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Safe haven or slow burn?

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1 **Status of mammals on Groote Eylandt: safe haven or slow burn?**

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9
10 **Abstract**

11 Native mammals across northern Australia have suffered severe decline, with feral cats (*Felis*
12 *catus*), introduced herbivores and changed fire regimes being implicated as drivers. However,
13 uncertainty surrounding the relative contribution of each of these threats, and the interactions
14 between them, is limiting the development of effective management strategies. The absence of
15 introduced herbivores and cane toads (*Rhinella marina*) on Groote Eylandt, Northern Territory,
16 provides an opportunity to evaluate some hypothesised threats in isolation of others. We used
17 camera traps to investigate the correlates of native mammal distribution and abundance at 112
18 lowland savanna sites across Groote Eylandt. Two large grids of camera traps were also
19 deployed to obtain estimates of feral cat density. We hypothesised that native mammal
20 populations would be negatively associated with feral cat occupancy as well as frequent, large
21 fires. Native mammal site-occupancy on Groote Eylandt was generally higher compared to
22 mainland Northern Territory. Feral cats were infrequently detected, precluding both an estimate

23 of feral cat density, or an evaluation of the relationship between feral cats and native mammals.
24 We found no evidence that native mammal site-occupancy or relative abundance are negatively
25 associated with frequent, large fires. The relatively healthy state of native mammal populations
26 on Groote Eylandt is likely due to the low density of feral cats, the benign fire regime and the
27 absence of large introduced herbivores and cane toads. However, due to a lack of historical
28 data, the current state of mammals should not be taken as evidence that these populations are
29 safe from decline. This study highlights that the apparent resilience of mammal populations is
30 a result of complex interactions between factors that vary substantially across the landscape.
31 Caution is therefore required when making broad inferences about the drivers of mammal
32 decline from studies that are spatially and temporally limited.

33

34 **Keywords:** islands, feral cats, fire, declines, threatened mammals.

35

36 **Introduction**

37 In the 230 years since European arrival, Australia has lost >10% of its terrestrial mammal fauna
38 and contributed more than 30% of global mammal extinctions recorded since 1500 (Woinarski
39 *et al.* 2015). In contrast to other continents, where large-bodied mammals near areas with high
40 human population density have been most prone to extinction (Cardillo *et al.*, 2005), Australian
41 species with body sizes between 35 – 5500 g (henceforth referred to as the critical weight range:
42 CWR), in remote and relatively unmodified areas, have suffered the highest extinction rates
43 (Woinarski *et al.*, 2015). Worryingly, this trend has continued in recent decades, with
44 widespread, significant declines of CWR mammals recorded across Australia's northern

45 savanna landscapes (Woinarski et al., 2010, Ziembicki et al., 2015, Fisher et al., 2014, Davies
46 et al., 2018).

47 Factors implicated in the current mammal decline across northern Australia include the higher
48 incidence of large-scale, intense fires occurring since the breakdown of traditional Aboriginal
49 burning practices (Russell-Smith and Edwards, 2006, Russell-Smith et al., 2003), habitat
50 degradation by large, feral herbivores and pigs (*Sus scrofa*) (Legge et al., 2011a, Kutt and
51 Woinarski, 2007), and predation by feral cats (*Felis catus*) (Ziembicki et al., 2015, Fisher et
52 al., 2014, Woinarski et al., 2011a, Frank et al., 2014). Due to a lack of empirical data, we do
53 not know if the initiation of mammal population declines in northern Australia coincided with
54 the establishment of any one of these hypothesised threats. Although northern Australian
55 mammal declines were quantitatively documented only relatively recently, it is plausible that
56 mammal populations have been declining over a much longer period. The uncertainty regarding
57 the relative contribution of each threat to northern mammal declines is limiting our ability to
58 develop and implement effective mitigation strategies.

59 Further complicating our ability to understand the factors implicated in declines of native
60 mammal populations across northern Australia are potentially complex interactions between
61 them. For example, frequent fire and feral herbivores may exacerbate the impact of feral cat
62 predation by simplifying vegetation structure (McGregor et al., 2014, McGregor et al., 2015,
63 Leahy et al., 2016, Davies et al., *in press*), while fire concurrently degrades the availability of
64 critical resources such as tree hollows (Woolley et al., 2018), perennial grasses and a fleshy
65 fruit-bearing shrub layer (Vigilante and Bowman, 2004). However, not only do fire regimes
66 vary significantly in frequency and intensity across northern Australian savanna landscapes, so
67 too does the occurrence and density of feral herbivores. Superimposed on these are a range of
68 environmental conditions (such as rainfall, climate, productivity and landscape complexity)
69 and land-use histories (i.e. indigenous management vs. pastoral use) that also influence the

70 resilience of mammal populations. Resolving the contribution of these factors in such a vast,
71 complex landscape is crucial to developing informed and effective management.

72 Islands provide important refugia for biota because factors responsible for mainland declines
73 are often absent or less intense (Legge et al., 2018, Ziembicki et al., 2015). However, as island
74 populations are generally small, with limited potential for recolonisation, they are often more
75 vulnerable to local extinction if threats do arrive (Woinarski et al., 2011b, Ziembicki et al.,
76 2015, Burbidge and Manly, 2002). For example, northern quolls (*Dasyurus hallucatus*) were
77 extirpated from Vanderlin Island in the Gulf of Carpentaria following the establishment of cane
78 toads (*Rhinella marina*), and native mammals declined to undetectable levels on West Island
79 following the introduction of feral cats (Paltridge et al., 2016, Woinarski et al., 2011b). Until
80 recently, Melville Island was also considered an important refuge for threatened mammal
81 species, however, Davies et al. (2017, 2018) reported evidence of population declines. This
82 pattern may indicate that declines may simply be lagging on these large northern Australian
83 islands compared to the mainland.

84 Groote Eylandt is Australia's fourth largest island and has high conservation values (Northern
85 Territory Government, 2017). It supports most of the global population of the northern
86 hopping-mouse (*Notomys aquilo*); one of few extant populations of the brush-tailed rabbit-rat
87 (*Conilurus penicillatus*); is an important refuge for the northern quoll; and several other small
88 and medium sized mammal species occur at seemingly much higher densities than on the
89 mainland (Diete et al., 2016, Mahney et al., 2009, Taylor and ALC, 2016). The relatively intact
90 state of the mammal fauna may be due to the absence, or low levels, of threatening processes
91 operating on Groote Eylandt. While feral cats are present, the island remains free of cane toads,
92 has no feral herbivores or pigs, and retains a relatively benign fire regime compared to the
93 mainland of northern Australia (Northern Territory Government, 2017, NAFI, 2017).
94 However, recent research suggests that some mammal declines may have occurred on Groote

95 Eylandt (Diete et al., 2016), and the presence of feral cats poses a potentially major threat to
96 CWR mammals. In light of recent findings on Melville Island (Davies et al., 2017), mammals
97 on Groote Eylandt may also be vulnerable to some of the processes driving declines elsewhere
98 across northern Australia.

99 Understanding the responses of species to different threats under varying environmental
100 conditions is crucial to optimising management strategies in different ecological settings.
101 Groote Eylandt provides a useful opportunity to evaluate some factors implicated in the decline
102 of native mammal species in isolation of other potentially interacting threats. We conducted a
103 survey of lowland forest and woodland habitats on Groote Eylandt to ascertain if frequent,
104 large fires and feral cats, are influencing native mammal distribution and abundance.

105

106 **Methods**

107 *Study site*

108 Groote Eylandt is in the Gulf of Carpentaria, approximately 50 km from the Northern Territory
109 mainland (Fig. 1). The island is of low relief (<220 m above sea level) and has a monsoonal
110 tropical climate (Bureau of Meteorology, 2017b). It is characterised by laterite plains and
111 sandstone plateaux, with eucalypt woodland the dominant vegetation. Several other habitats
112 are present, including mangroves, monsoon vine thickets, coastal grasslands and shrublands.
113 The Groote archipelago is an Indigenous Protected Area and is managed by the Anindilyakwa
114 Land Council. There is a large manganese mine (Groote Eylandt Mining Company: GEMCO)
115 with an associated port and settlement (Alyangula) on the western side of Groote Eylandt,
116 which has been a significant driver of economic and infrastructure development. Two other
117 settlements are present on the island; Umbakumba and Angurugu (Fig. 1).

119 We surveyed 112 lowland woodland sites across Groote Eylandt between April and September
120 2016 (Fig. 1). Lowland woodlands comprise a complex of vegetation associations that
121 collectively dominate the non-plateaux areas of Groote Eylandt. They are the preferred habitats
122 for the brush-tailed rabbit-rat and support a range of other CWR mammals, including the
123 northern hopping-mouse (Firth et al., 2006b, Dietsch et al., 2016). Surveying a broader range of
124 habitat types would have diluted our sampling effort and we were interested in investigating
125 environmental determinants of mammal species distribution rather than broad habitat
126 associations. Survey sites were stratified across land systems with lowland woodland (Lynch
127 and Wilson, 1998) by fire history (time since last fire; NAFI, 2017). All sites were a minimum
128 of 1 km apart and located within 2 km of vehicle access tracks.

129 At each site, six Reconyx Hyperfire camera traps (Reconyx Inc., Holmen, WI, USA) were
130 deployed for a minimum of 35 consecutive nights. Five cameras were deployed in a diamond
131 configuration with four cameras deployed approximately 50 m away from the centre camera.
132 Cameras were deployed facing south with a near-horizontal field of view; with the top of the
133 camera 35 cm above ground level and facing the base of a bait station 150 cm away containing
134 a mixture of peanut butter, honey and oats. Cameras comprised four white flash (either
135 Reconyx PC850 or HC550) and one infrared flash camera (either Reconyx HC500 or HC600).
136 This combination reflected camera availability and was the same at each site to control for
137 operational variability amongst models (Heiniger and Gillespie, 2018). This camera
138 configuration has been shown to adequately detect feral cats for occupancy modelling in
139 northern Australian (Stokeld et al., 2015), and to achieve high detection probabilities for a suite
140 of native species (Gillespie et al., 2015).

141 A sixth white flash camera was deployed within the diamond with a setup modified from
142 Welbourne (2013). A Reconyx PC850 camera modified for higher sensitivity and with a focal
143 length reduced to 90 cm (henceforth referred to as modified PC850) was deployed 65 cm from
144 ground level and angled downwards at 45° to face the middle of a corkboard 90 cm away. The
145 30 x 30 cm corkboard was used to improve small mammal detections in the tropical
146 environment by creating a substrate with a more homogenous temperature, therefore increasing
147 contrast with the thermal signature of small animals (Welbourne, 2013). A bait station was
148 placed at the centre of the rear edge of the corkboard, and drift fences extended 4 m either side
149 of the corkboard to direct mammals towards the detection zone.

150 All camera deployments were undertaken with high precision, using tape measures for
151 distances and test photos to ensure alignment of camera sensor zones with target areas.
152 Vegetation within each camera's field of view was cleared to increase detections, reduce false
153 triggers and risk of camera damage from fires. All cameras operated continuously and were set
154 to take three photos per trigger, with a one-second delay between each photo. Camera
155 sensitivities were set to high, with no quiet period.

156 *Feral cat density*

157 To further evaluate the relationships between feral cats and native mammal occurrence, we
158 investigated feral cat population density in two areas; (i) a northern site with high brush-tailed
159 rabbit-rat occupancy, and (ii) a southern site with no brush-tailed rabbit-rat detections (Fig. 1).
160 At each location camera trap arrays were established for a minimum of eight weeks from mid-
161 September to mid-November 2016, using methods modified from McGregor (2015). Each
162 array overlaid a vehicle track and comprised 70 camera traps arranged in 5 rows of 14 stations
163 spaced between 400 – 600 m apart. Each array contained the same combination of three white
164 flash camera models (PC850, modified PC850 and HC550), which were assigned randomly to

165 stations. Cameras were positioned locally to maximise feral cat detections, for example along
166 dry creek-lines, bush tracks or naturally open areas. Cameras were deployed at a height of 45
167 cm to the top of the casing, facing south and focused on an attractant 2.5 m away. The attractant
168 consisted of a non-toxic feral cat bait (kangaroo and chicken meat sausage; Scientec Research
169 Pty Ltd, Warrandyte, Australia) and a stick soaked in cat urine. Camera operating settings were
170 the same as the mammal survey.

171 *Data analysis*

172 We chose a set of environmental predictor variables that best described the fire regime, site-
173 specific habitat characteristics, landscape attributes and anthropogenic disturbances, based on
174 current knowledge of factors influencing northern Australian mammal declines (Kutt and
175 Woinarski, 2007, Woinarski et al., 2011a, Woinarski et al., 2010, Davies et al., 2017). It was
176 not possible to incorporate the occupancy of large mammalian predators (feral cats or dingoes)
177 as predictor variables in analyses because detections of these species during the survey were
178 too sparse.

179 Following Lawes et al. (2015), we derived multiple variables to quantify the fire regime at each
180 site, including the proportion of surrounding area burnt, patchiness, fire frequency and time
181 since fire. However, preliminary investigation of these fire variables demonstrated significant
182 collinearity. Therefore, we constrained our analyses to include one fire variable: the proportion
183 of the circular area (radius of 3200 m or 250 m depending on the species home range)
184 surrounding each site that is burnt each year, averaged over the five years preceding the
185 mammal surveys.

186 All predictor variables were centred and standardised by subtracting means and dividing by
187 standard deviations (Gelman and Hill, 2006). Collinearity was assessed amongst all variable
188 pairs and the most biologically relevant variable was retained for analysis when the Pearson

189 correlation coefficient was greater than 0.5 (positively or negatively). The resultant set of
190 predictor variables (Table 1) was used to develop occupancy models for species with adequate
191 detection probabilities (MacKenzie et al., 2002) and to evaluate patterns of species diversity
192 (Shannon diversity index). Occupancy modelling was conducted using the “unmarked”
193 package in R (Fiske and Chandler, 2011, R Core Team, 2017).

194 Single-season occupancy modelling was applied in two steps due to the large number of
195 predictor variables. First, the variables that best explained the detectability of each species were
196 determined by running all combinations of the eight predictor variables (i.e. 256 models) which
197 could potentially influence detectability (Table 1). This was done with occupancy constrained
198 to a saturated model of the eight occupancy variables. Model selection based on Akaike
199 Information Criteria (AIC) was then used to select the most parsimonious detectability model
200 in the candidate set. Second, all combinations of the eight occupancy variables were run (256
201 models) with detectability constrained to the most parsimonious model identified in step one.
202 Model selection based on AIC was used again to determine the best occupancy model. Where
203 no single model explaining the occurrence of the species emerged as superior ($\Delta AIC < 2$),
204 model averaging was performed to provide parameter estimates (Burnham and Anderson,
205 2002). The detection probability over the survey period was determined for the best and null
206 model using the formula: $1 - ((1-p)^n)$, where p is the nightly detection probability and n is the
207 number of survey nights. We assessed the goodness of fit of the most saturated model for each
208 species using three tests based on parametric bootstrapping: Pearson’s chi-square statistic, sum
209 of squared errors and Freeman-Tukey chi-square statistic. These tests repeatedly simulate
210 datasets based on the fitted model and then evaluate the probability that the observed history
211 of outcomes has a reasonable chance of happening (MacKenzie and Bailey, 2004).

212 For species with highly saturated occupancies, Royle-Nichols occupancy modelling was
213 applied, which assumes that heterogeneity in detection frequency is indicative of variability in

214 species abundance (Royle and Nichols, 2003). Modelling was otherwise conducted using the
215 same process as above.

216 Linear regression models were used to investigate the relationship between species diversity
217 and environmental parameters. Species diversity was modelled using the Shannon diversity
218 index (H), which takes into account the number of different species at a site and how even their
219 abundances are (Shannon, 1948). Because individuals of a species generally cannot be
220 distinguished using camera traps, we used the number of nights each species was detected as a
221 proxy for relative abundance. Model selection based on AIC was used to determine the best
222 model. Where no single model emerged as superior (i.e. $\Delta AIC < 2$), model averaging was
223 performed to provide parameter estimates (Burnham and Anderson, 2002).

224

225 **Results**

226 *Mammal survey*

227 Twelve native mammal species were detected (Table 2). Naïve occupancy rates varied from
228 2% for short-eared rock wallabies (*Petrogale brachyotis*) to 100% for northern brown
229 bandicoots (*Isodon macrourus*). Brush-tailed rabbit-rats were detected at 17% of survey sites,
230 mostly clustered on the northern peninsula (Appendix S1) and northern hopping-mice were
231 detected at only 3% of sites (Appendix S1). Feral cats were detected on nine occasions at eight
232 highly dispersed sites (Appendix S2), resulting in low overall detection probability (0.22).

233 *Correlates of species occupancy and relative abundance*

234 Data were adequate for single-season occupancy modelling for the delicate mouse (*Pseudomys*
235 *delicatus*), grassland melomys (*Melomys burtoni*), and the brush-tailed rabbit-rat. Nightly
236 detectability from the best model ranged from 0.13 for the grassland melomys to 0.18 for the

237 brush-tailed rabbit-rat (Table 3). Due to the length of time cameras were deployed (minimum
238 of 35 nights) the overall detectability of each species was very high (>0.99 ; Table 3). No single
239 occupancy model arose as superior for any of the three species (i.e. $\Delta AIC < 2$; Appendix S3),
240 so model averaging was conducted to calculate parameter coefficients. Distance from mine or
241 town was the strongest predictor variable for the brush-tailed rabbit-rat (Fig. 2a), with the
242 species occupying sites further from these features. Occurrence of brush-tailed rabbit-rat and
243 grassland melomys were also positively associated with shrubs (Fig. 2). In contrast, these
244 variables had only marginal influences on delicate mouse occurrence, which was positively
245 associated with proportion of area burnt (Fig. 2b).

246 Northern brown bandicoots were detected at every site and northern quolls at all but two.
247 Royle-Nichols occupancy modelling did not produce a single superior model for either species
248 (i.e. $\Delta AIC < 2$; Table 4 & Appendix S4) and model averaging was conducted. Northern brown
249 bandicoots had greater relative abundance at sites with more logs and shrubs, and a greater
250 proportion of the site burnt (Fig. 3a). Relative abundance of northern quolls increased with
251 ruggedness and proximity to major anthropogenic disturbance and roads (Fig. 3b).

252 Eight mammal species were included in species diversity analyses: northern quoll, northern
253 brown bandicoot, northern hopping-mouse, brush-tailed rabbit-rat, delicate mouse, grassland
254 melomys, common planigale (*Planigale maculata*) and short-beaked echidna (*Tachyglossus*
255 *aculeatus*). No single model of species diversity was superior and model averaging did not
256 identify any significant relationships between Shannon's diversity indices and predictor
257 variables.

258 *Feral cat density*

259 There were no feral cat detections on the northern camera array and only seven detections, at
260 four different camera stations, on the southern array (Appendix S2). Based upon distinct pelage

261 patterns, these detections comprised four individual cats, but detections were too sparse to
262 estimate density.

263

264 **Discussion**

265 Native mammal populations have suffered widespread contraction across mainland northern
266 Australia (Woinarski et al., 2001, Woinarski et al., 2010). Research suggests that mammal
267 populations on some large islands are now also exhibiting similar signs of decline to those
268 recorded earlier on the mainland (Davies et al. 2017; 2018). On Groote Eylandt, naïve
269 occupancy estimates of all CWR native mammals were higher compared to lowland savanna
270 woodland habitats across mainland Northern Territory (Table 2; Stokeld et al., 2016). This
271 reaffirms that, although fewer mammal species occur on Groote Eylandt (as with other large
272 Northern Territory islands), their populations remain healthier than those on the mainland. This
273 is likely related to several interrelated factors, including the low density of feral cats, the
274 relatively benign fire regime and the absence of large introduced herbivores and cane toads.

275 Feral cats have been implicated as a major driver in the decline of mammals across northern
276 Australia. Although widely distributed across Groote Eylandt, naïve occupancy and detection
277 probability of feral cats were low compared to similar habitats on mainland northern Australia
278 and the Tiwi Islands (Table 2). This precluded both an evaluation of environmental patterns of
279 feral cat occurrence, as well as our ability to investigate the relationship between feral cats and
280 the distribution/abundance of native mammals. The number of cat detections on camera grids
281 was also too low to estimate population density. In contrast, feral cat density estimates from
282 mainland Northern Territory using similar methods have ranged from 0.09 - 0.5 cats per km²
283 (Stokeld et al., 2016; Northern Territory Government, unpublished data, 2019) and McGregor
284 (2015) estimated a mean density of 0.18 cats per km² in woodland habitats in the Kimberley,

285 Western Australia. The detection of zero and four individual cats on our two camera grids,
286 combined with the low overall naïve occupancy, suggests that cat densities on Groote Eylandt
287 are far lower than those on the mainland. This finding contrasts with recent modelling
288 predicting that feral cat densities should be higher on islands than on the mainland (Legge et
289 al., 2017).

290 Interestingly, the density of feral cats remains low on Groote Eylandt despite well-established
291 populations of cats in two towns and one out-station (Anindilyakwa Land Council, unpublished
292 data, 2018), as well as high densities of their preferred prey (as inferred from the high
293 occupancy rates of CWR mammals presented in this study). This suggests that the population
294 dynamics of feral cats on Groote Eylandt is not simply influenced by prey availability. Due to
295 a range of factors (i.e. high prey availability, the absence of both cane toads and dingo control),
296 Groote Eylandt supports healthy populations of native predators that are known to prey on cats,
297 including dingoes (Kennedy et al., 2012, Moseby et al., 2012, Allen and Leung, 2012,
298 Paltridge, 2002, Wysong et al., 2019), olive pythons (H. McGregor, unpublished data, 2018)
299 and sand goannas (T. Jessop, unpublished data, 2018). It is plausible that the healthy
300 assemblage of native predators may suppress feral cat populations through both direct
301 predation and interference competition. The combination of a relatively benign fire regime and
302 the absence of large feral herbivores, may also have maintained the vegetation in a state that
303 reduces feral cat hunting success (McGregor et al., 2015, McGregor et al., 2017, McGregor et
304 al., 2016), although how these constraints may be offset by high prey availability is unknown.
305 The contrasting densities of feral cats on Groote Eylandt and the Northern Territory mainland
306 highlights our limited understanding of the factors that regulate their population dynamics.

307 In northern Australian savannas, frequent, high-intensity fires reduce the availability of critical
308 resources for native mammals, such as tree hollows (Woolley et al., 2018), fleshy-fruit bearing
309 shrubs (Vigilante and Bowman, 2004) and perennial grasses (Crowley, 2008). We found no

310 significant negative association between the occupancy or abundance of native mammals and
311 frequent, large fires on Groote Eylandt. In fact, we found a significant positive association
312 between our fire variable and northern brown bandicoot abundance and delicate mouse
313 occurrence. There are several potential explanations for these results. First, Groote Eylandt is
314 characterised as having a relatively benign fire regime compared to mainland northern
315 Australia. For example, the average annual area burnt on Groote Eylandt between 2000 and
316 2018 was 18.1% (ranging from as low as 1.5% to 40.1%; Department of Environment and
317 Natural Resources and Anindilyakwa Land Council, 2019), compared to Kakadu National Park
318 where around 50% is burnt annually (Russell-Smith et al., 1997). As such, native mammals
319 may simply not be strongly impacted by the fire regime on Groote Eylandt. Second, fire
320 influences fauna indirectly, via effects on vegetation structure and composition, including
321 complex interactions with other exacerbating factors such as predation (McGregor et al., 2017,
322 McGregor et al., 2015) and grazing by large introduced herbivores (Legge et al., 2019).
323 Therefore, given the absence of large introduced herbivores, as well as the low density of feral
324 cats on Groote Eylandt, such positive associations with fire are not necessarily surprising
325 (Radford, 2012). Third, while our fire variable, the proportion of area burnt averaged over the
326 preceding five years, captured the spatial and temporal variation in fire regimes on Groote
327 Eylandt, we do not have a firm understanding of how this variable encapsulates other
328 characteristics of the fire regime, such as intensity and patchiness. Due to issues of collinearity,
329 we did not investigate the influence of these other fire variables. In reality, the absence of strong
330 negative fire effects in our analyses likely reflects a combination of these explanations. We
331 suggest that future research should aim to elucidate how different fire characteristics influence
332 biodiversity on Groote Eylandt.

333 The high naïve occupancy rates of native mammals on Groote Eylandt suggest that populations
334 are relatively healthy when compared to mainland northern Australia (Table 2). However, due

335 to a lack of standardised historical data on Groote Eylandt, we cannot properly evaluate the
336 trajectory of native mammal populations. As such, the current state of native mammals on
337 Groote Eylandt should not be taken as evidence that these populations are safe from decline,
338 or that they are not currently declining. Despite the availability of seemingly suitable habitat,
339 the distribution of the northern hopping-mouse was highly restricted. This suggests that
340 populations of this species may have suffered declines on Groote Eylandt. However, the
341 reasons for this remain unclear.

342 Although less restricted, the brush-tailed rabbit-rat was absent from a large proportion of sites
343 in seemingly suitable lowland woodland. As with the findings of Davies et al. (2017), site-
344 occupancy of the brush-tailed rabbit-rat was positively associated with shrub density, which
345 has been hypothesised to reflect a greater availability of resources for native mammals (Friend,
346 1987, Davies et al., 2017), as well as shelter from predators (Briani et al., 2004). Our results
347 may also reflect a combination of these factors; however further research is required to
348 ascertain what factors may be limiting the distribution of this species on Groote Eylandt and
349 how they contrast with those operating on other extant populations.

350 Despite the seemingly low densities, cats could be impacting native mammal populations if
351 predation rates exceed recruitment and recolonisation (Ceballos and Cruzado 2004, Frank et
352 al., 2014, Short, 2016, Moseby et al., 2015). Both threatened rodent species may have relatively
353 limited dispersal capabilities (Firth et al., 2006a, Diete et al., 2016), and the brush-tailed rabbit-
354 rat has low fecundity, giving birth to one to three young each year (Taylor and Horner, 1971).
355 These species may therefore be limited in their ability to recolonise areas following disturbance
356 such as fire. Furthermore, studies have shown that cats selectively target CWR mammal species
357 (Kutt, 2012, Wysong et al., 2019), and that even at low densities, cats can exert significant
358 predation pressure on mammal populations (Frank et al., 2014). As such, despite their low

359 density on Groote Eylandt, feral cats could still be posing a significant threat to populations of
360 the brush-tailed rabbit-rat and northern hopping-mouse.

361 This research has identified important knowledge gaps that warrant further investigation to
362 better inform management:

- 363 • Greater understanding of the factors that regulate feral cat population densities in
364 northern Australia; in particular, to what extent are they limited by native predators;
- 365 • The impact of feral cats at varying densities on CWR mammal populations, and in
366 different environmental settings; and
- 367 • How fine-scale fire regimes are changing over time on Groote Eylandt and other
368 offshore islands, and what impacts these are having on biodiversity.

369 The greater resilience of mammal populations on Groote Eylandt compared to the northern
370 Australian mainland is likely due to the low density of feral cats, the relatively benign fire
371 regime and the absence of large introduced herbivores and cane toads. These factors have likely
372 benefited mammal populations by maintaining the availability of critical resources, while
373 concurrently reducing predation pressure. The resilience of mammal populations on Groote
374 Eylandt appears comparable to that of mammal populations on the Tiwi Islands. However, the
375 sources of resilience may differ between these areas. Compared to Groote Eylandt, there is a
376 greater number of threatening processes present on the Tiwi Islands, including a higher naïve
377 occupancy rate of cats, higher fire frequency, large introduced herbivores (buffalo and horse)
378 and feral pigs. While the Tiwi Islands have substantially higher rainfall (with some areas
379 receiving more than 2000 mm of annual rainfall compared to 1300 mm on Groote Eylandt),
380 they lack the rugged sandstone escarpment habitat that likely provide important refugia for
381 some native mammals on Groote Eylandt (Radford et al., 2014). As such, mammal populations
382 on Groote Eylandt may be more resilient to decline due to higher overall ecological integrity,

383 whereas mammal populations on the Tiwi Islands may be more resilient primarily due to higher
384 productivity. This contrast highlights that the way in which native mammal population declines
385 manifest themselves (in terms of severity or apparent resilience) is influenced by complex
386 interactions of factors that vary substantially across the landscape. Caution is therefore required
387 in making broad inferences about primary factors driving mammal species declines from a few
388 studies that are spatially and temporally limited. Management responses to conserve these
389 species need to be developed at appropriate ecological and management scales. They also need
390 to be adaptive to respond to new insights into threats and management responses as they
391 emerge.

392

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687

688 **Supporting information**

689 **Appendix S1.** Location of brush-tailed rabbit-rat and northern hopping-mouse records on
690 Groote Eylandt.

691 **Appendix S2.** Location of feral cat detections on Groote Eylandt.

692 **Appendix S3.** Occupancy covariates and AIC values of models with an AIC<2 for each
693 species.

694 **Appendix S4.** Occupancy covariates and AIC values of Royle-Nichols occupancy models
695 with an AIC<2 for each species.

696

697 **Tables**

698 **Table 1.** Description of landscape and site-specific environmental variables used in analyses.

Variable	Description	Rationale
Proportion burnt	Proportion of area surrounding each site that is burnt each year, averaged over the preceding five years. Area used was scaled to reflect different species home range sizes: 250 m radius for brush-tailed rabbit-rat, delicate mouse and grassland melomys (Firth et al., 2006a), and 3200 m radius for northern quoll, northern brown bandicoot and species diversity (Lawes et al., 2015b). Derived from	Too frequent and/or intense fires have been implicated in CWR mammal declines across northern Australia (Lawes et al., 2015a, Lawes et al., 2015b, Legge et al., 2011b, Andersen et al., 2005).

fine-scale (30 m x 30 m) LANDSAT imagery following Lawes *et al.* (2015b). This variable was correlated with fire frequency, total ground cover (perennial, annual, sedge, forb and herb cover) and perennial grass cover.

Ruggedness	Standard deviation in elevation (Geoscience Australia, 2017) estimated over 250 m and 3200 m radius, as per proportion burnt. Ruggedness was correlated with rainfall.	Rugged habitats provide refugia for CWR mammal species (Hohnen <i>et al.</i> , 2016, Braithwaite and Griffiths, 1994).
Shrubs	The presence of shrubs under 1.5 m was recorded every metre along two edges of a 50 x 50 m quadrat.	Shrubs provide shelter from predators and food resources for CWR mammal species (McGregor <i>et al.</i> , 2015), and predicted brush-tailed rabbit-rat occupancy on Melville Island (Davies <i>et al.</i> , 2017).

Logs	Number of logs (diameter ≥ 5 cm) crossing the perimeter of a 50 x 50 m quadrat.	Logs provide den sites and shelter for some CWR mammal species (Firth et al., 2006b).
Distance to anthropogenic disturbance	Minimum distance from each site to GEMCO mining operations or one of the three towns (Alyangula, Angurugu or Umbakumba). This covariate was not used to predict mammal detectability.	Disturbances from human settlements and roads may have pervasive effects on biodiversity proximal and distal from these sources (Sodhi et al., 2010, Laurance et al., 2009, Karanth et al., 2006, de Fretes, 1992).
Distance to roads	Minimum distance to a mapped road. This covariate was not used to predict mammal detectability.	
Distance to water	Distance to the closest permanent waterbody, defined by presence of water for more than 50% of all Landsat 5 and Landsat 7 satellite observations (Geoscience Australia, 2015). Permanent water body distribution was determined using the Australian Hydrological Geospatial Fabric (Bureau of Meteorology, 2017a).	Proximity to watercourses can influence the occurrence of CWR mammal species (Firth et al., 2006b).

Basal area	Calculated from the circumferences of all trees (diameter at 1.3 m > 5 cm) within a 5 m belt around the 50 x 50 m quadrat. Correlated with number of large trees (diameter at 1.3 m > 40 cm) within 5 m of the 50 x 50 m quadrat.	Tree basal area can influence the occurrence of CWR mammal species (Firth et al., 2006b).
Number of cameras operating	An observation-level covariate of the number of cameras operating at each site for each sampling day. Used as a covariate to estimate mammal detectability only.	Variation in detectability can arise from uneven numbers of cameras operating at sites due to camera malfunction (Stokeld et al., 2015).
Julian day	Date that sampling started at each site. Used as a covariate to estimate mammal detectability only.	Seasonal differences can influence mammal detectability (Einoder et al., 2018)

699

700 **Table 2.** Naïve occupancy estimates of mammal species detected during camera trapping
701 surveys in lowland woodland across the Northern Territory. Groote Eylandt estimates are from
702 the current survey, Tiwi Island estimates are derived from surveys conducted on Melville

703 (2015) and Bathurst Island (2014), and mainland estimates are derived from surveys conducted
 704 at Cobourg peninsula (2014), Fish River Station (2014), Kakadu National Park (2015),
 705 Litchfield National Park (2016), Nitmiluk National Park (2015), peri-urban areas of Darwin
 706 (2014) and Warddeken IPA (2013 – 2015).

707 ^{NA} Species is known to occur in the area, but naïve occupancy estimate is not available.

708 - Species not known to occur in the area.

709 ⁺ Estimate from Melville Island only as the species is not known to occur on Bathurst Island.

Common name	Scientific name	Naïve occupancy		
		Groote Eylandt (n=112)	Tiwi Islands (n=110)	Mainland (n=131)
Brush-tailed rabbit-rat	<i>Conilurus penicillatus</i>	0.17	0.318	0.128
Dingo	<i>Canis lupus dingo</i>	0.36	0.46	0.5
Northern quoll	<i>Dasyurus hallucatus</i>	0.98	-	0.015
Feral cat	<i>Felis catus</i>	0.07	0.24	0.23
Northern brown bandicoot	<i>Isoodon macrourus</i>	1.00	0.918	0.471
Agile wallaby	<i>Macropus agilis</i>	0.85	0.855	0.572
Grassland melomys	<i>Melomys burtoni</i>	0.08	0.091	0.056
Northern hopping-mouse	<i>Notomys aquilo</i>	0.03	-	NA

Sugar glider	<i>Petaurus breviceps</i>	0.05	NA	NA
Short-eared rock-wallaby	<i>Petrogale brachyotis</i>	0.02	-	NA
Common planigale	<i>Planigale maculata</i>	0.03	-	NA
Delicate mouse	<i>Pseudomys delicatulus</i>	0.47	0.027	NA
Short-beaked echidna	<i>Tachyglossus aculeatus</i>	0.39	-	0.05
Fawn antechinus	<i>Antechinus bellus</i>	-	-	NA
Water rat	<i>Hydromys chrysogaster</i>	NA	NA	0.03
Antilopine wallaroo	<i>Macropus antilopinus</i>	-	-	0.122
Black wallaroo	<i>Macropus bernardus</i>	-	-	0.036
Common wallaroo	<i>Macropus robustus</i>	-	-	0.121
Black-footed tree-rat	<i>Mesembriomys gouldii</i>	-	0.636 ⁺	0.315
Northern nail-tail wallaby	<i>Onychogalea unguifera</i>	-	-	0.007
Western chestnut mouse	<i>Pseudomys nanus</i>	-	0.009	0.013
Black rat	<i>Rattus rattus</i>	NA	NA	0.039
Pale field rat	<i>Rattus tunneyi</i>	NA	0.109	0.006
Butler's dunnart	<i>Sminthopsis butleri</i>	-	0.064	-
Red-cheeked dunnart	<i>Sminthopsis virginiae</i>	-	0.018	0.013
	<i>Trichosurus vulpecula</i>	-	0.393	0.05

Common brushtail

possum

711 **Table 3.** Comparison of ΔAIC , occupancy, nightly and overall detection probabilities (over 37
712 nights) for the null model (where occupancy and detectability parameters are assumed to be
713 constant across all survey sites), and the most parsimonious single-season occupancy model
714 for each species.

Species	Model	ΔAIC	Occupancy (Ψ) ($\pm SE$)	Nightly detection probability (p) (\pm SE)	Overall detection probability
Brush-tailed rabbit-rat	Null model	199.58	0.17 (0.04)	0.24 (0.02)	0.99
	Best model	0.0	0.20 (0.06)	0.18 (0.03)	0.99
Grassland melomys	Null model	18.33	0.09 (0.03)	0.07 (0.02)	0.94
	Best model	0.0	0.11 (0.05)	0.13 (0.06)	0.99
Delicate mouse	Null model	0.0	0.52 (0.08)	0.13 (0.02)	0.99
	Best model	129.04	0.47 (0.05)	0.15 (0.01)	0.99

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716

717 **Table 4.** Comparison of ΔAIC , relative abundance, nightly probability of detection and the
 718 overall probability of detection (over 37 nights) for the null model (where relative abundance
 719 and detectability parameters are assumed to be constant across all survey sites), and the most
 720 parsimonious Royle-Nichols occupancy model.

Species	Model	ΔAIC	Relative abundance (λ) ($\pm SE$)	Nightly detection probability (p) ($\pm SE$)	Overall detection probability
Northern brown bandicoot	Null model	55.24	3.76 (0.38)	0.14 (0.01)	0.99
	Best model	0	5.22 (1.15)	0.11 (0.02)	0.99
Northern quoll	Null model	34.99	3.06 (0.37)	0.09 (0.01)	0.96
	Best model	0	4.35 (1.27)	0.07 (0.01)	0.92

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727 **Figure legends**

728 **Figure 1.** Groote Eylandt and its location in Australia. Location of the 112 survey sites (black
729 circles) and cat density grids (black open rectangles). Light grey – lowland forest and
730 woodlands; clear – sandstone outcrop and coastal grassland and shrubland complex; dark grey
731 – GEMCO mining operation area; dashed lines – roads.

732 **Figure 2.** Model averaged regression coefficient estimates for (a) the brush-tailed rabbit-rat,
733 (b) the delicate mouse and (c) the grassland melomys. Error bars indicate 95% confidence
734 intervals and asterisks indicate significant parameters where confidence intervals do not
735 overlap zero.

736 **Figure 3.** Model averaged regression coefficient estimates of relative abundance for (a) the
737 northern brown bandicoot and (b) the northern quoll. Error bars indicate 95% confidence
738 intervals and asterisks indicate significant parameters where confidence intervals do not
739 overlap zero.

Figures

Figure 1:

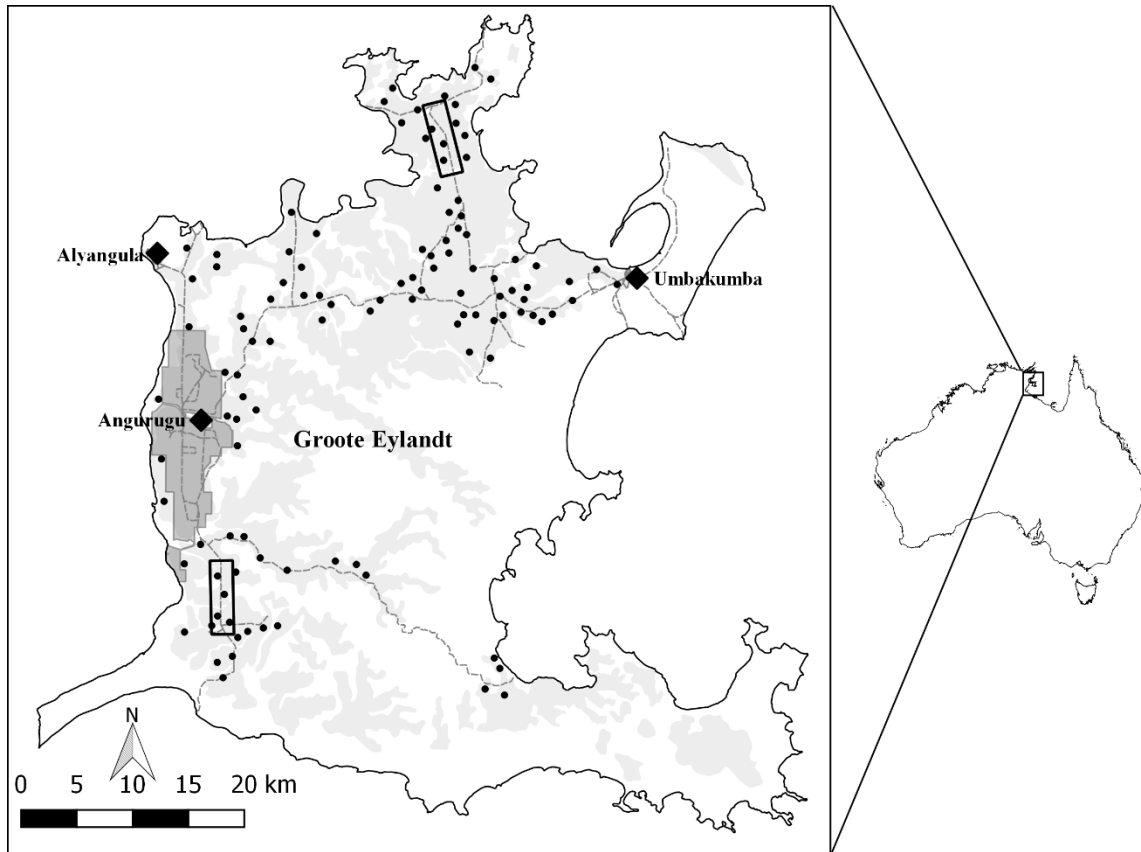


Figure 2:

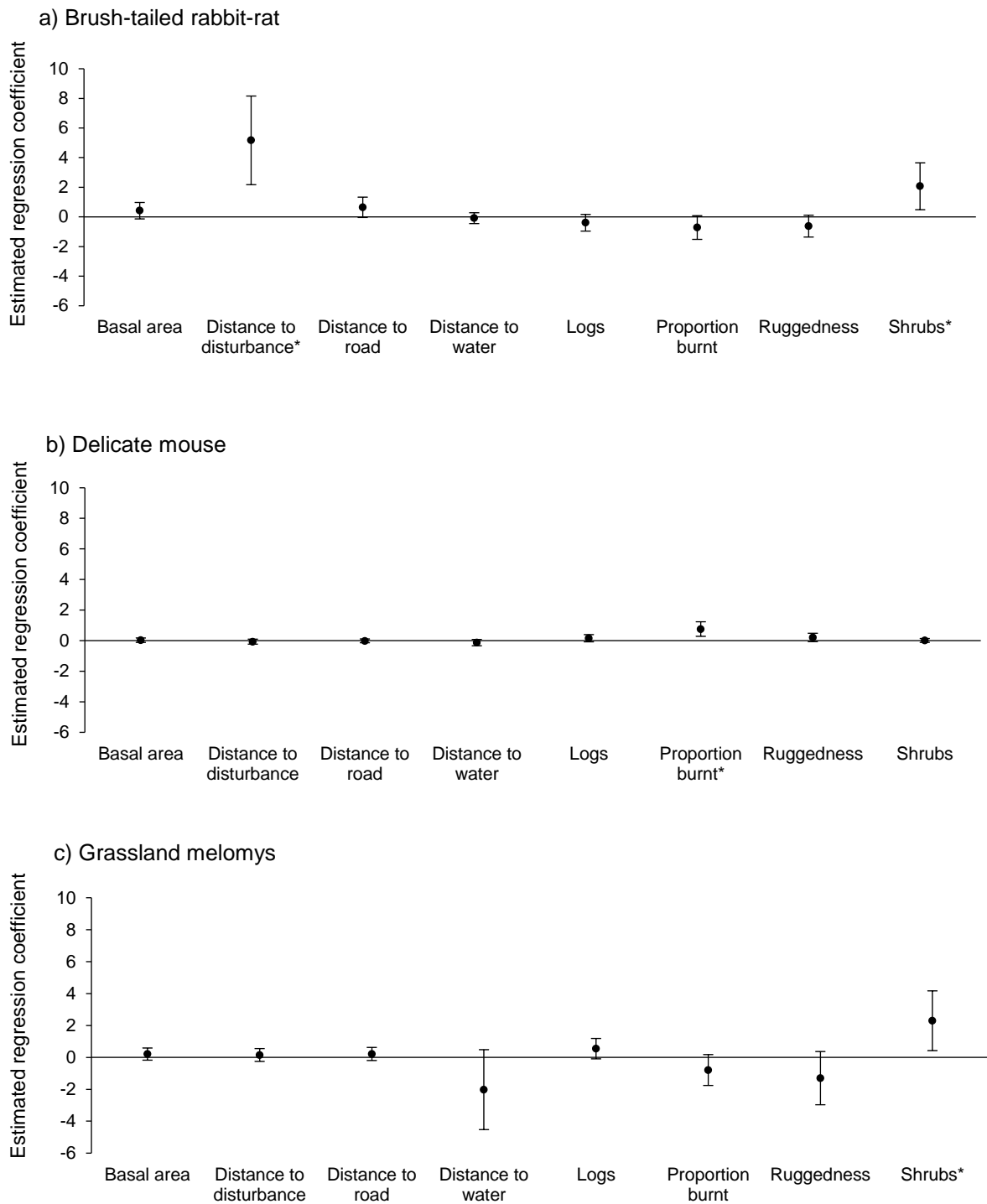
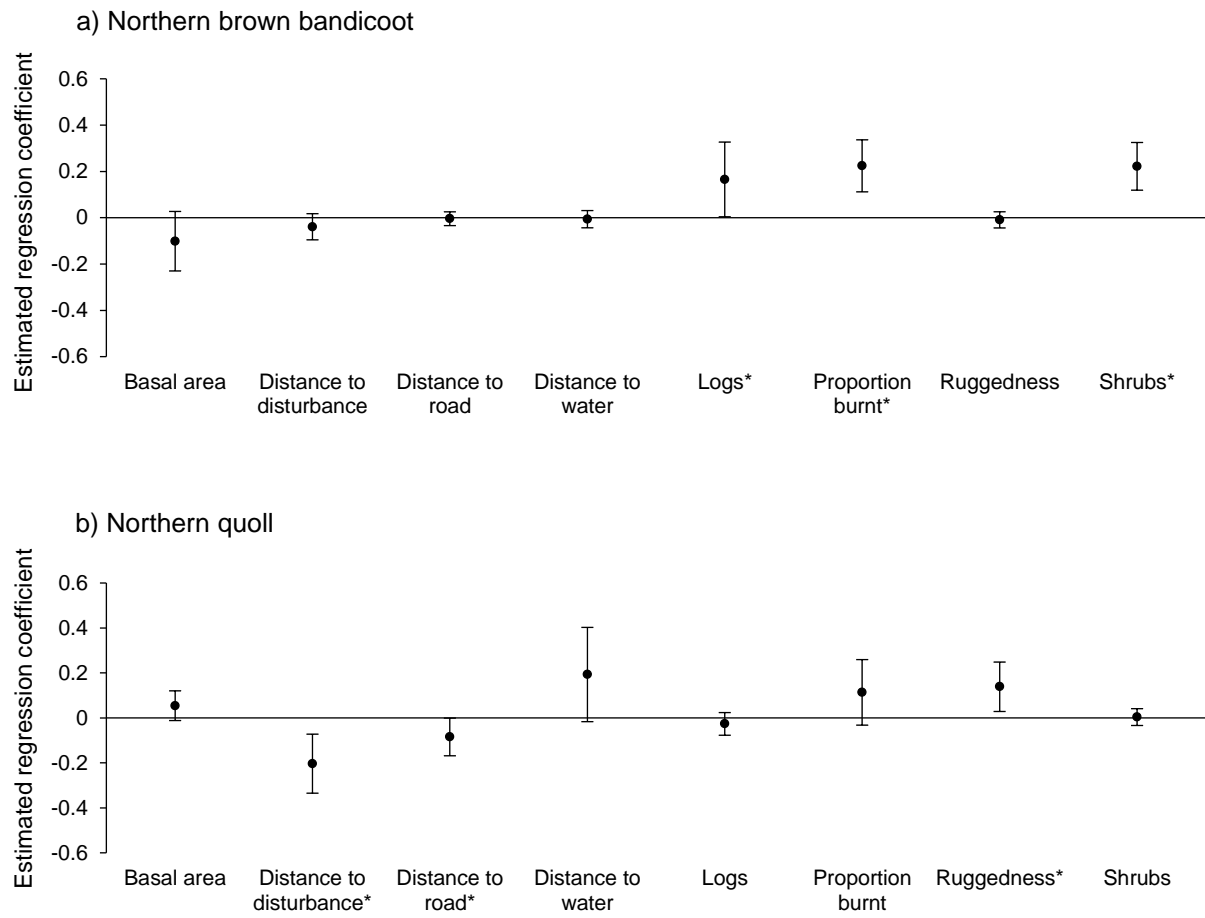


Figure 3:



Supporting information

Appendix S1. The locations of past and present records of (a) the brush-tailed rabbit-rat and (b) the northern hopping-mouse on Grootte Eylandt. Black diamonds - detected in the current study; open circles - previous records.

Appendix S2. Locations of feral cat detections on Grootte Eylandt. Black diamonds - mammal survey; filled circles - cat density array records.

Appendix S3: The occupancy variables, number of parameters (K), AIC, Δ AIC and AIC weight for the occupancy models with an AIC < 2 for each species.

Occupancy variables	K	AIC	ΔAIC	AIC weight
Brush-tailed rabbit-rat				
<i>proportion burnt + ruggedness + disturbance + basal area + roads + shrubs</i>	13	707.64	0	0.097
<i>proportion burnt + ruggedness + disturbance + basal area + logs + roads + shrubs</i>	14	708.26	0.62	0.071
<i>proportion burnt + ruggedness + water + disturbance + basal area + roads + shrubs</i>	14	709.38	1.74	0.041
<i>proportion burnt + ruggedness + disturbance + basal area + shrubs</i>	12	709.5	1.86	0.038
<i>proportion burnt + ruggedness + disturbance + roads + shrubs</i>	12	709.64	2	0.036
Grassland melomys				
<i>proportion burnt + ruggedness + water + shrubs</i>	8	238.82	0	0.086
<i>proportion burnt + water + logs + shrubs</i>	8	238.91	0.085	0.083
<i>proportion burnt + ruggedness + water + roads + shrubs</i>	9	239.36	0.534	0.066
<i>proportion burnt + ruggedness + water + disturbance + basal area + logs + shrubs</i>	11	239.87	1.048	0.051
<i>water + logs + shrubs</i>	7	240	1.179	0.048
<i>proportion burnt + water + logs + roads + shrubs</i>	9	240.17	1.352	0.044
<i>proportion burnt + ruggedness + water + disturbance + shrubs</i>	9	240.21	1.384	0.043
<i>proportion burnt + ruggedness + water + disturbance + roads + shrubs</i>	10	240.57	1.744	0.036
<i>ruggedness + water + logs + roads + shrubs</i>	9	240.71	1.884	0.034
Delicate mouse				
<i>proportion burnt + logs</i>	10	1714.19	0	0.038
<i>proportion burnt + ruggedness + water</i>	11	1714.27	0.076	0.037
<i>proportion burnt + ruggedness</i>	10	1714.45	0.256	0.033
<i>proportion burnt</i>	9	1714.45	0.256	0.033
<i>proportion burnt + ruggedness + water + logs</i>	12	1714.97	0.781	0.026
<i>proportion burnt + ruggedness + logs</i>	11	1714.98	0.785	0.026
<i>proportion burnt + water + logs</i>	11	1715.01	0.815	0.025
<i>proportion burnt + water</i>	10	1715.26	1.071	0.022

<i>proportion burnt + ruggedness + disturbance</i>	11	1715.36	1.165	0.021
<i>proportion burnt + ruggedness + disturbance + logs</i>	12	1715.43	1.238	0.020
<i>proportion burnt + ruggedness + water + disturbance</i>	12	1715.55	1.354	0.019
<i>proportion burnt + disturbance + logs</i>	11	1715.61	1.419	0.019
<i>proportion burnt + ruggedness + water + disturbance + logs</i>	13	1715.88	1.689	0.016
<i>proportion burnt + basal area</i>	10	1716.01	1.816	0.015
<i>proportion burnt + logs + roads</i>	11	1716.07	1.883	0.015
<i>proportion burnt + basal area + logs</i>	11	1716.08	1.892	0.015
<i>proportion burnt + logs + shrubs</i>	11	1716.09	1.894	0.015
<i>proportion burnt + ruggedness + shrubs</i>	11	1716.1	1.909	0.015
<i>proportion burnt + ruggedness + basal area</i>	11	1716.11	1.919	0.015
<i>proportion burnt + ruggedness + water + basal area</i>	12	1716.15	1.956	0.014

Appendix S4: The occupancy variables, number of parameters (K), AIC, Δ AIC and AIC weight for the Royle-Nichols occupancy models with an AIC < 2 for each species.

Occupancy variables	K	AIC	Δ AIC	AIC weight
Northern quoll				
<i>proportion burnt + ruggedness + water + disturbance + basal area + roads</i>	11	4189.22	0	0.062
<i>proportion burnt + ruggedness + water + disturbance + roads</i>	10	4189.54	0.32	0.053
<i>ruggedness + water + disturbance + roads</i>	9	4189.9	0.68	0.044
<i>ruggedness + water + disturbance + basal area + roads</i>	10	4190.1	0.88	0.040
<i>proportion burnt + ruggedness + water + disturbance + basal area + logs + roads</i>	12	4190.38	1.16	0.035
<i>ruggedness + water + disturbance + basal area + logs + roads</i>	11	4190.68	1.46	0.030
<i>ruggedness + disturbance + basal area + logs + roads</i>	10	4190.94	1.72	0.026
<i>proportion burnt + ruggedness + disturbance + basal area + roads</i>	10	4190.97	1.76	0.026
<i>proportion burnt + ruggedness + disturbance + basal area + logs + roads</i>	11	4191.05	1.84	0.025
<i>proportion burnt + ruggedness + water + disturbance + basal area + roads + shrubs</i>	12	4191.22	2	0.023
Northern brown bandicoot				
<i>proportion burnt + basal area + logs + shrubs</i>	10	5157.47	0	0.069
<i>proportion burnt + disturbance + basal area + logs + shrubs</i>	11	5157.49	0.023	0.069
<i>proportion burnt + shrubs</i>	8	5158.12	0.658	0.050
<i>proportion burnt + logs + shrubs</i>	9	5158.39	0.924	0.044
<i>proportion burnt + disturbance + shrubs</i>	9	5158.44	0.977	0.043
<i>proportion burnt + disturbance + logs + shrubs</i>	10	5158.67	1.205	0.038
<i>proportion burnt + water + basal area + logs + shrubs</i>	11	5158.89	1.426	0.034
<i>proportion burnt + ruggedness + basal area + logs + shrubs</i>	11	5159	1.529	0.032
<i>proportion burnt + ruggedness + disturbance + basal area + logs + shrubs</i>	12	5159.29	1.822	0.028
<i>proportion burnt + water + disturbance + basal area + logs + shrubs</i>	12	5159.3	1.83	0.028
<i>proportion burnt + ruggedness + shrubs</i>	9	5159.44	1.979	0.026