

Variation in feral cat density between two large adjacent islands in Australia's monsoon tropics

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Abstract. Despite contributing to the ongoing collapse of native mammal populations across northern Australian savannas, we have limited understanding of the ecological constraints of feral cat population density in this system. Addressing such knowledge gaps is a crucial step towards mitigating the impacts of feral cats, and is particularly important for the large islands off northern Australia that remain as strongholds for numerous species vulnerable to cat predation. Here, we investigated cat density across Melville and Bathurst Island, two large islands in Australia's monsoon tropics. We deployed large grids (~13 km²) of 70 camera-traps at four locations to investigate how feral cat density varies under different combinations of fire frequency, and feral herbivore presence. Using spatially-explicit capture-recapture models, we estimated feral cat density on Melville Island to be 0.15 cats km⁻². We did not record any cat detections on Bathurst Island. Using simulations, we predicted that if cat density on Bathurst Island was equal to that on Melville Island, we would have expected to record 27.9 detections of 9.9 individual cats. Our results, coupled with other recent surveys, suggest that the density of cats is much lower on Bathurst Island than the adjacent Melville Island. The absence of feral herbivores on Bathurst Island may have contributed to this variation in cat density. Management that enhances understorey vegetation density, through feral herbivore control, as well as fire management, could help mitigate the impact of feral cats on northern Australian savanna biodiversity.

Keywords: Bathurst Island, feral cat, fire management, grazing, herbivores, Melville Island, native mammals, northern Australia, population density.

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Introduction

Feral cats (*Felis catus*) have had a devastating impact on global biodiversity (Nogales *et al.* 2004; Medina *et al.* 2011). The significant impacts of feral cats are typified by the dire state of many native mammal species across Australia. Since their introduction following European arrival in 1788, feral cats have proliferated across the Australian mainland, Tasmania and most other large islands (Legge *et al.* 2017). Over this period, feral cats have been a primary contributor to Australia's extraordinarily high rate of mammal extinction (Woinarski *et al.* 2015), and directly caused the failure of numerous threatened species reintroduction programs (Hardman *et al.* 2016; Short 2016). Despite their impact on Australian biodiversity, there are limited options currently available for the broad-scale control of feral cats

(Legge *et al.* 2017). As a result, the ecological impacts of feral cats are continuing largely unabated.

The widespread and ongoing collapse of native mammal populations across the savanna landscapes of northern Australia remains a significant conservation issue (Woinarski *et al.* 2015). Given the similarities with previous mammal extinctions (Murphy and Davies 2014; Woinarski *et al.* 2015), it seems likely that if these declines continue unabated, more species will be lost forever. Although predation by feral cats has been implicated in these declines (Ziembicki *et al.* 2015), the movement, activity and impact of feral cats in northern Australian savannas is strongly influenced by fire and grazing by feral herbivores (Leahy *et al.* 2016; McGregor *et al.* 2015a, 2016b), and there is growing evidence that such processes are important

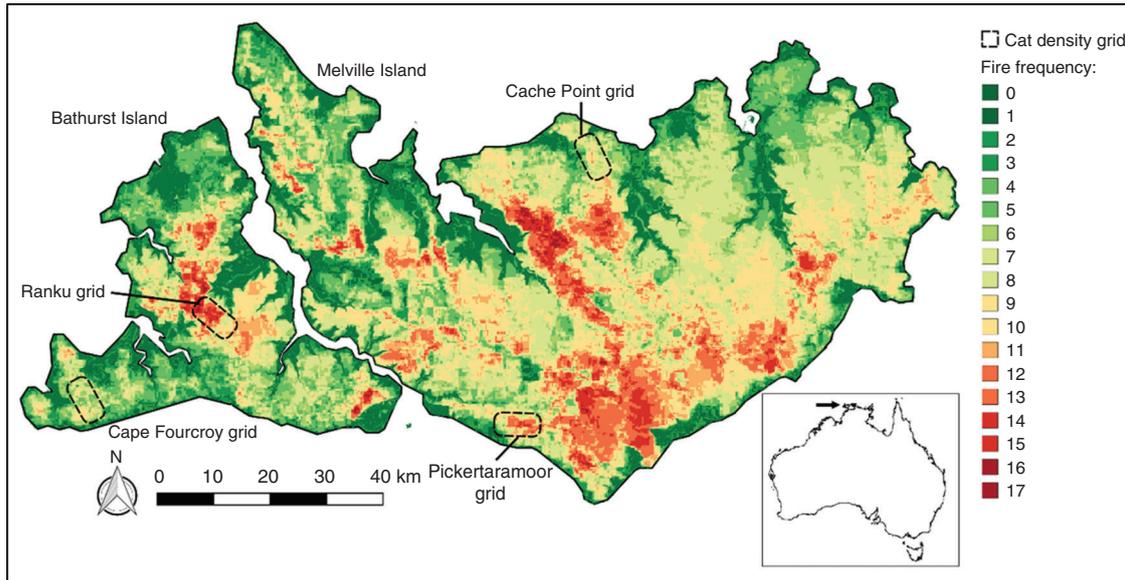


Fig. 1. The location of the four grids of camera-traps deployed to estimate the density of feral cats on the Tiwi Islands. The MODIS satellite-derived fire frequency across the Tiwi Islands (number of times burnt in the 17-year period 2000–2016, inclusive), and the location of the Tiwi Islands relative to mainland Australia are also shown.

drivers of spatial variation in feral cat occupancy (Stobo-Wilson *et al.* 2020) and density (Heiniger *et al.* 2020). This is thought to reflect the heightened predation efficiency afforded to predators by processes that reduce the density of understorey vegetation. However, despite the contribution of feral cats to the ongoing collapse of native mammal populations across northern Australian savanna landscapes, we have limited understanding of the ecological constraints of feral cat population density in this system (as well as across Australia more broadly). For example, while fire and grazing may be important drivers of feral cat populations, the relative influence of each of these factors is often difficult to disentangle from each other due to their near ubiquitous occurrence across northern Australian savannas. Addressing such knowledge gaps is a crucial step towards both understanding and mitigating the impacts of feral cats, and is therefore particularly important for the large islands off northern Australia that have remained as strongholds for many species vulnerable to cat predation.

The Tiwi Islands, located in the Australian monsoon tropics, remain a stronghold for numerous species that are vulnerable to predation by cats, and are one of the last remaining areas in Australia to support an intact native mammal assemblage. However, there are worrying initial signs of decline for the northern brown bandicoot (*Isodon macrourus*), black-footed tree-rat (*Mesembriomys gouldii*), and brush-tailed rabbit-rat (*Conilurus penicillatus*) (Davies *et al.* 2018), with evidence that cats have contributed to the decline of at least one species (brush-tailed rabbit-rat, Davies *et al.* 2017), as well as evidence that feral cat activity and abundance are higher in areas that have experienced frequent severe fires and heavy grazing by feral herbivores (Davies *et al.* 2020). Importantly, fire activity is spatially variable across both Melville and Bathurst Island (the two largest of the Tiwi Islands), and feral herbivores are only present on Melville Island. As such, these large adjacent islands,

provide a useful ‘natural experiment’ where we can investigate how feral cat density varies under different combinations of fire frequency, and feral herbivore presence. To increase our understanding of the ecological constraints of feral cat populations across northern Australian savannas, we aimed to obtain robust estimates of feral cat density from across Melville and Bathurst Island. We surveyed feral cats at four locations: one with high fire frequency with no feral herbivores, one with low fire frequency with no feral herbivores, one with high fire frequency with feral herbivores, and one with low fire frequency with feral herbivores.

Materials and methods

Study site

Our study was conducted on Melville (5786 km²) and Bathurst Island (2600 km²), Australia’s second and fifth largest islands, respectively. They are the two largest of the group of islands collectively known as the Tiwi Islands, located 20 km off the north coast of Australia’s Northern Territory (Fig. 1). The main vegetation type of the Tiwi Islands is lowland savanna dominated by *Eucalyptus miniata*, *Eucalyptus tetrodonta* and *Corymbia nesophila* with a predominantly grassy understorey. The islands experience a tropical monsoonal climate with a humid wet season (November–March) in which over 90% of the annual rainfall occurs, followed by a dry season (April–October). Fire frequency is high but there are significant gradients across the islands (Fig. 1). Feral cats are present on both islands. Feral herbivores (Asian water buffalo (*Bubalus bubalis*) and horse (*Equus caballus*)) are only present on Melville Island. Feral pigs (*Sus scrofa*) are widespread on Bathurst Island, but localised to the western half of Melville Island. Cane toads (*Rhinella marina*) are absent from both islands. Dingoes (*Canis familiaris*) are widespread across both islands. The introduced red fox

Table 1. Summary of the camera-trap survey data recorded at each of the four grids across the Tiwi Islands
Dashes indicate where grids are located outside of the current range of a particular feral species

	Pickertaramoor	Cache Point	Ranku	Cape Fourcroy
Island	Melville	Melville	Bathurst	Bathurst
Fire frequency	High	Low	High	Low
Other feral animals detected	Horse, buffalo	Buffalo	Pig	Pig
Feral herbivore nightly detections	214 (134 buffalo, 80 horse)	156 (all buffalo)	–	–
Dingo nightly detections	51	25	36	12
Pig nightly detections	–	–	1	23
Number of cameras	70	70	70	70
Survey duration (days)	62	61	61	64
Number of cat detections	21	5	0	0
Number of identifiable cat detections	18	3	0	0
Number of unidentifiable cat detections	3	2	0	0
Number of identifiable cats	7	3	0	0

(*Vulpes vulpes*) is absent from monsoonal northern Australia, including the Tiwi Islands.

Data collection

To estimate the density of feral cats, we deployed four grids of motion-activated cameras (camera-traps) across the Tiwi Islands: two on Melville Island (Pickertaramoor and Cache Point) and two on Bathurst Island (Ranku and Cape Fourcroy) (Fig. 1). Each camera-trap grid consisted of 14 rows of five camera stations (70 cameras in total) spaced between 400 and 600 m apart, covering an area of approximately 13 km². This configuration was chosen to increase the detection of cats by targeting natural edges of vegetation and trails. Grids were deployed for between 61 and 64 consecutive days with cameras operating continuously. We used a combination of Reconyx Hyperfire PC550 white-flash and PC850 infrared cameras (Reconyx, Holmen, WI, USA) programmed to take 10 immediately consecutive photographs per trigger, with no quiet period between triggers and sensitivity set to high. Alternating cameras on each grid were baited with a standard mammal bait of oats, peanut butter and honey.

The locations of the four camera-trap grids were chosen as they represent different combinations of fire frequency and feral herbivore presence, but are largely similar in vegetation type, weather, geology, soil and topography (Table 1). The Pickertaramoor and Ranku grids were characterised by high fire frequency, with the number of times burnt in the 17-year period from 2000 to 2016 inclusive, averaging 10.7 and 11.4, respectively. The Cache Point and Cape Fourcroy grids were placed in areas with lower fire frequency, with the number of times burnt in the 17-year period from 2000 to 2016 inclusive, averaging 7.9 and 6.7, respectively. The Pickertaramoor and Ranku grids were surveyed from July to September 2017, whereas the Cache Point and Cape Fourcroy grids were surveyed from August to October 2018.

Feral cats are generalist carnivores that eat a wide variety of prey (including mammals, birds, reptiles, frogs and invertebrates). Given there are no robust estimates of prey abundance at each plot, we do not have a firm understanding of how prey availability varies across our sites. However, we note that mammalian prey remains abundant across all four sites (H. Davies, unpubl. data).

Individual cat identification

Individual cats were identified by unique pelage markings by three independent observers. Discrepancies between observers were reviewed until a consensus was reached. Detections of cats which could not be identified to the individual level were omitted from the analysis.

Data analysis

As data limitations (zero cat detections on some grids) precluded a simultaneous analysis of our four grids, we explored the density of feral cats across Melville Island and Bathurst Island separately. First, we investigated feral cat density across the two grids on Melville Island. We fitted spatially-explicit capture-recapture models using the ‘secr’ package (Efford 2020b) in the statistical program R (R Development Core Team 2013), with capture histories collapsed in 24-h sampling occasions. Following McGregor *et al.* (2015b), we used a 3.5 km buffer around the outermost coordinates of the camera-trap grids. This buffer distance was based on the average maximum width of male feral cat home ranges estimated by GPS tracking in north-western Australia (McGregor *et al.* 2015b), and ensured that density was estimated over a large enough area to include the activity centres of all cats exposed to our survey (Royle *et al.* 2013). We restricted our buffers to exclude all uninhabitable areas (e.g. ocean, mangrove, swamps). Using a half-normal detection function, we fit a model where density differed between the two grids (Density ~ grid) and another where density was constant (Density ~ 1) on Melville Island. Model selection based on Akaike’s Information Criterion adjusted for small sample size (AIC_c) was used to identify the best fit model (Burnham and Anderson 2002), from which an estimate of feral cat density was obtained.

As cats were not recorded on either grid on Bathurst Island we could not directly estimate density for these two grids. Instead, we explored the density of feral cats on Bathurst Island in relation to Melville Island with a simulated scenario constructed using the ‘secrdesign’ package (Efford 2020a). These simulations predicted the average number of individual cats, and the total number of cat detections, we would have expected to observe on Bathurst Island if feral cat density was equal to that

Table 2. Summary of the models investigating feral cat density across Melville Island

k , number of parameters; AICc, Akaike's information criterion adjusted for small sample size; Δ AICc, difference between the AICc of this model and the model with the smallest AICc; w_i , Akaike weight. The estimated feral cat density from each model is also shown

Model	k	Δ AICc	w_i	Grid	Density (cats km ⁻²) (95% CI)
Density ~ 1	3	0.0	0.90	Both Melville grids	0.15 (0.07–0.34)
Density ~ grid	4	4.5	0.10	Pickertaramoor Cache Point	0.21 (0.08–0.51) 0.10 (0.03–0.32)

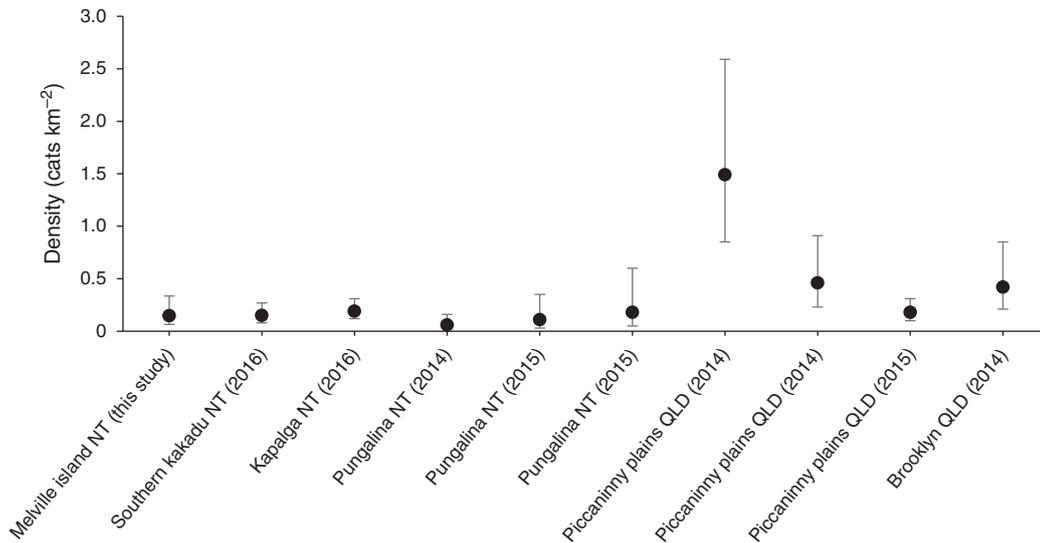


Fig. 2. The mean density of feral cats estimated for Melville Island compared with other spatially-explicit capture-recapture estimates of feral cat density from across northern Australia (Stokeld *et al.* 2016; McGregor *et al.* 2016a; Legge *et al.* 2017). Error bars indicate the 95% confidence interval.

estimated by the best-fit model of cat density on Melville Island. To do this we built a scenario with two detector grids of 70 camera-traps spaced 500 m apart (deployed in 14 rows of 5), deployed for 61 consecutive days, a buffer of 3.5 km, with the detection parameters (g_0 and σ) of the best-fit model of cat density on Melville Island. We replicated this scenario 1000 times. As the detection parameters (g_0 and σ) describe the rate at which detection probability changes with the distance from the centre of a cat's home range, and cat home range is influenced by density (Bengsen *et al.* 2016), these detection parameters are expected to be highly-specific to a particular estimate of cat density. Importantly, our simulations used the exact detection parameters derived for the specific cat density estimated on Melville Island.

Results

We recorded 26 detections of 10 individual cats on Melville Island, but did not detect any cats on Bathurst Island. Overall, the rate of feral cat detection was very low. From a total of 17 360 camera-trap nights, feral cats were detected at a rate of only 1 cat detection per 667 camera-trap nights. Of these cat detections on Melville Island, 21 (81%) were recorded on the Pickertaramoor grid, with the remaining five (19%) recorded at Cache Point (Table 1). Of the 21 cat detections at Pickertaramoor, there was a

total of 18 detections of seven individually identifiable cats. Of the cat detections at Cache Point, there were three individually identifiable cats that were each only recorded once. As the remaining five cat detections involved only a partial view of a cat, they were classified as unidentifiable and removed from the analyses.

There was no statistically significant difference in feral cat density between the two grids on Melville Island (Table 2). The density estimate from the most parsimonious model was 0.15 cats km⁻² (95% CI 0.07–0.34) (Fig. 2). The size of our buffer was sufficient for an unbiased density estimate. The session-specific model indicated that feral cat density at Pickertaramoor (0.21 cats km⁻²) was more than double that of Cache Point (0.09 cats km⁻²), however confidence intervals overlapped substantially (Table 2). Given our survey design and effort on Bathurst Island, our simulations predicted that if cat density was equal to that estimated by the best-fit model on Melville Island (i.e. 0.15 cats km⁻²) we would have observed on average 27.9 detections (95% CI 27.2–28.6) of 9.9 individual cats (95% CI 9.7–10.1).

Discussion

Our study provides the first robust estimate of feral cat population density from the largest island off the northern Australian coast, Melville Island. Our estimate of feral cat density for

Melville Island ($0.15 \text{ cats km}^{-2}$) is comparable to estimates from mainland northern Australia. However, although cats are known to be present, and despite comparable survey effort, we recorded zero cat detections on Bathurst Island. Our simulations predicted that if cat density on Bathurst Island was equal to that on Melville Island, we would have observed on average 27.9 detections of 9.9 individual cats. Our results suggest that the density of cats is much lower on Bathurst Island than the adjacent Melville Island. This variation in cat density provides valuable insight into the ecological constraints of feral cat populations across northern Australian savannas, with important implications for mitigating the impacts of feral cats on savanna biodiversity.

The observed difference in cat populations between Melville and Bathurst Island may be driven by detectability rather than density. However, recent camera-trap surveys conducted across these islands do not support this explanation. For example, there has been zero feral cat detections from around 12 600 camera-trap nights conducted on Bathurst Island since 2014; this is despite stray cats being present in and around the community of Wurrumiyanga (Kennedy *et al.* 2018) and feral cats being occasionally sighted away from communities (C. Kerinauia, pers. comm.). By comparison, there have been 65 recent detections of feral cats on Melville Island from 24 010 camera-trap nights ($0.27 \text{ cats per } 100 \text{ camera-trap nights}$) (Davies *et al.* 2020). As such, the detection rate of feral cats has been more than 30 times higher on Melville Island compared with the adjacent Bathurst Island (i.e. $65/24\,010$ vs $<1/12\,600$). The magnitude of the difference in cat detection rates between these islands is difficult to reconcile due solely to variation in feral cat behaviour. Although cat activity patterns and movement could indeed vary between these islands, the most plausible explanation, is that cat density is much lower on Bathurst Island compared with Melville Island. This explanation is also supported by the predictions of our simulations; however, we acknowledge that there remains some uncertainty around how feral cat detection parameters and densities vary across these islands.

In northern Australian savannas, feral cat site-occupancy is higher in areas with lower understorey vegetation density (Stobo-Wilson *et al.* 2020). As such, productivity-driven variation in vegetation density across the islands could have contributed to the observed variation in cat density. If this were the case, we would expect both Bathurst Island grids to have higher vegetation density than the grids on Melville Island. Unfortunately, we do not have ground-based data with which to compare the density of understorey vegetation across our four grids. However, a remote-sensed measured response of habitat productivity, that correlates with the density of green vegetation (Pickett-Heaps *et al.* 2014; Stobo-Wilson *et al.* 2020), does not support this. Instead, it suggests that the average vegetation density across the Ranku grid is more comparable with that of the Pickertaramoor grid, while the vegetation density at Cache Point is comparable to that of the Cape Fourcroy grid (H. Davies, unpubl. data). As the density of understorey vegetation varies between habitat types, the presence and extent of other habitat types in proximity to each of our grids may also have contributed to the observed variation in cat density between Melville and Bathurst Island. The proximity of the Pickertaramoor grid to

habitat with an open understorey such as plantations of *Acacia mangium* and *Pinus caribaea*, as well as stands of native *Callitris intratropica*, may indicate that the area surrounding this grid may simply be a more favourable habitat for feral cats than the other surveyed areas. However, we note that the Ranku grid was similarly placed near habitat with an open understorey, including plantations of *Acacia mangium* and treeless plain. Although vegetation density influences feral cat movement, activity and occupancy in northern Australian savannas (McGregor *et al.* 2014; Stobo-Wilson *et al.* 2020), the extent to which natural variation in vegetation density (due to productivity and/or between habitat types) influences feral cat density warrants further investigation.

Processes that influence the density of understorey vegetation could also have contributed to the observed variation in feral cat density between these islands (McGregor *et al.* 2014). High fire activity and grazing by feral herbivores, are important predictors of feral cat occupancy across northern Australian savannas, especially in areas of high productivity (Stobo-Wilson *et al.* 2020). This is thought to reflect the heightened prey accessibility afforded to feral cats due to the simplification of vegetation associated with fire and grazing. Importantly, due to their preference to graze on the palatable, nutrient-rich regenerating vegetation following fire, feral herbivores may enhance the benefits afforded to feral cats by fire, by extending the amount of time the vegetation remains in an open, suppressed state (McGregor *et al.* 2014; Legge *et al.* 2019; Davies *et al.* 2020). The hypothesis that feral cat populations are strongly influenced by the interaction between fire activity and grazing is supported by our observation of highest feral cat density at the Pickertaramoor grid, characterised by both high fire frequency and the highest activity of feral herbivores (buffalo and horse). McGregor *et al.* (2015b) found no evidence that grazing by feral herbivores influenced feral cat density in the central Kimberley, but our results align with those of Stobo-Wilson *et al.* (2020), who showed that factors that simplify understorey vegetation density become increasingly important predictors of feral cat occurrence in areas of high productivity such as the Tiwi Islands.

Recent research from another of northern Australia's largest and most important strongholds for native mammals, Groote Eylandt, demonstrated that the density of feral cats is likely far lower than on the northern Australian mainland (Heiniger *et al.* 2020). They hypothesised this was due to 'top-down' pressure from a healthy assemblage of native predators, as well as 'bottom-up' constraints of feral cat hunting success due to a relatively benign fire regime and absence of feral herbivores (Heiniger *et al.* 2020). Heiniger *et al.* (2020) attributed the healthy assemblage of native predators on Groote Eylandt to the abundant prey, the absence of cane toads, and absence of dingo population control. For these same reasons, both Melville and Bathurst Islands support healthy assemblages of native predators (e.g. dingoes, pythons, goannas and birds of prey). As such, the apparent variation in feral cat density between Bathurst and Melville Island better aligns with the 'bottom-up' hypothesis of Heiniger *et al.* (2020); that landscape modification by feral herbivores is a key contributing factor in determining feral cat population density on these islands. The 'game-trails' that are created by feral herbivores through thick vegetation may create an ideal edge habitat that affords feral cats significantly

improved hunting conditions (Doherty *et al.* 2015). Importantly, as these game trails occur year-round, they could maintain hunting areas that are more seasonally-reliable for feral cats, compared with the favourable hunting conditions created by fire, which predominantly occurs in the dry season (April–October).

Our results concur with recent research that suggests feral cats are particularly reliant on processes that simplify vegetation structure in productive areas of northern Australia (Davies *et al.* 2020; Stobo-Wilson *et al.* 2020). As such, the effective management of these processes could prove particularly effective at mitigating the impact of feral cats on native biodiversity. The concurrent management of fire and feral herbivores has proved beneficial to native mammal populations in north-western Australia (Legge *et al.* 2019), and is a feasible management option for Melville Island. However, as buffalo and horse both hold an important place in Tiwi culture, support for their eradication is unlikely. Instead, the development of management objectives and actions in direct consultation with Tiwi traditional owners, is critical to ensure management is both effective and culturally appropriate.

The density of mesopredators is driven by a complex interplay of ‘top-down’ and ‘bottom-up’ factors (Ritchie and Johnson 2009). As such, the density of feral cats on the Tiwi Islands, and across Australia more broadly, is a result of multiple, interacting factors. As our study was conducted at only four locations, further research is needed to better understand the ecological constraints of feral cat populations across northern Australian savannas. The low density of feral cats in areas that continue to support healthy populations of species vulnerable to cat predation (such as Groote Eylandt and Bathurst Island) suggests that the density of feral cats in northern Australian savannas is not predominantly driven by the abundance of prey. Unfortunately, we have limited robust data on the abundance of feral cat prey across our four sites. However, we note that compared with other areas of northern Australia, small native mammals (i.e. a preferred prey type of feral cats) remain abundant across our four sites (H. Davies, unpubl. data). This may suggest that feral cat population density on the Tiwi Islands is more strongly influenced by prey accessibility rather than prey abundance. Although McGregor *et al.* (2015a) demonstrated that feral cat hunting success in areas with an open microhabitat was four times higher than in areas with a complex microhabitat, the extent to which such variation in prey accessibility influences feral cat populations remains to be tested.

We suggest future research aims to better understand the drivers of prey accessibility, and the implications for feral cat populations. This could be achieved by the concurrent monitoring of feral cat and prey populations in an experimental framework of fire and feral herbivore control/exclusion. Such research should also aim to understand the benefits afforded to feral cat populations by enhanced prey accessibility in the context of the ‘top-down’ predation pressure imposed on feral cat populations by native predators. It is important to note that there are a number of other hypothesised factors that could have contributed to our results that we could not interrogate, such as the level of predation imposed on feral cat populations by native predators, disease and parasites, and the availability of feral cat denning sites. We also have limited understanding of temporal trends of feral cat population density. Future work investigating

the constraints of feral cat population density in tropical savannas should strive to elucidate these factors.

The three largest islands off northern Australia (Bathurst Island, Melville Island and Groote Eylandt) have all remained as strongholds for many species that are vulnerable to feral cat predation. Compared with both Melville Island and areas of mainland northern Australia, feral cat density appears to be particularly low on Groote Eylandt (Heiniger *et al.* 2020) and Bathurst Island. This may be related to the absence of feral herbivores from both of these islands, though further research is needed to test this hypothesis. Due to their large size, cat eradication is currently not a feasible option for any of these islands. However, there is growing evidence that enhancing understorey vegetation density, through the concurrent management of fire and feral herbivores, could help mitigate the impact of feral cats on northern Australian savanna biodiversity.

Conflicts of interest

The authors declare no conflicts of interest.

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