) to have the strongest influence on mammal populations.	• Feral cat activity • Mammal occupancy and detectability
Rainfall	Mean annual rainfall (Australian Bureau of Meteorology 2015). Throughout Australia, feral cat densities tend to be lower in areas of high rainfall (Legge et al., 2016) and mammal species in areas of high rainfall have declined the least (Fisher et al., 2013).	• Feral cat activity • Mammal occupancy and detectability
Basal area	Calculated as the sum of the basal area (m^2/ha) of 50 trees (with a diameter at breast height greater than 5 cm) measured within a quadrat 5 m wide with a length equal to the distance to the 50th measured tree or a maximum of 200 m. Firth et al. 2006a demonstrated the influence of basal area on the occurrence of mammals.	• Mammal occupancy and detectability
Dingo activity	The proportion of nights that dingos were recorded on camera at each site. This was taken as an approximation of dingo activity at each site. Included in analyses to investigate the potential negative influence of dingos on feral cats and potential benefits for mammal populations (Johnson, 2006, Kennedy et al., 2012).	• Feral cat activity • Mammal occupancy and detectability
Shrub density	A count of the number of shrubs in a 1 × 100 m quadrat at each site. Shrubs were defined as anything greater than 20 cm in height with a diameter at breast height of less than 5 cm. Shrubs with multiple stems were counted as a single	• Feral cat activity • Mammal occupancy and

	individual. Vegetation structure has been demonstrated to reduce feral cat hunting success, and therefore influence the distribution of feral cats as well as the occupancy and detectability of mammals (McGregor et al., 2015).	detectability
Distance to water	A remote-sensed variable measuring the distance (m) from each site to the closest permanent water body. The distance to water was demonstrated by Firth et al. (2006a) to strongly influence a number of mammals on Melville Island.	• Mammal occupancy and detectability
Coarse woody debris (CWD)	A count of the number of logs with a diameter of greater than 5 cm that crossed a 200 m transect at each site. Included in analyses due to Firth et al. (2006b) demonstrating the reliance of some mammals on fallen logs as den sites.	• Mammal occupancy and detectability
Feral cat activity	As an index of feral cat activity, we used the predicted probability of detecting feral cats at each site, derived from spatially explicit generalised linear models (Murphy et al., 2010). The probability of feral cat detection was included in the analyses as cats have been implicated as a major factor in the northern mammal decline (Woinarski et al., 2011a, Ziembicki et al., 2014). SeeDavies et al. (2016).	• Mammal occupancy and detectability
Julian day	The Julian day of the calendar year that sampling started at each site. Recent work by Geyle (2015) demonstrated that the detectability of the brush-tailed rabbit-rat (Conilurus penicillatus) increases throughout the dry season (May – November).	• Mammal detectability
Number of cameras operating	An observation level covariate to account for the variation in detectability arising from uneven numbers of cameras operating at different sites due to camera malfunction and destruction.	• Mammal detectability

Table 2: Summary of the changes in the native mammal populations of Melville Island recorded with live-trapping between 2000–02 and 2015. Naïve occupancy was calculated as the percentage of the 82 live-trapped sites where a species was detected. * = p < 0.05, *** = p < 0.001. Decreases denoted by -, increases denoted by +. Species in bold indicate a body-size outside the critical weight range. Dashes indicate species for which a proportional change in trap-success could not be calculated.

Species	Naïve occupancy 2000-02 (%)	Naïve occupancy 2015 (%)	Change in naïve occupancy (%)	Trap-success 2000-02 (%)	Trap-success 2015 (%)	Change in trap-success (%)

				(±SE)	(±SE)	
Northern brown bandicoot (Isoodon macrourus)	49	12	- 75	6.91 (0.99)	0.71 (0.23)	- 90***
Black-footed tree-rat (Mesembriomys gouldii)	38	23	- 39	3.69 (0.59)	1.38 (0.33)	- 63***
Common brushtail possum (Trichosurus vulpecula)	27	38	+ 29	3.78 (0.88)	3.32 (0.73)	- 12
Brush-tailed rabbit-rat (Conilurus penicillatus)	17	9	- 50	0.53 (0.15)	0.19 (0.08)	- 64*
Grassland melomys (Melomys burtoni)	7	4	- 50	0.69 (0.31)	0.10 (0.06)	- 88
Delicate mouse (Pseudomys delicatulus)	7	12	+ 29	0.20 (0.09)	0.30 (0.10)	+ 33
Pale field-rat (Rattus tunneyi)	6	1	- 80	0.10 (0.05)	0.02 (0.02)	- 80
Red-cheeked dunnart (Sminthopsis virginiae)	5	1	- 75	0.10 (0.06)	0.03 (0.03)	- 70
Northern sugar glider (Petaurus breviceps)	2	0	-	0.03 (0.02)	0	-
Northern brush-tailed phascogale (Phascogale pirata)	2	0	-	0.03 (0.02)	0	-
Butler's dunnart (Sminthopsis butleri)	1	0	-	0.03 (0.02)	0	-
Western chestnut mouse (Pseudomys nanus)	0	2	-	0	0.03 (0.02)	-



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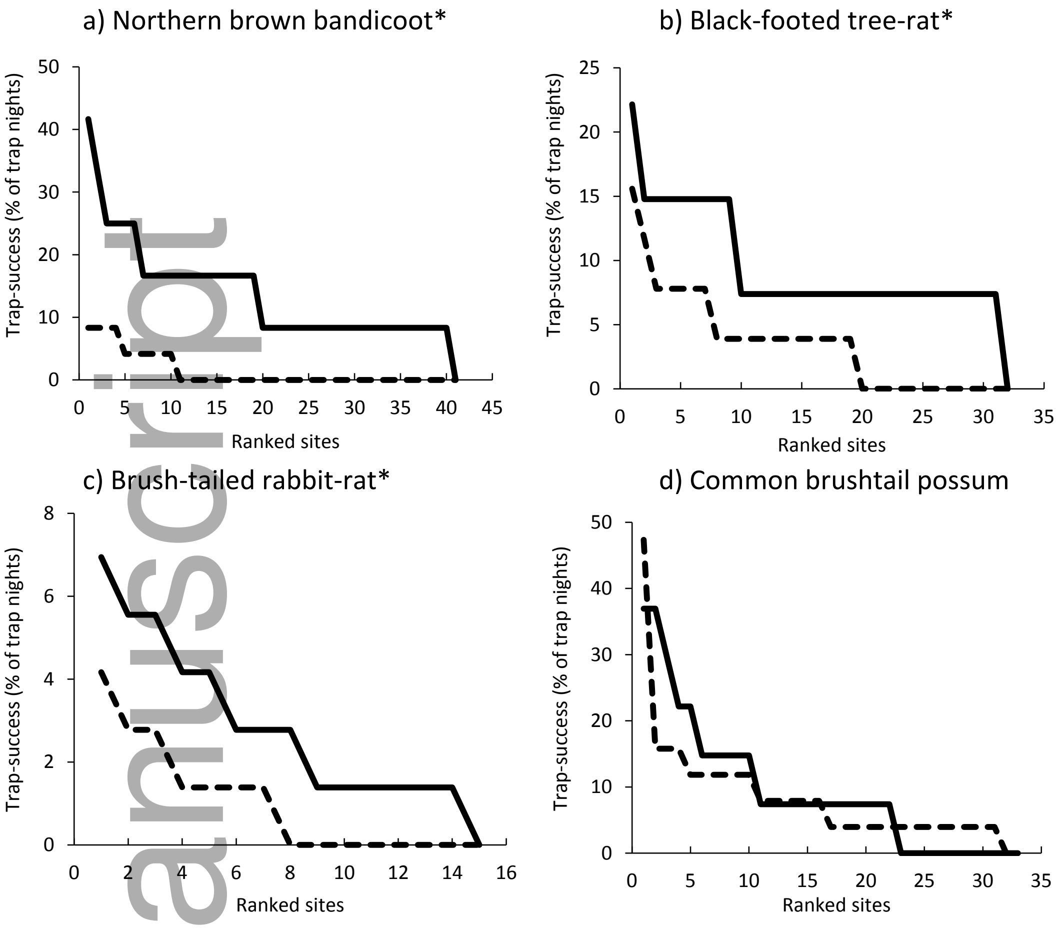

a) Northern brown bandicoot*

b) Black-footed tree-rat*

c) Brush-tailed rabbit-rat*

d) Common brushtail possum

Figure 2: The difference in live trap-success in 2000-02 (solid line) and 2015 (dashed line) for a) northern brown bandicoot b) black-footed tree-rat c) brush-tailed rabbit-rat and d) common brushtail possum. Asterisks indicate a statistically significant ($p < 0.05$) change in trap-success.

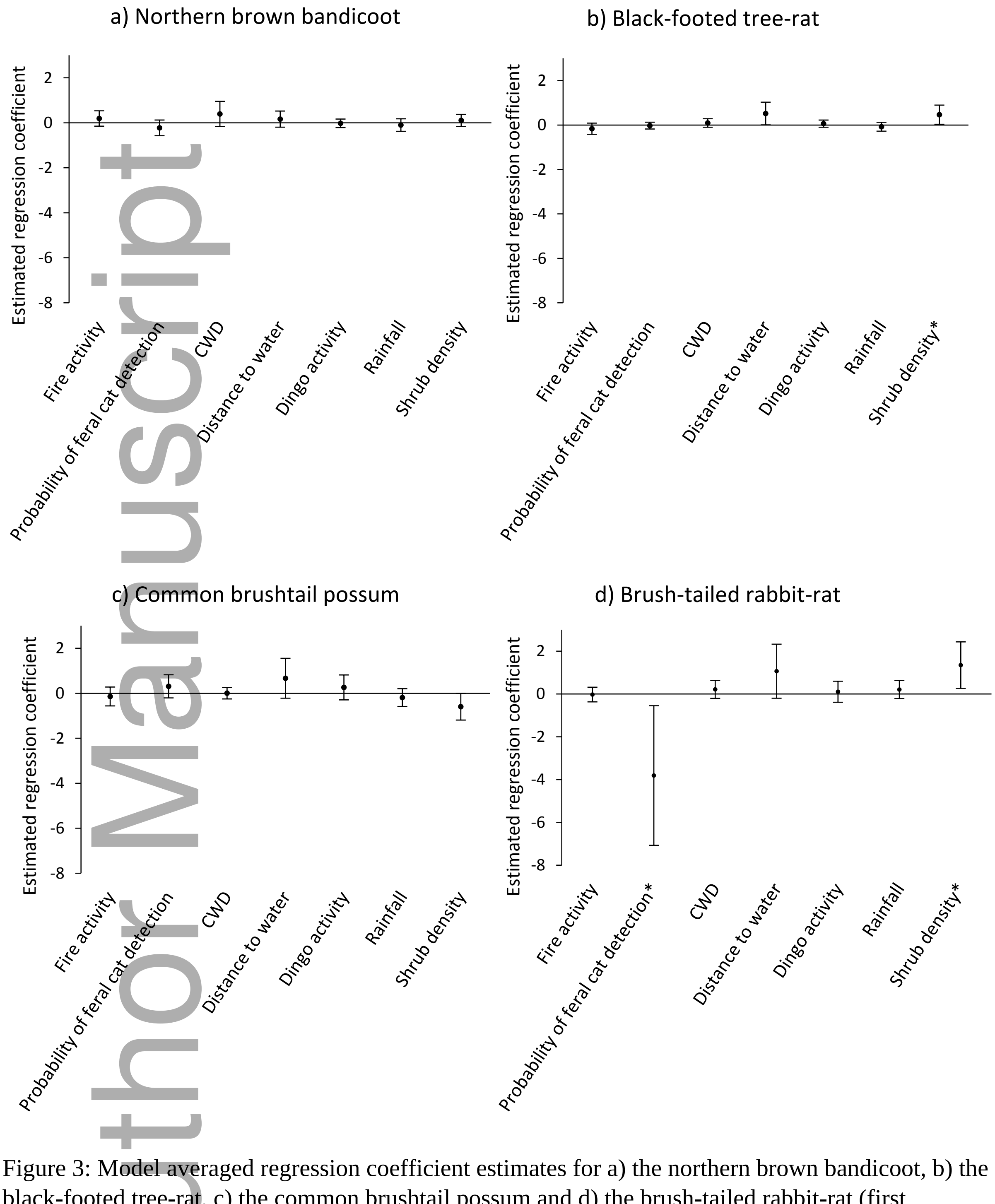

Figure 3: Model averaged regression coefficient estimates for a) the northern brown bandicoot, b) the black-footed tree-rat, c) the common brushtail possum and d) the brush-tailed rabbit-rat (first published in Davies et al. (2016)). Error bars indicate 95% confidence intervals; asterisks indicate where they do not overlap zero, i.e. a statistically significant effect. Data sourced from 2015 camera-trapping.