

1 Feral cats are more abundant under severe disturbance regimes in an Australian
2 tropical savanna

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9 **Abstract**

10 There is an increasing awareness that feral cats play a key role in driving the ongoing decline of small
11 mammals across northern Australia, yet the factors that control the distribution, abundance and
12 behaviour of feral cats are poorly understood. These key knowledge gaps make it near-impossible for
13 managers to mitigate the impacts of cats on small mammals. We investigated the environmental
14 correlates of feral cat activity and abundance across the savanna woodlands of Melville Island, the larger
15 of the two main Tiwi Islands, northern Australia. We conducted camera-trap surveys at 88 sites, and
16 related cat activity and abundance to a range of biophysical variables. We found that feral cat activity
17 and abundance tended to be highest in areas characterised by relatively severe disturbance regimes,
18 namely high frequencies of severe fires and/or high feral herbivore activity. Our results contribute to
19 the growing body of research demonstrating that in northern Australian savanna landscapes, disturbance
20 regimes characterised by frequent high-severity fires and grazing by feral herbivores may advantage
21 feral cats. This is most likely a result of high-severity fire and grazing removing understorey biomass,
22 which increases the time that the understorey remains in an open state in which cats can hunt more
23 efficiently, due to both the frequent and extensive removal of ground layer vegetation by severe fires,
24 as well as the suppressed post-fire recovery of ground layer vegetation due to grazing by feral
25 herbivores. Management that reduces the frequency of severe fires and the density of feral herbivores
26 could suppress feral cat populations on Melville Island. A firm understanding of how threatening
27 processes interact, and how they vary across landscapes with different environmental conditions, is
28 critical for ensuring management success.

29 **Introduction**

30 Since European colonisation 230 years ago, the unique mammal fauna of the Australian continent has
31 proven extremely susceptible to novel threats and disturbance regimes. Ten percent of Australia's
32 terrestrial mammals have been driven to extinction, amounting to over a third of all historical mammal
33 extinctions globally (Woinarski et al., 2015). Ground-dwelling mammals with a body size within the

34 'critical weight range' (35–5500 g) in southern and arid parts of Australia have been most prone to
35 extinction (Burbidge and McKenzie, 1989, Johnson and Isaac, 2009). Predation by the feral cat (*Felis*
36 *catus*) and red fox (*Vulpes vulpes*), changed fire regimes, habitat loss and exotic herbivores rank among
37 the top factors threatening Australian mammals (Woinarski et al., 2015).

38 Numerous mammals have suffered widespread decline across the savannas of tropical northern
39 Australia (Woinarski et al., 2011, Ziembicki et al., 2014), and there are worrying similarities between
40 the species most affected by these declines and the species earlier driven to extinction in central and
41 southern Australia. First, mammal decline in northern Australia has been most severe in areas of low
42 rainfall (Woinarski et al., 2011, Stobo-Wilson et al., 2019). Second, the species that have suffered the
43 greatest decline in northern Australia are again those with a body size in the critical weight range
44 (Fitzsimons et al., 2010, Murphy and Davies, 2014). The urgent need to mitigate the northern mammal
45 decline has stimulated much research over the last decade, significantly increasing our understanding
46 of the factors involved (Woinarski et al., 2015, Legge et al., 2019). A key hypothesis that has emerged
47 is that the decline of native mammals across northern Australian savannas is the result of the interaction
48 between feral cats and anthropogenic disturbance, namely frequent, large-scale, high-severity fires and
49 grazing by large feral herbivores (Legge et al., 2011a, McGregor et al., 2016a, McGregor et al., 2016b,
50 Legge et al., 2019). According to this hypothesis, the impact of disturbance regimes on native mammal
51 populations likely arises due to the concurrent depletion of critical resources and enhanced predation
52 pressure, especially by feral cats.

53 In northern Australian savannas, feral cats appear to benefit from fire. For example, in the central
54 Kimberley region of northwestern Australia, feral cats make large movements outside their normal
55 home range to hunt in recently burnt areas, especially areas that have recently experienced a high-
56 severity fire (McGregor et al., 2016b). The selection of recently burnt areas has also been demonstrated
57 for feral cats on Cape York Peninsula, northeastern Australia (McGregor et al., 2016a). This behaviour
58 likely reflects the short-term, heightened hunting efficiency afforded to predators (especially feral cats)
59 due to the removal of ground layer vegetation in recently burnt areas (McGregor et al., 2015). Feral cat

60 activity also tends to be higher in heavily grazed areas, most likely due to the improved hunting success
61 associated with reduced grass biomass (McGregor et al., 2014). Furthermore, feral herbivores
62 preferentially graze on the nutrient-rich regenerating grass and shrubs following fire, thereby extending
63 the amount of time the vegetation remains in an open, suppressed state (Legge et al. 2019).

64 The Tiwi Islands are an excellent model system to understand the drivers of the decline of small
65 mammal in northern Australian savannas. Despite the presence of frequent fire, large introduced
66 herbivores and feral cats, the Tiwi Islands remain one of the last parts of northern Australia to retain a
67 complete assemblage of native mammals, and most Tiwi mammals remain abundant and widespread.
68 However, while mammal populations on the Tiwi Islands have been relatively resilient compared to
69 those on the mainland of northern Australia, they are showing the initial signs of decline, suggesting
70 that similar threatening processes are present on both the mainland and the Tiwi Islands (Davies et al.,
71 2017, Davies et al., 2018). Earlier work has shown that across the Tiwi Islands there is strong variation
72 in feral cat abundance, and areas of high cat abundance have experienced greater rates of mammal
73 decline (Davies et al., 2017); however, a key unresolved question is what controls that geographic
74 variation in the abundance of feral cats. Here, we explore the variation in the activity and abundance of
75 feral cats across a range of biophysical gradients on Melville Island, the larger of the two main Tiwi
76 Islands. We test the hypothesis that feral cat activity and abundance are highest in areas of frequent,
77 high-severity fires, and high feral herbivore activity.

78 **Methods**

79 *Study site*

80 Melville Island, the larger of the two main Tiwi Islands, is located 80 km north of Darwin, in Australia's
81 Northern Territory (Figure 1). The island is of low relief (≤ 103 m above sea level) and experiences a
82 tropical monsoonal climate with over 90% of annual rainfall occurring in the 5-month wet season
83 (November–April) (Australian Bureau of Meteorology, 2015). There is a substantial gradient in annual

84 rainfall, from 1400 mm in the east, to 2000 mm in the northwest. The major vegetation types are savanna
85 woodlands and open forests dominated by *Eucalyptus miniata*, *E. tetradonta* and *Corymbia nesophila*,
86 with a predominantly grassy understorey. Shrub density is highly variable, and studies on the mainland
87 have shown that this is influenced by the fire regime (Russell-Smith et al., 2003, Woinarski et al., 2004).
88 Recent fire mapping of the Tiwi Islands from 2000–2013 estimated that, on average, 54% of the
89 savannas burn annually, mostly in the late dry season (i.e. after July 31st) (Richards et al., 2015).

90 *Data collection*

91 In 2015, camera trap surveys were conducted at 88 sites across the savannas of Melville Island (Fig. 1).
92 Camera trapping involved five horizontally facing motion-sensor cameras that were deployed at each
93 site for at least 35 consecutive days. Each camera faced a bait station, containing a mixture of peanut
94 butter, oats and honey. To increase the likelihood of being triggered, each camera was carefully
95 positioned to ensure the base of its bait station was in the centre of the field of view (Gillespie et al.,
96 2015). Vegetation within each camera's field of view was cleared to reduce the chance of false triggers
97 and to reduce the risk posed by fire. Of the five cameras deployed at each site, two were Reconyx™
98 HC550 Hyperfire white-flash cameras (Reconyx Inc., Holmen, USA), while the remaining three
99 cameras were Reconyx™ PC800 Hyperfire Professional infra-red flash cameras (Reconyx Inc.,
100 Holmen, USA). All cameras could be triggered at any time of day and were set to take three image
101 bursts per trigger, with a 1-sec time delay interval between images. The sensitivity of each camera was
102 set to high, with cameras re-arming instantly after being triggered.

103 <<< Insert Figure 1 about here>>>

104 *Frequency of high-severity fires*

105 The decline of native mammal species in Kakadu National Park was originally shown to be correlated
106 with point-based fire frequency (Woinarski et al., 2010). However, Lawes et al. (2015) demonstrated

107 that spatial metrics of fire regimes are more strongly associated with mammal declines than point-based
108 fire frequency. To date, few studies have investigated the influence of satellite-derived measures of fire
109 severity, despite observations that cats show a much stronger attraction to areas burnt by high-severity
110 fires (McGregor et al., 2016a, McGregor et al., 2016b).

111 To estimate fire severity, we used data from the satellite-based Moderate Resolution Imaging
112 Spectroradiometer (MODIS) (Justice et al., 1998). Pre-processing, consisting of radiometric and
113 geometric calibration as well as atmosphere correction, was undertaken as described in Maier (2010).
114 Using a spectral un-mixing approach, we derived an estimate of the fraction burnt of each 250×250 m
115 pixel. We note that while this variable has been verified opportunistically on the ground, it has yet to
116 be rigorously and systematically validated with ground-based data from across northern Australian
117 savannas. In this study, we defined fires as high-severity when $>50\%$ of a pixel is burnt. Frequency of
118 high-severity fires was the number of times each 250×250 m grid cell was mapped as $>50\%$ burnt over
119 the five years preceding the fauna surveys. This value was averaged over a 3.2 km radius around each
120 site, as areal estimates are likely to provide better representations of the elements of the fire regime
121 most relevant to highly mobile animals, such as cats, than point based metrics (Lawes et al., 2015).

122 *Data analysis*

123 We used the statistical program R (R Development Core Team, 2013) to analyse two response variables.
124 The first was the number of days on which feral cats were detected at each site (henceforth called ‘feral
125 cat activity’). Once confirming there was no evidence of overdispersion or zero inflation in our data,
126 we analysed this response variable using generalised linear models with a Poisson error structure and
127 log link-function. We examined all combinations of the five explanatory variables outlined in Table 1,
128 with no interactions (32 models in total), and based model selection on Akaike’s Information Criterion
129 corrected for small sample size (AIC_c). Where no single model was clearly superior to other models
130 (i.e. multiple models with a $\Delta AIC_c < 2$), we used model averaging to obtain parameter estimates
131 (Burnham and Anderson, 2002).

132 <<<Insert Table 1 about here>>>

133 The second response variable we analysed was feral cat abundance. To analyse this response variable
134 we used Royle-Nichols abundance-induced heterogeneity models (Royle and Nichols, 2003) in the R
135 package ‘unmarked’ (Fiske and Chandler, 2011). We created a feral cat detection history for each site
136 by dividing the camera surveys into 24-hour sampling occasions. Cat detections were combined for all
137 cameras at each site. Again, we ran all combinations of the five variables hypothesised to influence the
138 abundance of feral cats. To account for potential effects of season and camera effort on feral cat
139 detectability, we included as detectability covariates the Julian day (i.e. day of year) on which that
140 survey commenced and the number of cameras operating at each site, each day. Where no single model
141 was clearly superior to other models (i.e. multiple models with a $\Delta AICc < 2$), we used model averaging
142 to obtain parameter estimates (Burnham and Anderson, 2002).

143 As correlates of feral cat activity and abundance, we compared the frequency of high-severity fires with
144 overall fire frequency (i.e. frequency of all fires, regardless of their severity), which is a much more
145 easily-derived, and commonly used, metric of fire activity in tropical savannas. To do this, we
146 investigated how the $AICc$ value of the best models changed in response to substituting frequency of
147 high-severity fires with overall fire frequency.

148 Prior to analyses, we centred and standardised all explanatory variables, and confirmed that there was
149 not excessive collinearity among them (Zuur et al., 2010).

150 **Results**

151 Feral cats were recorded at 26 out of the 88 sites (29.6%), on 39 separate sampling occasions. At sites
152 where feral cats were detected, the mean number of sampling occasions on which they were detected
153 was 1.5 (range = 1–4).

154 Inspection of the raw data suggested that two variables that were positively (albeit weakly) correlated
155 with feral cat activity: frequency of high-severity fires and feral herbivore activity (Fig. 2). Formal
156 modelling confirmed that the frequency of high-severity fires and herbivore activity were the only clear
157 correlates of feral cat activity. All well-supported models of feral cat activity (i.e. $\Delta AIC_c < 2$) contained
158 these two variables (Table 2a). There was a positive relationship between feral cat activity and the
159 frequency of high-severity fires (Fig. 3a; Fig. 4a), and feral herbivore activity (Fig. 3a; Fig. 4b).
160 Replacing frequency of high-severity fires with overall fire frequency increased the AIC_c of the best
161 model by 3.4, indicating that frequency of high-severity fires was clearly a better predictor of feral cat
162 activity than overall fire frequency.

163 There was a very similar pattern for the second response variable, feral cat abundance. The same two
164 variables were clearly identified as correlates: frequency of high-severity fires and feral herbivore
165 activity. Again, all well-supported models of feral cat abundance (i.e. $\Delta AIC_c < 2$) contained these two
166 variables (Table 2b). There was a positive relationship between feral cat activity and the frequency of
167 high-severity fires (Fig. 3b; Fig. 5b), and feral herbivore activity (Fig. 3b; Fig. 5b). Again, replacing
168 frequency of high-severity fires with overall fire frequency increased the AIC_c of the best fit model by
169 4.1, very substantially reducing the support for this model.

170 Feral cats were detected on four separate sampling occasions at only one site. To investigate whether
171 this site had a large influence on our conclusions, we repeated the analysis excluding this site. Excluding
172 the potentially influential observation (i.e. the site at which feral cats were detected on four sampling
173 occasions) did not markedly change the modelling results.

174 <<<Insert Table 2 about here>>>

175 <<<Insert Figure 2 about here>>>

176 <<<Insert Figure 3 about here>>>

177 <<<Insert Figure 4 about here>>>

178 <<<Insert Figure 5 about here>>>

179 **Discussion**

180 The rapid ongoing decline of small mammals in northern Australia is one of our most pressing
181 biodiversity conservation issues. While there is a growing body of evidence to suggest that feral cats
182 might play a central role in the mammal declines, we have a poor understanding of the factors that
183 influence the distribution, abundance and behaviour of feral cats, severely limiting our ability to
184 effectively mitigate their impacts on small mammals. We have demonstrated that on Melville Island –
185 a part of northern Australia that has retained a diverse assemblage of small mammals, yet has
186 experienced significant mammal declines in recent decades – high feral cat activity and abundance is
187 associated with frequent high-severity fires and high feral herbivore activity. This finding contributes
188 to the growing body of research suggesting that in northern Australian savanna landscapes, disturbances
189 such as high-severity fire and heavy grazing by feral herbivores may offer significant advantages to
190 feral cats.

191 While ours is the first study to demonstrate a positive association between feral cat activity and
192 abundance and a satellite-derived metric of fire severity, our findings strongly align with those of other
193 recent studies. For example, in the central Kimberley region of northwestern Australia, feral cats have
194 been shown to make large movements outside their normal home range to hunt in recently burnt areas,
195 especially areas that have experienced a high-severity fire (McGregor et al., 2016b). The selection of
196 recently burnt areas has also been demonstrated for feral cats on Cape York Peninsula, northeastern
197 Australia (McGregor et al., 2016a). Current evidence suggests that this behaviour reflects the short-
198 term, heightened hunting efficiency afforded to predators (especially feral cats) due to the removal of
199 ground layer vegetation in recently burnt areas (McGregor et al., 2015). Furthermore, while there is a
200 significant negative correlation between feral cat site-occupancy and vegetation density across the

201 Northern Territory, this effect is diminished in areas with high fire frequency over the preceding decade,
202 indicating that frequent fire might be especially important for the maintenance of feral cat populations
203 in areas with dense understorey vegetation, as it enables them access to prey which would otherwise be
204 less accessible (Stobo-Wilson et al. unpublished). Currently, we do not know whether this is
205 predominantly due to the consistent removal of ground-cover or a gradual, longer-term reduction in
206 understorey density and complexity (e.g. reduction in shrub biomass). Importantly, taken together, these
207 studies highlight how feral cats likely benefit from frequent fires, especially those of high severity.

208 We have also demonstrated a significant positive association between feral cat activity and abundance
209 and feral herbivore activity on Melville Island. Again, our results strongly align with other recent studies
210 from northern Australia. McGregor et al. (2014) demonstrated that GPS-tracked cats selected heavily-
211 grazed areas, most likely due to improved hunting success in such areas. The impacts of livestock
212 grazing on vegetation structure and composition have been well-studied across many habitats
213 (Dambach, 1944, Yates et al., 2000). Pastoral leases cover more than 70% of the Australian continent
214 (Martin and Possingham, 2005) and northern Australian savannas have been subject to high levels of
215 degradation due to high densities of introduced ungulates (Freeland, 1990, Kutt and Woinarski, 2007).
216 The impact of feral herbivore grazing on vegetation structure in northern Australian savannas is often
217 complex due to the interacting effects of fire, however cattle grazing in the absence of fire has been
218 shown to significantly reduce the cover of ground-layer vegetation (Kutt and Woinarski, 2007). As feral
219 cats in northern Australian savannas appear to prefer open areas in which to hunt (McGregor et al.,
220 2015, McGregor et al., 2016b), grazing by feral herbivores on Melville Island may benefit feral cat
221 hunting efficiency via changes to vegetation structure (Legge et al., 2011a, Legge et al., 2019).
222 Additionally, feral herbivores may create 'game trails' through thick grass, which facilitate movements
223 of feral cats.

224 Importantly, our analysis demonstrates that the frequency of high-severity fires is a much stronger
225 predictor of feral cat activity and abundance than overall fire frequency, a much more commonly used
226 and readily available metric of fire activity. Fire displays a very high level of spatial and temporal

227 variability in a range of attributes, including severity. As such, it is important to ensure that fire regimes
228 are characterised in a way that properly encompasses their potential impacts on biota. For example, as
229 fire severity increases, so too might the biotic impacts. In the past, correlational studies in northern
230 Australian using satellite-derived fire variables have attempted to capture this variation in fire severity
231 by grouping mapped fire scars into early dry season (those occurring before the 1st of August) and late
232 dry season (those occurring after the 31st of July) (Russell-Smith and Edwards, 2006). However, this
233 early/late dichotomy may be an oversimplification as relatively high-severity fires can occur in the early
234 dry season, just as low-severity fires can occur in the late dry season (Murphy and Russell-Smith, 2010,
235 Oliveira et al., 2015). As there is significant variation in a range of factors that influence fire behaviour
236 across landscapes (climate, rainfall, rockiness, vegetation etc.), this simple dichotomy may be more of
237 an issue in studies over large geographic areas. For example, due to the consistent formation of catabatic
238 storm clouds, Melville Island receives more dry-season rainfall than adjacent mainland areas of northern
239 Australia (Brocklehurst, 1998). Due to these climatic conditions, a fire occurring late in the dry season
240 may be of much lower severity, and therefore not directly comparable to a fire occurring at the same
241 time of year in an area that receives less dry-season rainfall. We again note that as our satellite-derived
242 metric of the frequency of high-severity fires has only been validated opportunistically, our results
243 should be interpreted with some caution. Nonetheless, this metric holds promise as a useful remotely-
244 sensed measure of fire impact and warrants further investigation and validation.

245 The decline of native mammals across northern Australian savannas is most likely the result of several
246 interacting factors. While we have presented evidence that suggests both severe fire and feral herbivores
247 could be benefiting feral cats on Melville Island, several important knowledge gaps remain. For
248 example, we do not know whether severe fires or feral herbivores offer the greatest potential benefits
249 to cats, or whether fire may benefit feral cats in the absence of feral herbivores, and vice versa. We note
250 that it is difficult for correlative studies, like ours, to resolve interacting threats, such as frequent high-
251 severity fires, feral herbivores and feral cats. These threats are almost ubiquitous across northern
252 Australia savannas, and therefore very difficult to tease apart. Importantly, some large offshore islands
253 remain free of feral herbivores and have low feral cat abundance, namely Groote Eylandt (J. Heiniger,

254 pers. comm.) and Bathurst Island (H. Davies, unpublished data), and we currently have no data relating
255 to native mammal population trajectories on those islands. Future research in such areas (where certain
256 threats are absent), coupled with manipulative experiments (e.g. involving fenced enclosures) could be
257 particularly informative. Such research will continue to develop our understanding of how native
258 mammals respond to different threats, under varying environmental conditions (i.e. across gradients of
259 feral herbivore density, fire severity and feral cat density). Doing so is a crucial step towards optimising
260 management strategies in different ecological settings.

261 Our results suggest that frequent severe fires and feral herbivores could be benefiting feral cat
262 populations on Melville Island. As in the Kimberley region of Western Australia (Legge et al., 2011a,
263 Legge et al., 2019), reducing both fire severity and the density of feral herbivores on Melville Island
264 could offer significant benefits to native mammal populations, potentially via negative flow-on effects
265 to feral cat populations. Importantly, both fire severity and the density of feral herbivores can feasibly
266 be manipulated through management actions; in contrast, the direct control of feral cats is notoriously
267 difficult and expensive, especially in the tropical savannas (Woinarski et al., 2019). The current
268 approach to fire management on Melville Island involves the application of low-severity prescribed
269 fires in the early dry season to reduce the extent of high-severity fires later in the dry season under more
270 severe fire-weather conditions. While the motivation for this is partly driven by the economic potential
271 of greenhouse gas abatement, it is plausible that this fire management could also disadvantage feral
272 cats, and therefore have significant positive effects on Melville Island mammal populations (Legge et
273 al., 2011b). Such fire management may be more effective when coupled with the removal of feral
274 herbivores (Legge et al., 2019). However, it is important to note that we currently have only a limited
275 understanding of how the density of feral cats translates into population-level impacts on native
276 mammals, and further research quantifying the magnitude this effect would help refine potential
277 management options.

278 As native mammal populations across northern Australian savannas continue to decline, there is an
279 urgent need to develop and implement effective management actions. Our findings suggest that

280 frequent, severe fires and grazing by feral herbivores may benefit feral cat populations on Melville
281 Island. These results highlight the potential of threatening process to interact to drive biodiversity
282 decline (Legge et al., 2019). A firm understanding of these interactions, and how they vary across
283 landscapes with different environmental conditions, is critical for ensuring management success.

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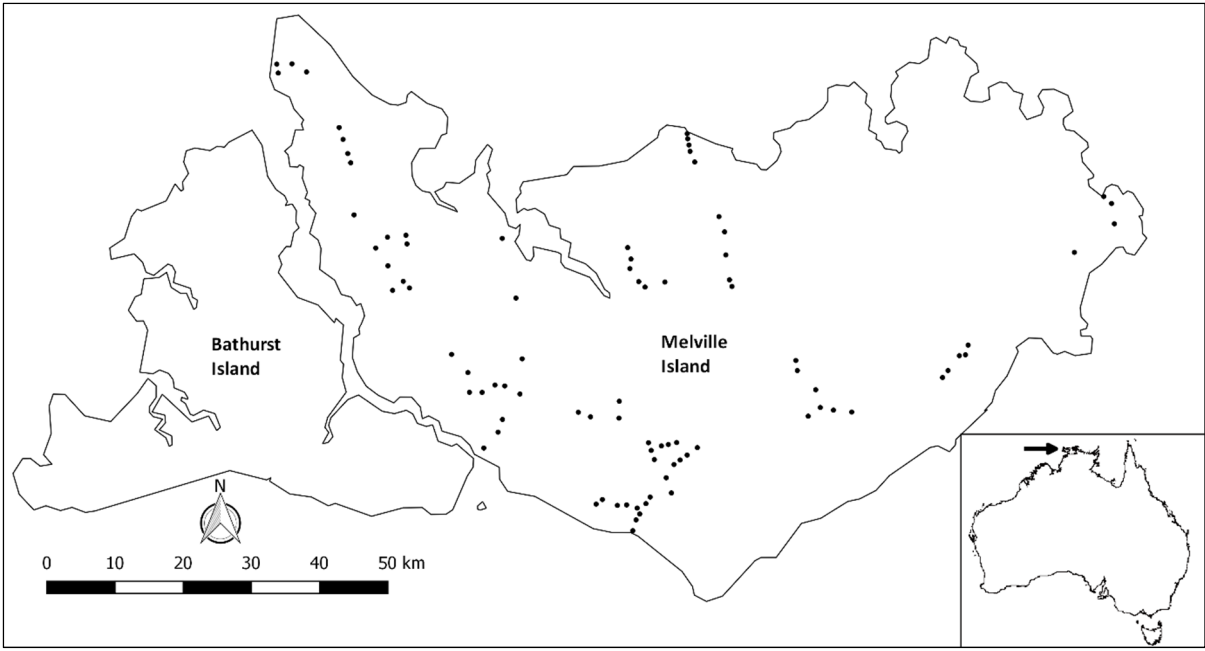
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413 Table 1: Description and justification of the variables used in analyses to investigate the correlates of
 414 feral cat activity and abundance on Melville Island.

<u>Explanatory variable</u>	<u>Description and justification for inclusion</u>	<u>Variable used in analyses to investigate:</u>
Rainfall (mm)	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., 2017) 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 • Feral cat abundance
Shrub density (100 m ⁻²)	The number of shrubs in a 1 × 100 m quadrat at each site. Shrubs were defined as anything taller than 20 cm but shorter than 1.3 m, or taller than 1.3 m 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 could influence the distribution of feral cats as well as the occupancy and detectability of small mammals (McGregor et al., 2015).	<ul style="list-style-type: none"> • Feral cat activity • Feral cat abundance
Dingo activity (%)	The percentage of days that dingoes 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 dingoes on feral cats and potential benefits for small mammal populations (Johnson, 2006, Kennedy et al., 2012).	<ul style="list-style-type: none"> • Feral cat activity • Feral cat abundance
Frequency of high-severity fires (fires year ⁻¹)	Number of times a 250 m x 250 m grid cell was mapped as >50% burnt over the five years preceding surveys. This value was averaged over a 3.2 km radius around each site as areal estimates are better representations of fire regimes than point based metrics	<ul style="list-style-type: none"> • Feral cat activity • Feral cat abundance
Overall fire frequency (fires year ⁻¹)	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 small mammal populations.	<ul style="list-style-type: none"> • Feral cat activity • Feral cat abundance
Herbivore activity (%)	The percentage of days on which feral herbivores were detected at each site. Feral herbivores were water buffalo (<i>Bubalus bubalis</i>) and horse (<i>Equus caballus</i>). Feral herbivores potentially influence small mammal populations via impacts on vegetation structure (Legge et al., 2011a).	<ul style="list-style-type: none"> • Feral cat activity • Feral cat abundance
Julian day	The day of the calendar year that sampling started at each site. Included to account for potential seasonal differences in detectability (Geyle et al., 2018).	<ul style="list-style-type: none"> • Feral cat 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"> • Feral cat detectability

416 Table 2: Well-supported models of (a) feral cat activity and (b) feral cat abundance. $\Delta AICc$ represents
 417 the difference between the model's $AICc$ value and that of the top-ranking model; K indicates the
 418 number of model parameters; w_i is the Akaike weight. Well-supported models ($\Delta AICc \leq 2$) are shown
 419 in bold. Only models with $\Delta AICc \leq 5$ are shown.

<u>Response</u>	<u>Model</u>	<u>$\Delta AICc$</u>	<u>K</u>	<u>w_i</u>
(a) Feral cat activity				
	~ Frequency of severe fires + Herbivore activity	0.0	3	0.30
	~ Shrub density + Frequency of severe fires + Herbivore activity	1.2	4	0.16
	~ Rainfall + Frequency of severe fires + Herbivore activity	2.0	4	0.11
	~ Dingo activity + Frequency of severe fires + Herbivore activity	2.2	4	0.10
	~ Rainfall + Shrub density + Frequency of severe fires + Herbivore activity	3.4	5	0.05
	~ Shrub density + Dingo activity + Frequency of severe fires + Herbivore activity	3.5	5	0.05
	~ Herbivore activity	4.0	2	0.04
	~ Rainfall + Dingo activity + Frequency of severe fires + Herbivore activity	4.2	5	0.04
	~ Frequency of severe fires	5.0	2	0.02
(b) Feral cat abundance				
	~ Rainfall + Frequency of severe fires + Herbivore activity	0.0	7	0.20
	~ Frequency of severe fires + Herbivore activity	0.5	6	0.16
	~ Rainfall + Shrub density + Frequency of severe fires + Herbivore activity	0.5	8	0.16
	~ Shrub density + Frequency of severe fires + Herbivore activity	1.7	7	0.09
	~ Rainfall + Dingo activity + Frequency of severe fires + Herbivore activity	1.9	8	0.08
	~ Rainfall + Shrub density + Dingo activity + Frequency of severe fires + Herbivore activity	2.3	9	0.06
	~ Dingo activity + Frequency of severe fires + Herbivore activity	2.4	7	0.06
	~ Shrub density + Dingo activity + Frequency of severe fires + Herbivore activity	3.6	8	0.03
	~ Frequency of severe fires	3.9	5	0.03



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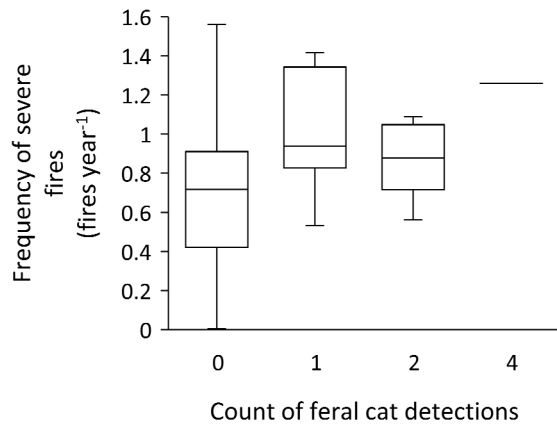
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423 Figure 1: The location of the 88 sites surveyed across Melville Island in 2015. The location of Melville

424 Island relative to mainland Australia is shown in the inset.

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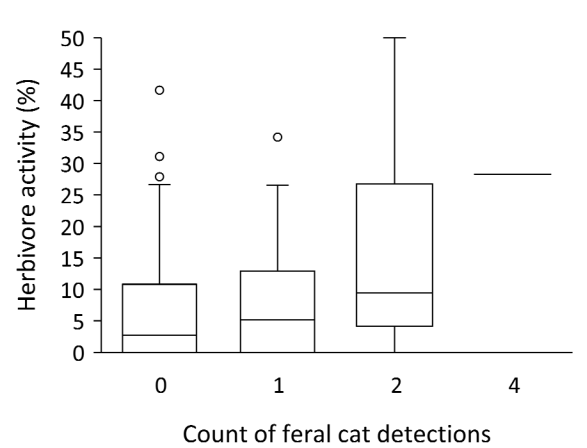
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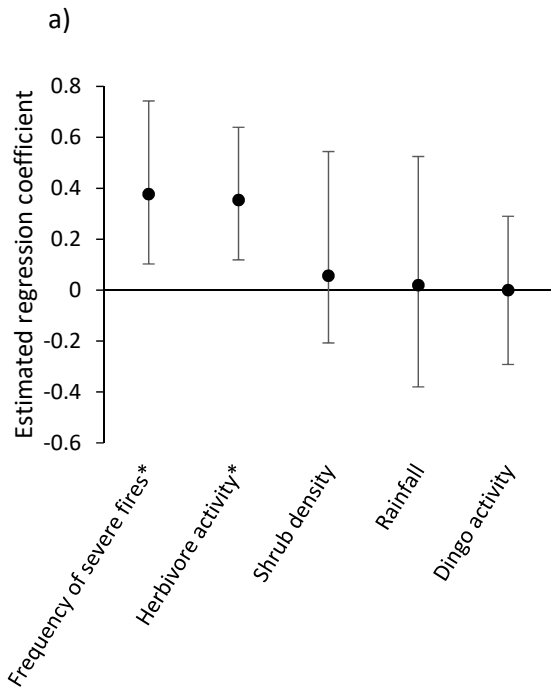
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428 Figure 2: 'Box and whisker' plots of the raw data, showing the positive relationship between: a) the
429 frequency of severe fires; and b) herbivore activity and the count of feral cat detections. The rectangular
430 'boxes' indicate the second and third quartiles, with the horizontal line indicating the median. The
431 whiskers indicate $\pm 1.5 \times$ interquartile range, and open circles indicate outliers.

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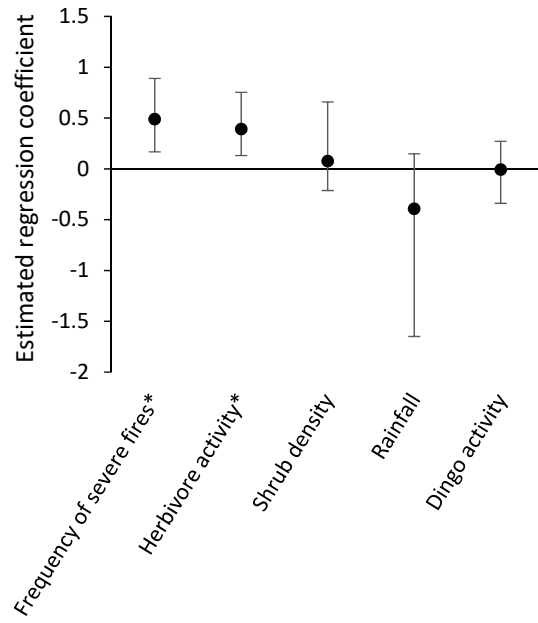
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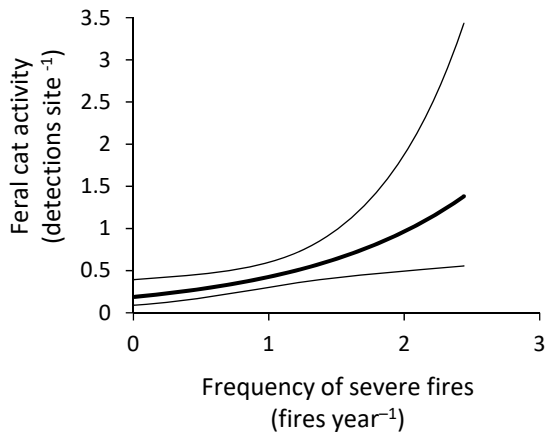
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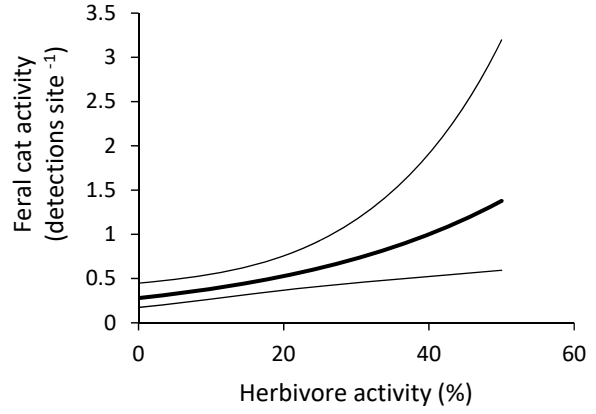
436 Figure 3: Model averaged regression coefficient estimates for: a) the number of sampling occasions on
437 which feral cats were detected; b) feral cat abundance. Error bars indicate 95% confidence intervals;
438 asterisks indicate where they do not overlap zero.

439

a)



b)



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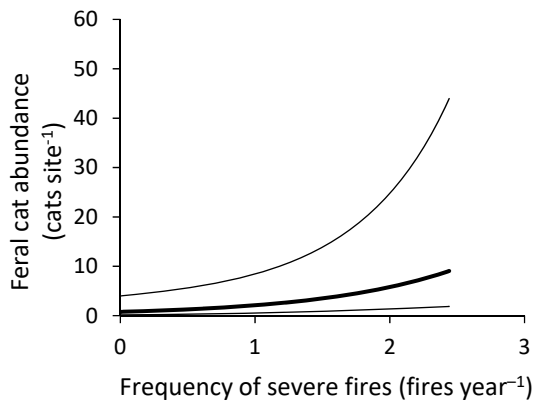
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442 Figure 4: Modelled relationship between feral cat activity and: a) the frequency of severe fires; and b)

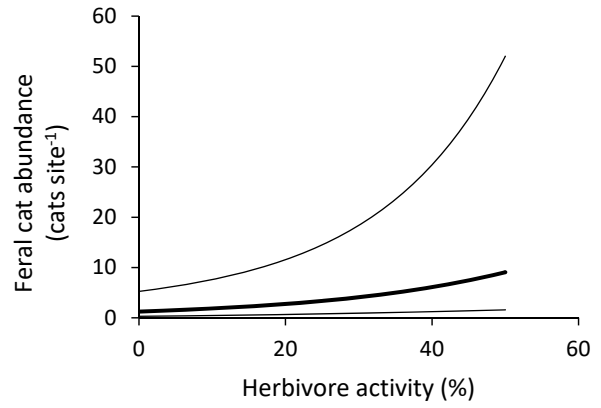
443 herbivore activity. Thin lines indicate 95% confidence intervals.

444

a)



b)



445

446

447 Figure 5: Modelled relationship between feral cat abundance and: a) the frequency of severe fires; and

448 b) herbivore activity. Thin lines indicate 95% confidence intervals.