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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

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

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

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

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

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

## **Methods**

### *Study site*

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

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

#### *Data collection*

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

<<< Insert Figure 1 about here>>>

#### *Frequency of high-severity fires*

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

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

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

#### *Data analysis*

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

<<<Insert Table 1 about here>>>

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

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

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

## Results

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



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

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

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

<<<Insert Table 2 about here>>>

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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

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

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

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

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

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

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

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

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

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

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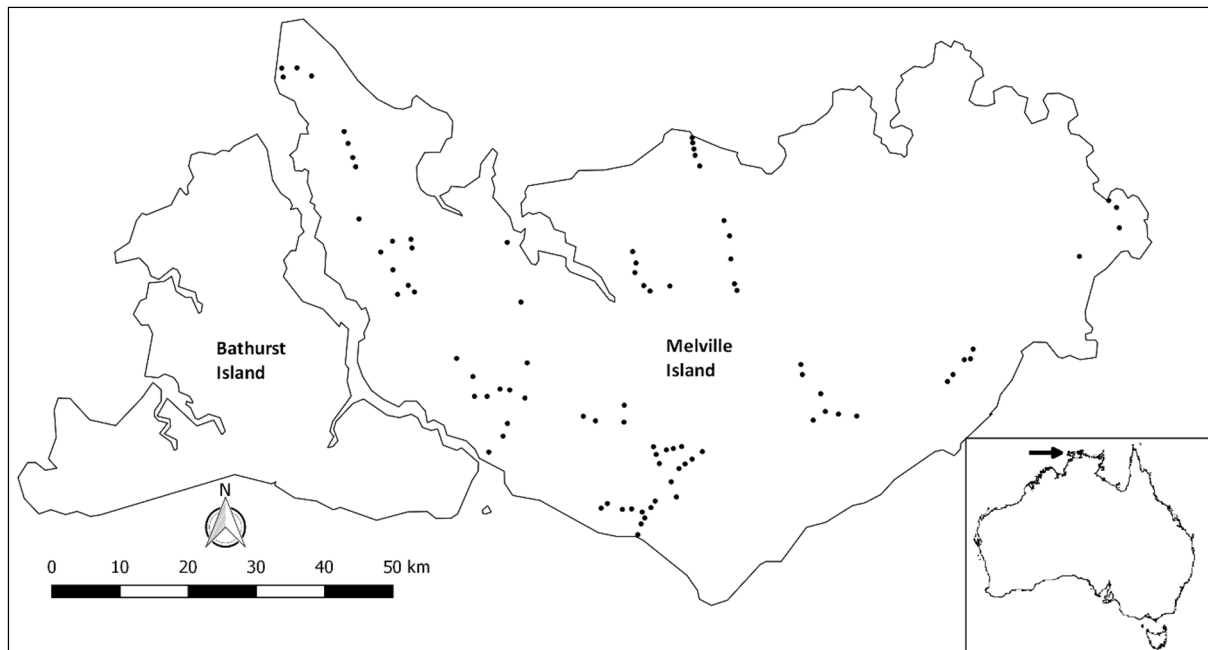
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413 Table 1: Description and justification of the variables used in analyses to investigate the correlates of  
 414 feral cat activity and abundance on Melville Island.

<b><u>Explanatory variable</u></b>	<b><u>Description and justification for inclusion</u></b>	<b><u>Variable used in analyses to investigate:</u></b>
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"> <li>• Feral cat activity</li> <li>• Feral cat abundance</li> </ul>
Shrub density (100 m <sup>-2</sup> )	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"> <li>• Feral cat activity</li> <li>• Feral cat abundance</li> </ul>
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"> <li>• Feral cat activity</li> <li>• Feral cat abundance</li> </ul>
Frequency of high-severity fires (fires year <sup>-1</sup> )	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"> <li>• Feral cat activity</li> <li>• Feral cat abundance</li> </ul>
Overall fire frequency (fires year <sup>-1</sup> )	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"> <li>• Feral cat activity</li> <li>• Feral cat abundance</li> </ul>
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"> <li>• Feral cat activity</li> <li>• Feral cat abundance</li> </ul>
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"> <li>• Feral cat detectability</li> </ul>
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"> <li>• Feral cat detectability</li> </ul>

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

<b>Response</b>	<b>Model</b>	<b><math>\Delta AIC_c</math></b>	<b><math>K</math></b>	<b><math>w_i</math></b>
(a) Feral cat activity				
	~ <b>Frequency of severe fires + Herbivore activity</b>	<b>0.0</b>	<b>3</b>	<b>0.30</b>
	~ <b>Shrub density + Frequency of severe fires + Herbivore activity</b>	<b>1.2</b>	<b>4</b>	<b>0.16</b>
	~ <b>Rainfall + Frequency of severe fires + Herbivore activity</b>	<b>2.0</b>	<b>4</b>	<b>0.11</b>
	~ 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				
	~ <b>Rainfall + Frequency of severe fires + Herbivore activity</b>	<b>0.0</b>	<b>7</b>	<b>0.20</b>
	~ <b>Frequency of severe fires + Herbivore activity</b>	<b>0.5</b>	<b>6</b>	<b>0.16</b>
	~ <b>Rainfall + Shrub density + Frequency of severe fires + Herbivore activity</b>	<b>0.5</b>	<b>8</b>	<b>0.16</b>
	~ <b>Shrub density + Frequency of severe fires + Herbivore activity</b>	<b>1.7</b>	<b>7</b>	<b>0.09</b>
	~ <b>Rainfall + Dingo activity + Frequency of severe fires + Herbivore activity</b>	<b>1.9</b>	<b>8</b>	<b>0.08</b>
	~ 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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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.

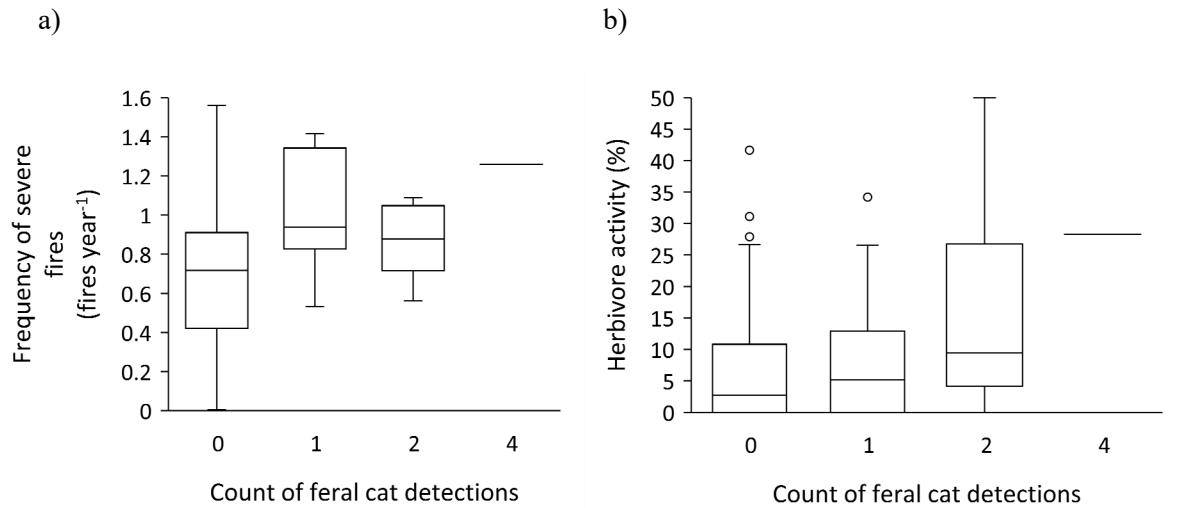


Figure 2: ‘Box and whisker’ plots of the raw data, showing the positive relationship between: a) the frequency of severe fires; and b) herbivore activity and the count of feral cat detections. The rectangular ‘boxes’ indicate the second and third quartiles, with the horizontal line indicating the median.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

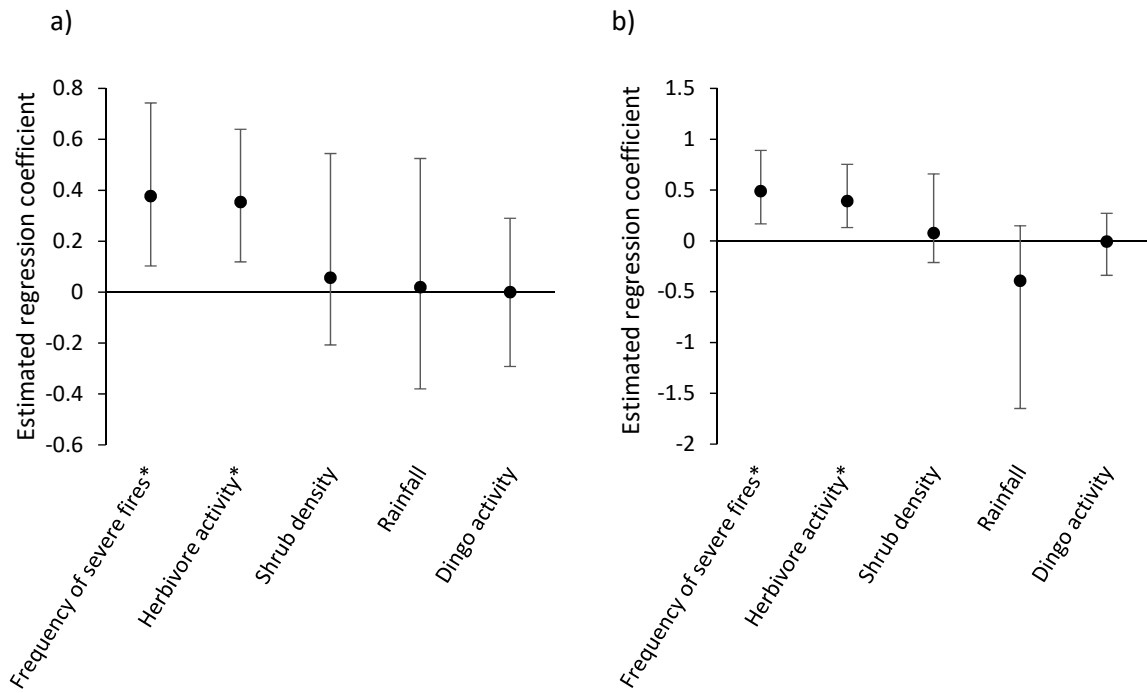
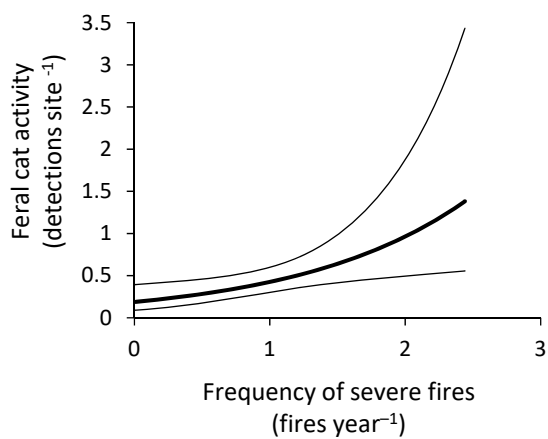


Figure 3: Model averaged regression coefficient estimates for: a) the number of sampling occasions on which feral cats were detected; b) feral cat abundance. Error bars indicate 95% confidence intervals; asterisks indicate where they do not overlap zero.

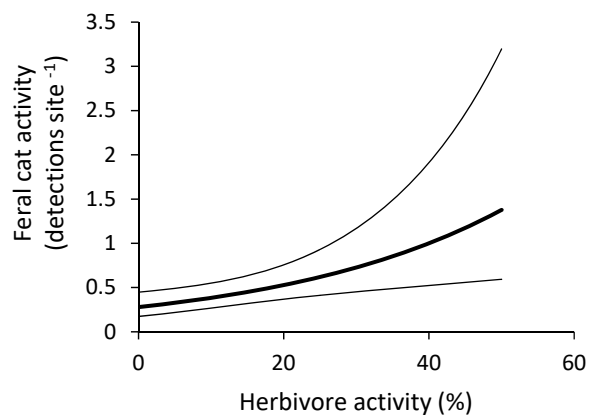
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a)



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b)



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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.

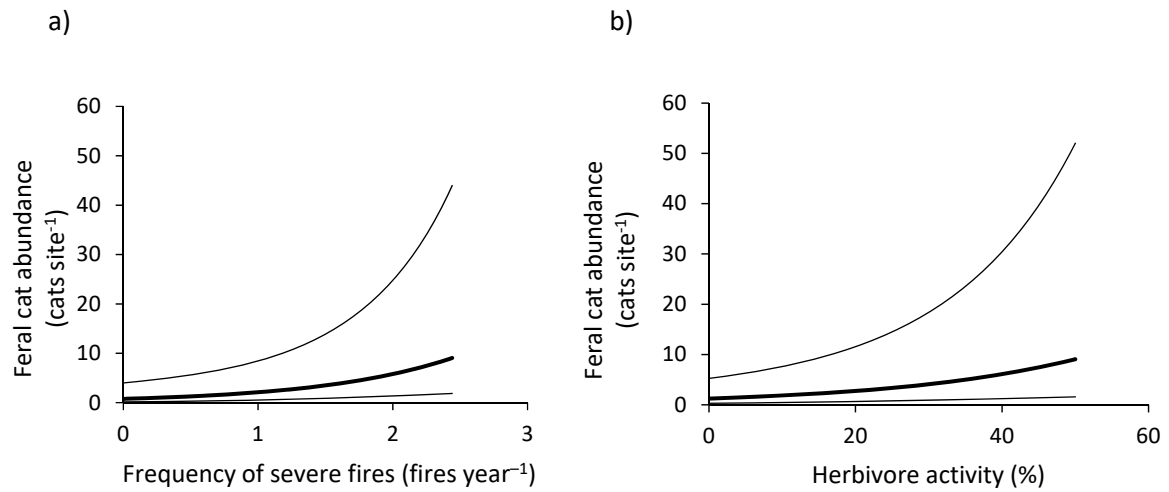


Figure 5: Modelled relationship between feral cat abundance and: a) the frequency of severe fires; and b) herbivore activity. Thin lines indicate 95% confidence intervals.