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

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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

32 remaining areas that support an intact mammal assemblage, Melville Island, the largest island off the
33 northern Australian coast. We have previously reported a marked decline on Melville Island of the
34 threatened brush-tailed rabbit rat (*Conilurus penicillatus*) over the period 2000 to 2015, linked to
35 predation by feral cats. We now report a 62% reduction in small mammal trap-success and a 36%
36 reduction in site-level species richness over this period. There was a decrease in trap-success of 90%
37 for the northern brown bandicoot (*Isoodon macrourus*), 64% for the brush-tailed rabbit-rat and 63%
38 for the black-footed tree-rat (*Mesembriomys gouldii*), but no decline for the common brushtail possum
39 (*Trichosurus vulpecula*). These results suggest that populations of native mammals on Melville Island
40 are exhibiting similar patterns of decline to those recorded in Kakadu National Park two decades
41 earlier, and across the northern Australian mainland more generally. Without the implementation of
42 effective management actions, these species are likely to be lost from one of their last remaining
43 strongholds, threatening to increase Australia's already disproportionate contribution to global
44 mammal extinctions.

45 Keywords: Threatened mammals, extinction, refuge, northern Australia

46 **Introduction:**

47 Australia has experienced the highest number and proportion of mammal extinctions of any continent
48 over the past two centuries (IUCN, 1996), having lost around 10% of its native mammal species
49 (Short et al., 2002, Woinarski et al., 2014). While most of these mammal extinctions occurred from
50 the mid 19th to early 20th Centuries and were concentrated in the southern and arid parts of Australia,
51 over the past three decades severe declines have occurred further north in the monsoonal tropics
52 (Woinarski et al., 2001, Woinarski et al., 2010). Given that the current decline of mammals in
53 northern Australia is most evident in taxa similar to those driven to extinction and severe decline
54 elsewhere in Australia (e.g. bandicoots, large rodents and dasyurids in the 'critical weight range'
55 (CWR) of 35–5500 g) (Burbidge and McKenzie, 1989, Woinarski et al., 2010, Murphy and Davies,
56 2014), similar factors may be responsible. There is compelling evidence that predation by the
57 introduced red fox (*Vulpes vulpes*) and feral cat (*Felis catus*) was the driver of decline and extinction
58 of many mammal species in temperate, arid and semi-arid Australia (Johnson, 2006, Hardman et al.,
59 2016, Short, 2016). Red foxes do not occur in monsoonal Australia, but the feral cat has been present
60 across the northern Australian mainland since the 19th Century (Abbott, 2002, Abbott, 2008).

61 There is accumulating evidence that predation by feral cats is a key factor in the current declines
62 across northern Australia. Recent studies have demonstrated extirpations of some native mammal
63 species on islands recently colonised by cats, but persistence on islands without cats, with this pattern
64 especially strong for mammal species that have declined extensively across mainland areas (Southgate
65 et al., 1996, Woinarski et al., 1999, Woinarski et al., 2011b). An experimental reintroduction of the
66 long-haired rat (*Rattus villosissimus*) on the northern Australian mainland failed outside predator

67 enclosure areas, due primarily to predation by feral cats (Frank et al., 2014). At another mainland site,
68 Leahy et al. (2016) demonstrated that predation by feral cats and dingoes (*Canis dingo*) was the
69 primary cause of local population declines of two native mammal species over the 12-month study
70 period. Fire was also a significant factor, but its influence was not through direct fire-related
71 mortality, nor fire-induced reductions in food availability or reproductive success, or emigration.
72 Rather, the influence of fire was related to cat predation, the effects of which were most severe in
73 areas subject to high-intensity fire that removed a greater proportion of vegetation cover (Leahy et al.,
74 2016). The synergistic relationship between fire and predation was further supported by McGregor et
75 al. (2016), who demonstrated that feral cats concentrated their hunting activity to areas recently burnt
76 by high-intensity fires.

77 Despite the accumulating evidence that predation by feral cats is a key factor in the current declines
78 across northern Australia, the apparent asynchrony between the establishment of the feral cat in
79 monsoonal northern Australia and the late 20th Century mammal declines, suggests other factors may
80 be involved. Frequent, high-intensity fires, such as those characterising the fire regime across northern
81 Australia since the breakdown of traditional Aboriginal burning practices, significantly alter the
82 availability of critical resources, including fleshy-fruit bearing shrubs, logs and tree hollows (Russell-
83 Smith et al., 2003b, Vigilante and Bowman, 2004, Firth et al., 2006b, Woinarski and Westaway,
84 2008). Any species with a strong reliance on such resources may be strongly disadvantaged by current
85 northern Australian fire regimes, even in the absence of predation. However, species that are both
86 dependent on these fire-mediated resources and also susceptible to predation are likely to be
87 particularly threatened, and expected to be the first to exhibit decline and range contraction.

88 Predation by feral cats and frequent high-intensity fire both occur throughout far northern Australia,
89 and therefore are potential threats to areas that currently still retain their full mammalian fauna. One
90 such area is Australia's second-largest island, Melville Island, where the threatened brush-tailed
91 rabbit-rat (*Conilurus penicillatus*) has recently contracted to areas where feral cats were rarely
92 detected and shrub density was high (Davies et al. 2016). Here we build on that study by investigating
93 changes in the broader mammal assemblage on Melville Island, which includes many species that
94 have declined extensively across mainland northern Australia (Firth et al., 2006a, Woinarski et al.,
95 2010, Firth et al., 2010) and several endemic subspecies. We predict that: (1) a range of native
96 mammals on Melville Island, and not just the brush-tailed rabbit-rat, will be in decline; (2) declines
97 will be most evident in those species that have declined most dramatically on the mainland; (3) the
98 current distribution of small mammals on Melville Island will be inversely related to the presence of
99 feral cats and frequent fire.

100

101 **Methods:**

102 Study site:

103 Melville Island (5788 km²) is the larger of the two main Tiwi Islands, located ~20 km off the coast of
104 Australia's Northern Territory (Figure 1). The Tiwi Islands became separated from mainland
105 Australia relatively recently (between 12,000 and 8,000 years ago) (Woodroffe et al., 1992), and
106 hence have an environment and a mammal assemblage largely comparable to the mainland (with the
107 notable absence of the northern quoll (*Dasyurus hallucatus*). The islands are of low relief (≤ 103 m
108 above sea level) and experience a tropical monsoonal climate with an intense wet season (November–
109 April) in which over 90% of the annual rainfall occurs. There is a substantial rainfall gradient on
110 Melville Island, from 1400 mm in the east, to 2000 mm in the northwest. The major vegetation types
111 are savanna woodlands and open forests dominated by *Eucalyptus miniata*, *E. tetradonta* and
112 *Corymbia nesophila*, with a predominantly grassy understorey. Shrub density is highly variable, and
113 studies on the mainland have shown that it is negatively affected by frequent, high-intensity fires
114 (Russell-Smith et al., 2003a, Woinarski et al., 2004). Fire mapping of the Tiwi Islands, has shown that
115 an average of 54% of the savannas were burnt each year from 2000-2013, with 65% of this area
116 burning in the late dry season (Richards et al., 2015).

117 There is currently no evidence to suggest any recent change in fire intensity or frequency, feral animal
118 densities or invasive weeds on the Tiwi Islands (see Woinarski et al. (2001) for further details on
119 introduced species). Over the past two decades, the expansion of the forestry industry across the
120 western half of Melville Island, has seen the replacement of around 30,000 ha of eucalypt tall open
121 forest with short-rotation plantations of exotic *Acacia mangium* (Woinarski and Tiwi Land Council,
122 2001). Due to a lack of historical records (Abbott and Burbidge, 1995), the timing of the arrival of
123 feral cats on Melville Island is unknown. While cats could have arrived as far back as the
124 establishment of a British military outpost at Fort Dundas in 1824 (Brocklehurst, 1998), they also
125 could have arrived appreciably later than in other parts of northern Australia (Davies et al. 2016).

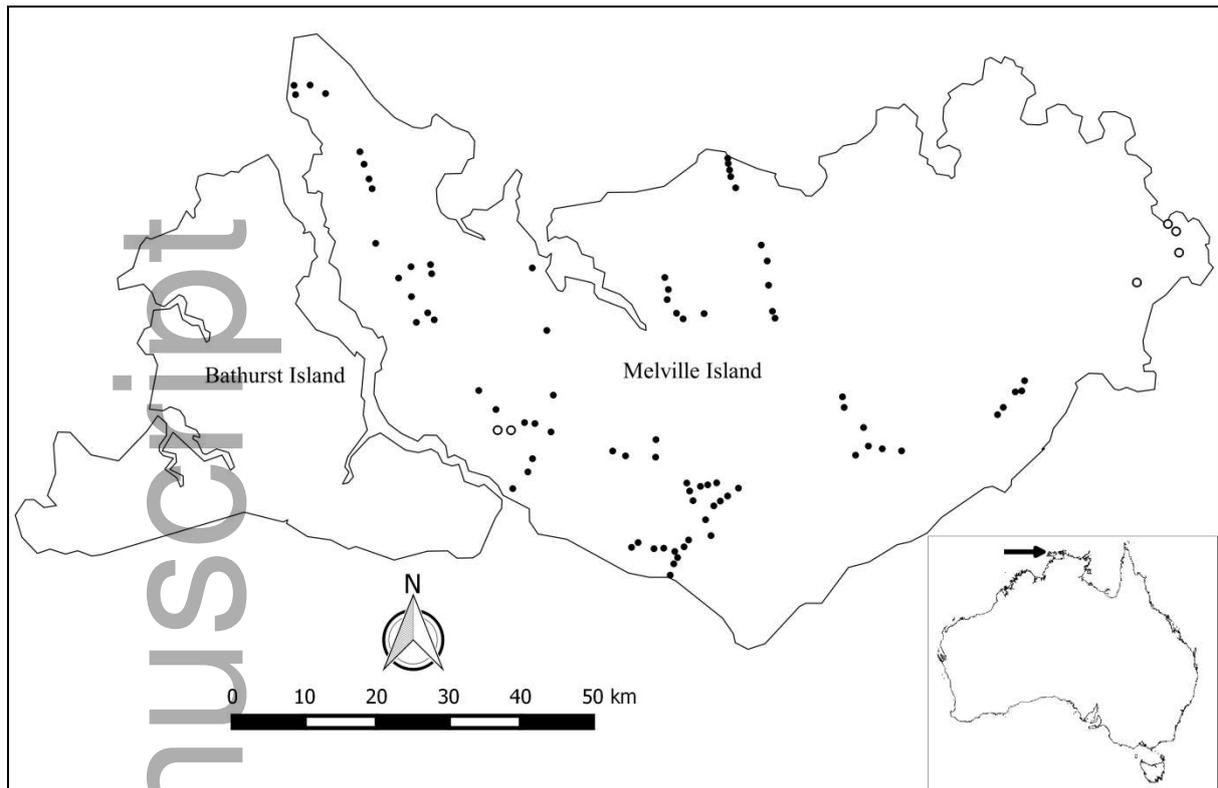
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127 Data collection:

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

136 Between April and December 2015, 88 of the original 351 sites were revisited (Davies et al. 2016), all
137 located in the savanna woodland and open forests of Melville Island (Figure 1). These 88 sites were
138 chosen to capture the large variation in both annual rainfall and fire history on Melville Island.
139 Eighty-two of these sites were surveyed using both live-trapping and camera-trapping, with the
140 remaining six sites being surveyed using only camera-trapping. Live-trapping followed the 2000–
141 2002 protocol but was conducted over four consecutive nights instead of three, and used eight cage
142 traps and 16 Elliott traps. To avoid bias relating to possible seasonal differences in trap-success, re-
143 visited sites were trapped at a comparable time of year to when they were originally surveyed. In
144 2015, no pitfall traps were used or site searches undertaken. Camera-trapping involved five
145 horizontally facing motion-sensor cameras left continuously recording (24-hours per day) for a
146 minimum 35 consecutive day period that overlapped with each site’s live-trapping survey. Camera
147 traps were baited with a mixture of peanut butter, oats and honey. To ensure maximum likelihood of
148 being triggered, each camera was carefully positioned to ensure the bait was in the centre of the field
149 of view (Gillespie et al., 2015). Vegetation within each camera’s field of view was cleared to reduce
150 the chance of false triggers and to reduce the risk posed by fire. Of the five cameras deployed at each
151 site, two were Reconyx™ HC550 Hyperfire white flash cameras (Reconyx Inc., Holmen, USA), while
152 the remaining three were Reconyx™ PC800 Hyperfire Professional infra-red flash cameras. All
153 cameras were set to take three image bursts per trigger, with a 1-second delay between images. The
154 sensitivity of each camera was set to high, with cameras re-arming instantly after being triggered.

155 To allow for direct comparison of the live-trapping results, we excluded captures from the original
156 surveys arising from methods not repeated in 2015 (i.e. pitfall traps and site searches). We
157 acknowledge here a potential source of bias arising from the exclusion of the pitfall records. On any
158 given night, a particular animal caught in a pitfall trap is no longer able to be trapped in an Elliott or
159 cage trap. Therefore the number of animals caught in pitfall traps could have influenced the 2000–
160 2002 trap-success. We highlight that this source of bias relates only to those species small enough to
161 be caught in pitfall traps (i.e. mice and dunnarts), and note that the number of mammals caught in
162 pitfall traps in 2000–2002 was low and therefore not a large source of bias. As trap-success and
163 species richness do not increase linearly with the number of nights that traps are deployed, we also
164 excluded all captures recorded on the fourth night of live-trapping in 2015. The initial sampling
165 derived an abundance measure from the number of captures and noted the possibility that multiple
166 captures could include the same individual. For consistency we derived trap success the same way.



167

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

172

173 Table 1: Description and justification of the variables used in analyses to assess the correlates of
 174 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.	<ul style="list-style-type: none"> • Feral cat activity • Mammal occupancy and detectability
Rainfall	Mean annual rainfall (Australian Bureau of Meteorology	<ul style="list-style-type: none"> • 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).	<ul style="list-style-type: none"> 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 50 th measured tree or a maximum of 200 m. Firth et al. 2006a demonstrated the influence of basal area on the occurrence of mammals.	<ul style="list-style-type: none"> 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).	<ul style="list-style-type: none"> 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).	<ul style="list-style-type: none"> 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.	<ul style="list-style-type: none"> 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.	<ul style="list-style-type: none"> 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, Ziemnicki et al., 2014). See Davies 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 (<i>Conilurus penicillatus</i>) 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

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178 Data analysis:

179 1) Trends in trap-success

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

191 of cage traps in 2015, Elliott traps accounted for only 2.7% of black-footed tree-rat captures.
192 Therefore the effective trap-success in each year for this species was calculated as:

193 $\text{Effective trap-success} = \text{number of captures} \div (\text{number of cage trap nights} + 0.027 * \text{number of Elliott}$
194 $\text{trap nights}) * 100$

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

198 2) Correlates of mammal distribution in 2015

199 Davies et al. (2016) investigated a range of environmental correlates of the distribution of the brush-
200 tailed rabbit-rat on Melville Island. Here we use the same approach to investigate the 2015
201 distribution of three other mammal species that were detected by camera traps sufficiently to permit
202 occupancy modelling: the northern brown bandicoot, black-footed tree-rat and common brushtail
203 possum. Single-season occupancy models were used to investigate how each predictor variable (Table
204 1) influenced site occupancy. For comparison, we also present results published by Davies et al.
205 (2016) for the brush-tailed rabbit-rat. Occupancy modelling was conducted using only the 2015
206 camera trapping data (88 sites) in the package “unmarked” in R (Fiske and Chandler, 2011).
207 Explanatory variables were centred and standardised prior to analysis.

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

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

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

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

233

234 **Results:**

235 1) Trends in trap-success

236 A total of twelve mammal species were recorded, two of which do not have a mean body size within
237 the CWR: delicate mouse and Butler's dunnart. Overall trap-success was 62% lower in 2015 ($6.1 \pm$
238 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
239 ten sites across the sampling periods, exhibited a significant decrease in trap-success, with northern
240 brown bandicoot decreasing by 90% ($Z = 5.42$, $p < 0.001$), brush-tailed rabbit-rat by 64% ($Z = 1.97$, p
241 < 0.05) and black-footed tree-rat by 63% ($Z = 3.33$, $p < 0.001$) (Figure 2). The remaining five species
242 (mostly reported from few sites) showed no significant change (Table 2).

243 Site-level species richness decreased by 36% between 2000-02 (1.6 ± 0.1) and 2015 (1.0 ± 0.1 ; $Z =$
244 3.82 , $p < 0.001$). The proportion of sites where no native mammals were trapped doubled from 13% to
245 26%. Six species exhibited a large decrease in naïve occupancy (39 – 80%), while the common
246 brushtail possum and delicate mouse were recorded at 29% more sites in 2015 than in 2000-02 (Table
247 2).

248 2) Correlates of mammal distribution in 2015

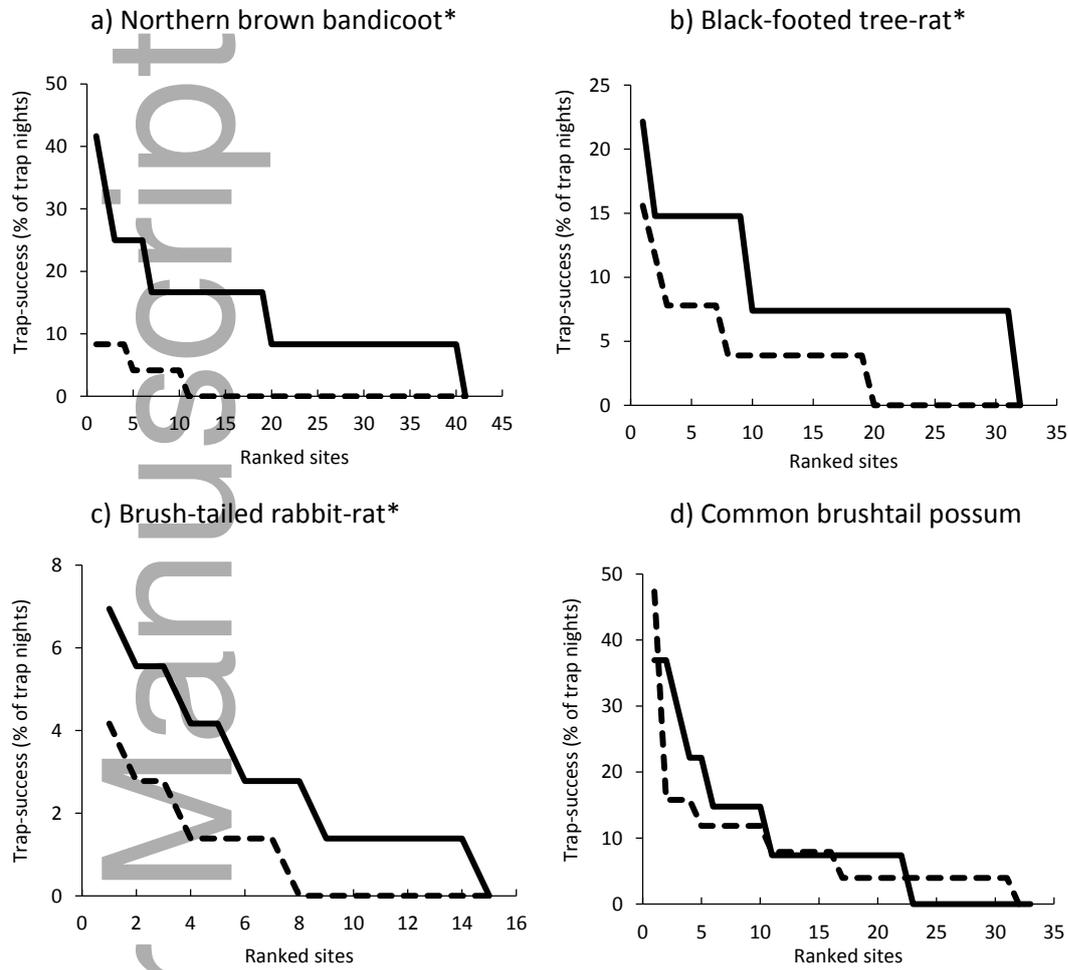
249 Given the overall high detectability for all species, the estimated rate of occupancy by the respective
250 best model for each species was very similar to the naïve and null model estimates (See Table S2 in
251 supplementary material). As such, the effect of each covariate on site-occupancy was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

253 Shrub density was a (borderline) significant predictor of site-occupancy by the black-footed tree-rat,
254 as it was for the brush-tailed rabbit-rat, but not for the northern brown bandicoot or common brushtail
255 possum (Figure 3). Unlike the situation for the brush-tailed rabbit rat, feral cat detection was not a
256 significant predictor variable for any of the other species (Figure 3). Fire was not a significant

257 predictor for any species, and neither the inclusion of neither tree-basal area nor an interaction
 258 between fire and shrubs with feral cat activity improved the model fit for any species.

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

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269

270 Table 2: Summary of the changes in the native mammal populations of Melville Island recorded with
 271 live-trapping between 2000–02 and 2015. Naïve occupancy was calculated as the percentage of the 82
 272 live-trapped sites where a species was detected. * = $p < 0.05$, *** = $p < 0.001$. Decreases denoted by -
 273 , increases denoted by +. Species in bold indicate a body-size outside the critical weight range. Dashes
 274 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 (<i>Isoodon macrourus</i>)	49	12	- 75	6.91 (0.99)	0.71 (0.23)	- 90***
Black-footed tree-rat (<i>Mesembriomys gouldii</i>)	38	23	- 39	3.69 (0.59)	1.38 (0.33)	- 63***
Common brushtail possum (<i>Trichosurus vulpecula</i>)	27	38	+ 29	3.78 (0.88)	3.32 (0.73)	- 12
Brush-tailed rabbit- rat (<i>Conilurus penicillatus</i>)	17	9	- 50	0.53 (0.15)	0.19 (0.08)	- 64*
Grassland melomys (<i>Melomys burtoni</i>)	7	4	- 50	0.69 (0.31)	0.10 (0.06)	- 88
Delicate mouse (<i>Pseudomys delicatulus</i>)	7	12	+ 29	0.20 (0.09)	0.30 (0.10)	+ 33
Pale field-rat (<i>Rattus tunneyi</i>)	6	1	- 80	0.10 (0.05)	0.02 (0.02)	- 80
Red-cheeked dunnart (<i>Sminthopsis virginiae</i>)	5	1	- 75	0.10 (0.06)	0.03 (0.03)	- 70
Northern sugar glider (<i>Petaurus breviceps</i>)	2	0	-	0.03 (0.02)	0	-
Northern brush-tailed phascogale (<i>Phascogale pirata</i>)	2	0	-	0.03 (0.02)	0	-
Butler's dunnart (<i>Sminthopsis butleri</i>)	1	0	-	0.03 (0.02)	0	-

Western chestnut

mouse
(*Pseudomys nanus*)

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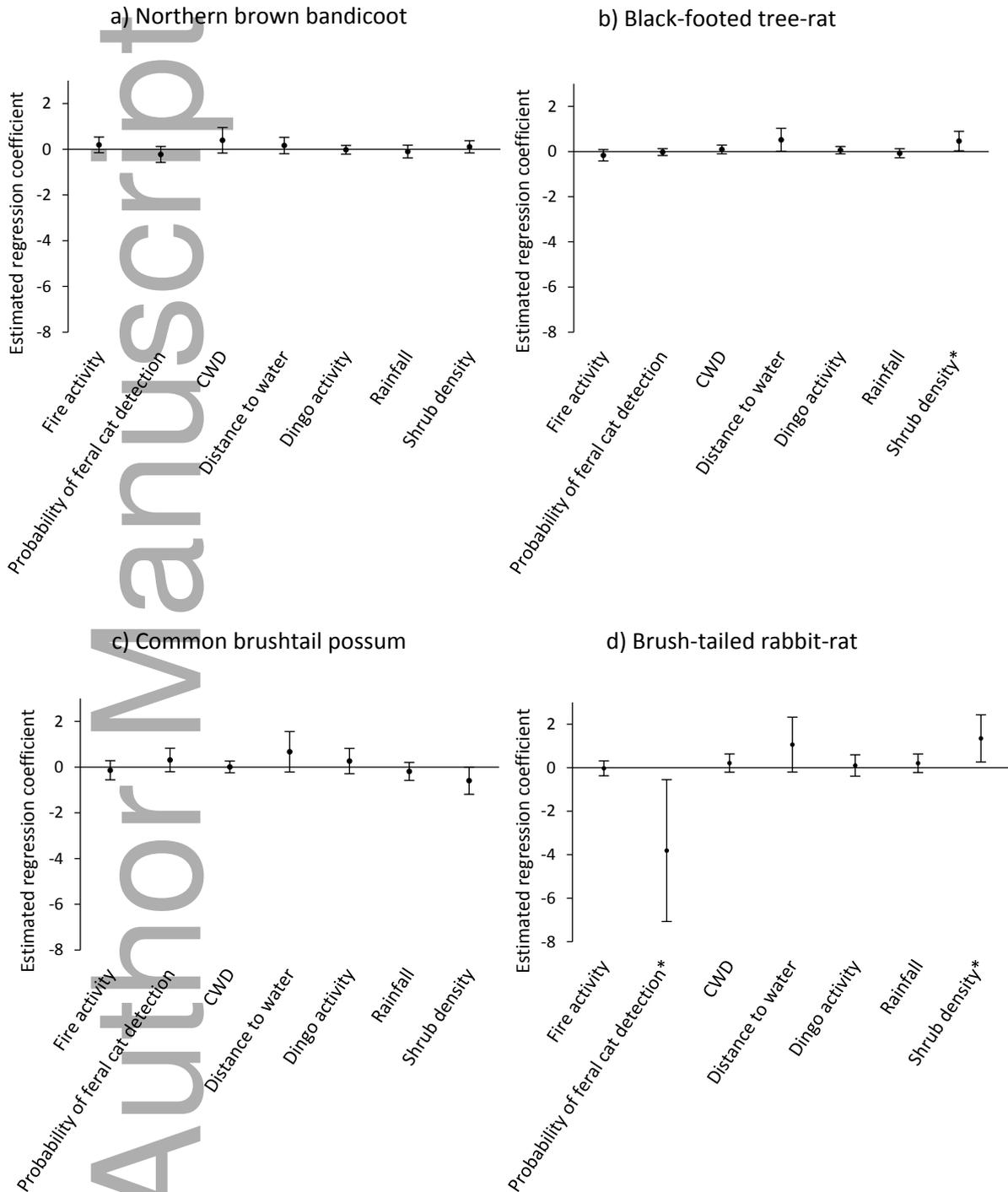
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282 Figure 3: Model averaged regression coefficient estimates for a) the northern brown bandicoot, b) the
283 black-footed tree-rat, c) the common brushtail possum and d) the brush-tailed rabbit-rat (first
284 published in Davies et al. (2016)). Error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

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

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289 **Discussion:**

290 Many native mammal species have recently experienced severe range contractions across northern
291 Australia, and Melville Island is one of the few remaining areas to have retained an intact mammal
292 fauna (Woinarski et al. 2010, Ziembicki et al. 2014). However, Davies et al. (2016) demonstrated that
293 the Melville Island population of the brush-tailed rabbit-rat had retracted to areas where feral cats
294 were rarely detected and shrub density was high. Here we build on that study to report evidence of
295 broader decline in the mammal assemblage of Melville Island. We found that trap-success and species
296 richness at the site-level decreased by 62% and 36% respectively from 2000-02 to 2015. As predicted,
297 declines were most evident for three species that have suffered considerable declines on mainland
298 northern Australia: northern brown bandicoot (90% decrease in trap-success), brush-tailed rabbit-rat
299 (64%) and black-footed tree-rat (63%). These severe declines are particularly notable because the
300 local subspecies of black-footed tree-rat (*M. gouldii melvillensis*) is endemic to the island, and the
301 local subspecies of brush-tailed rabbit-rat (*C. penicillatus melibius*) is endemic to Melville Island and
302 the adjacent Bathurst Island. However, inconsistent with our prediction, there was no such decline for
303 the common brushtail possum, a comparably-sized species that has also exhibited marked decline on
304 the northern Australian mainland (Woinarski et al., 2010).

305 We acknowledge the limitations associated with inferring mammal decline with only two data points
306 spaced 15 years apart. However, the pattern of decline observed on Melville Island is very similar to
307 that recorded in Kakadu National Park between 2001 and 2009. Over this period in Kakadu, the
308 brush-tailed rabbit-rat and black-footed tree-rat were not recorded frequently enough to permit
309 statistical analysis (despite both species being common 30–40 years previously) (Woinarski et al.,
310 2010), and the abundance of the northern brown bandicoot and common brushtail possum decreased
311 by 88 and 86% respectively (Woinarski et al., 2010). This suggests that in Kakadu, the brush-tailed
312 rabbit-rat and black-footed tree-rat were among the first mammal species to decline. It is therefore
313 plausible that Melville Island is currently experiencing the pattern of decline that occurred in Kakadu
314 National Park over a decade earlier.

315 Unlike the brush-tailed rabbit-rat (Davies et al. 2016) and despite substantial decreases in trap-
316 success, neither the northern brown bandicoot nor black-footed tree rat appear to have suffered
317 marked range contractions on Melville Island. This suggests that their declines have not yet
318 progressed to the point of influencing their distribution. The lack of change in the occurrence of these

319 species (as opposed to abundance) can explain why we failed to detect relationships between
320 environmental variables, including the presence of feral cats or frequent fire, and site occupancy.

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

329 Second, and also related to the higher rainfall, much of Melville Island has a particularly dense
330 understorey and midstorey of shrubs and small trees (Richards et al., 2012, Davies et al., 2016). As a
331 result, the predation pressure imposed on mammal populations, particularly by feral cats, may be
332 lower on Melville Island compared with the mainland (McGregor et al., 2015, Hohnen et al., 2016,
333 Leahy et al., 2016). This is supported by evidence that site occupancy by the brush-tailed rabbit-rat
334 and the black-footed tree-rat on Melville Island is positively related to shrub density (Davies et al.,
335 2016).

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

347 Finally, it is likely that cats have not been on Melville Island for as long as they have on the mainland
348 (Abbott and Burbidge, 1995, Abbott, 2002, Abbott, 2008), and although there have been some
349 anecdotal reports that cats were introduced to Tiwi islands only within the past few decades (Firth,
350 2010), definitive evidence of an introduction date is not available. It is also plausible that feral cat
351 populations (and their impact on native mammals) on Melville Island have been suppressed by high
352 dingo densities (Kennedy et al., 2012).

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

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

389 improve our understanding of the factors driving these declines, and to implement management
390 actions before these species are lost from one of the last remaining areas in Australia with an intact
391 small mammal fauna.

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413

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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.

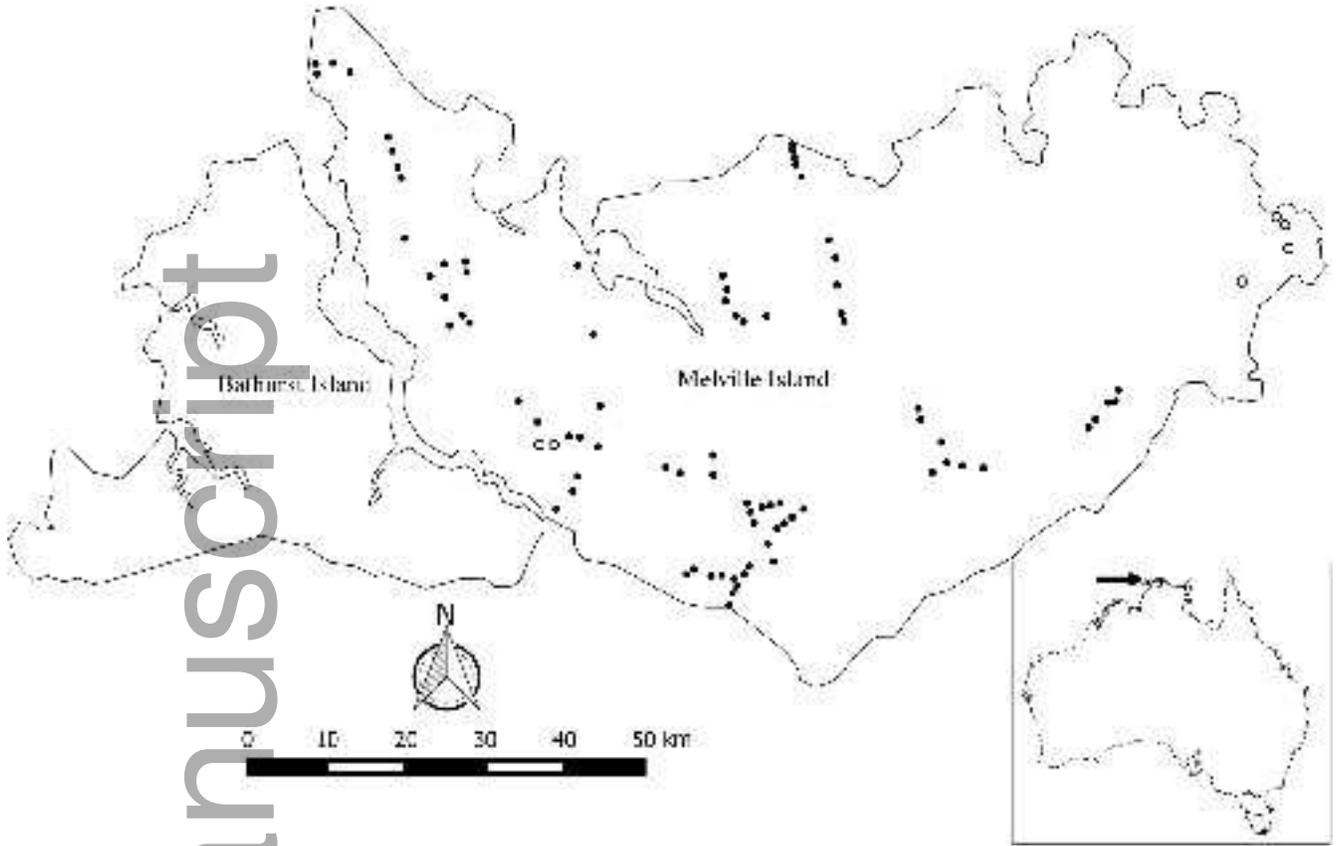
Explanatory variable	Description and justification for inclusion	Variable used in analyses to predict:
Fire activity	Following Lawes et al. (2015), a remote-sensed fire variable derived from fine-scale (30 × 30 m) LANDSAT satellite imagery, representing the proportion of the area surrounding each site 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.	<ul style="list-style-type: none"> • 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).	<ul style="list-style-type: none"> • 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 50 th measured tree or a maximum of 200 m. Firth et al. 2006a demonstrated the influence of basal area on the occurrence of mammals.	<ul style="list-style-type: none"> • 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).	<ul style="list-style-type: none"> • 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	<ul style="list-style-type: none"> • 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.	<ul style="list-style-type: none"> • 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.	<ul style="list-style-type: none"> • 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). See Davies et al. (2016).	<ul style="list-style-type: none"> • 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 (<i>Conilurus penicillatus</i>) increases throughout the dry season (May – November).	<ul style="list-style-type: none"> • 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.	<ul style="list-style-type: none"> • 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 (<i>Isoodon macrourus</i>)	49	12	- 75	6.91 (0.99)	0.71 (0.23)	- 90***
Black-footed tree-rat (<i>Mesembriomys gouldii</i>)	38	23	- 39	3.69 (0.59)	1.38 (0.33)	- 63***
Common brushtail possum (<i>Trichosurus vulpecula</i>)	27	38	+ 29	3.78 (0.88)	3.32 (0.73)	- 12
Brush-tailed rabbit-rat (<i>Conilurus penicillatus</i>)	17	9	- 50	0.53 (0.15)	0.19 (0.08)	- 64*
Grassland melomys (<i>Melomys burtoni</i>)	7	4	- 50	0.69 (0.31)	0.10 (0.06)	- 88
Delicate mouse (<i>Pseudomys delicatulus</i>)	7	12	+ 29	0.20 (0.09)	0.30 (0.10)	+ 33
Pale field-rat (<i>Rattus tunneyi</i>)	6	1	- 80	0.10 (0.05)	0.02 (0.02)	- 80
Red-cheeked dunnart (<i>Sminthopsis virginiae</i>)	5	1	- 75	0.10 (0.06)	0.03 (0.03)	- 70
Northern sugar glider (<i>Petaurus breviceps</i>)	2	0	-	0.03 (0.02)	0	-
Northern brush-tailed phascogale (<i>Phascogale pirata</i>)	2	0	-	0.03 (0.02)	0	-
Butler's dunnart (<i>Sminthopsis butleri</i>)	1	0	-	0.03 (0.02)	0	-
Western chestnut mouse (<i>Pseudomys nanus</i>)	0	2	-	0	0.03 (0.02)	-



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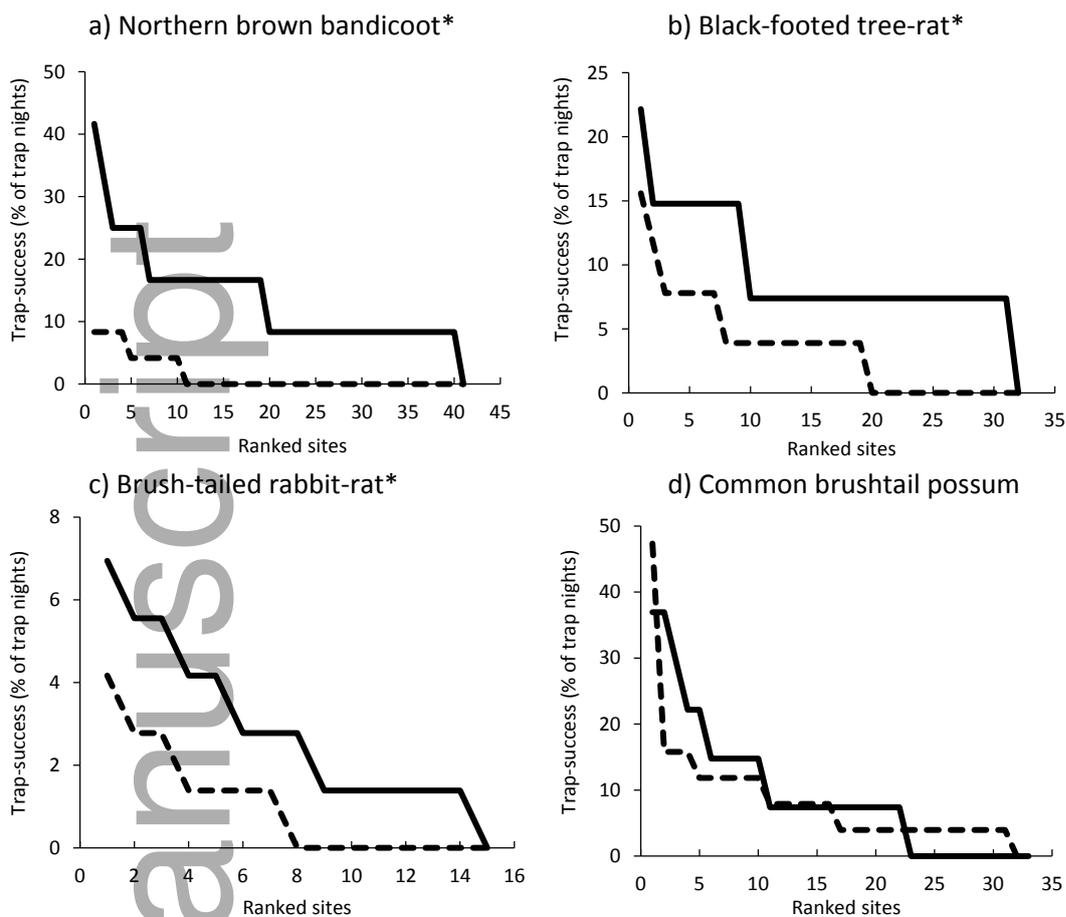


Figure 2: The difference in live trap-success in 2000-02 (solid line) and 2015 (dashed line) for a) northern brown bandicoot b) black-footed tree-rat c) brush-tailed rabbit-rat and d) common brushtail possum. Asterisks indicate a statistically significant ($p < 0.05$) change in trap-success.

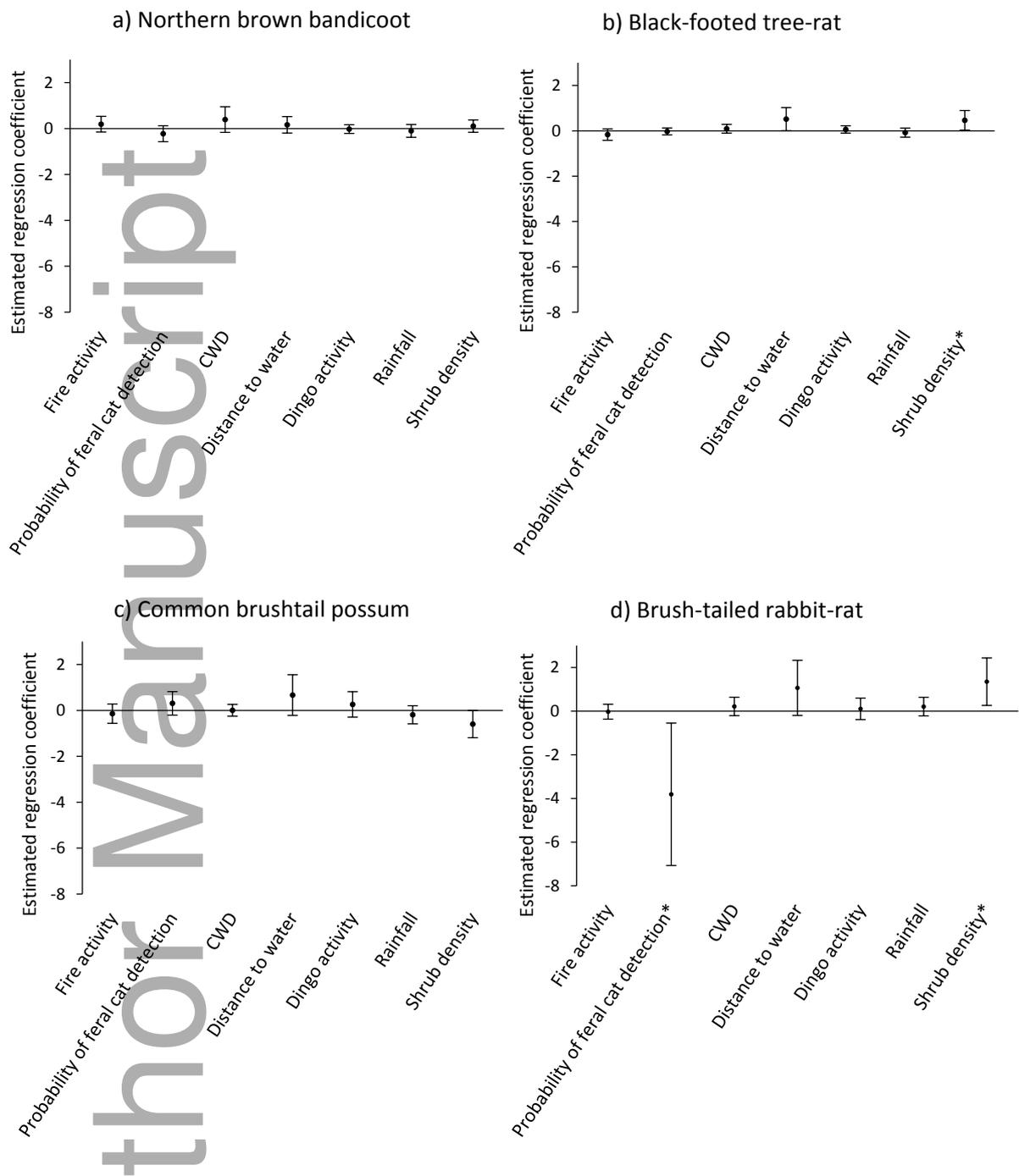


Figure 3: Model averaged regression coefficient estimates for a) the northern brown bandicoot, b) the black-footed tree-rat, c) the common brushtail possum and d) the brush-tailed rabbit-rat (first published in Davies et al. (2016)). Error bars indicate 95% confidence intervals; asterisks indicate where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