Title

What do predator diets tell us about mammal declines in Kakadu National Park?

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Abstract

Context.

Small and medium-sized native mammals have suffered severe declines in much of northern Australia, including within protected areas such as Kakadu National Park. Several factors have been implicated in these declines but predation, particularly by feral cats *Felis catus*, has been identified as potentially the most direct cause of decline for many species.

Aims.

We evaluated how prey frequency changed in cat and dingo scats in Kakadu from the early 1980s to 2013-15, with this period spanning a severe decline in the small- and medium-sized mammal fauna.

Methods.

Chi-squared test of independence and Fisher's exact test were used to compare prey frequencies between dingoes and cats, and among years to assess significance of temporal change.

Key Results.

Small-sized native mammals were the prey item occurring at the highest frequency in scats for both dingoes and cats in the 1980s. Prey content in dingo and cats scats differed in the 2010s with macropods predominating in the scats of dingoes, and medium-sized native mammals predominating in cat scats. The frequency of occurrence of small-sized native mammals declined in both dingo and cat scats between the 1980s and 2010 sampling periods, while the frequency of occurrence of medium-sized native mammals remained constant in dingo scats and increased in cat scats.

Conclusions.

Small mammals were a major component of the diets of both dingoes and cats at Kapalga in the 1980s, when small mammals were much more abundant. Despite marked reduction from the 1980s to the 2010s in the capture rates of both small- and medium-sized native mammals, some species continue to persist in the diets of cats and dingoes at disproportionally high frequencies. Both predators continue to exert predatory pressure on mammal populations that have already experienced substantial declines.

Implications.

Although predation by feral cats is a major threat to small- and medium-sized native mammals, dingoes may also play an important role in limiting their recovery. Disturbance from fire and grazing by introduced herbivores have been shown to augment predatory impacts of feral cats on native

mammals. Predation more generally, not just by feral cats, may be exacerbated by these disturbance processes. Management programs that solely focus on mitigating the impact of feral cats to benefit threatened species may be inadequate in landscapes with other significant disturbance regimes and populations of predators.

Introduction

The small- to medium-sized mammal fauna of northern Australia has undergone widespread catastrophic decline over the past ca. 20-30 years (Woinarski *et al.* 2014). Unlike declines in southern Australia where large-scale habitat loss and predation by the introduced red fox (*Vulpes vulpes*) have been key drivers (Fisher *et al.* 2003; Johnson and Isaac 2009), declines of native mammals in northern Australia have occurred where foxes are absent and in areas with extensive intact native vegetation, including large protected areas such as Kakadu National Park and adjacent Indigenous Protected Areas. The declines are most likely the consequence of complex interactions occurring between several factors, including predation, fire, introduced livestock and poisoning by cane toads (Ziembicki *et al.* 2015). Resolving uncertainty in the relative importance of these factors, their interactions with each other and their environmental context is critical for the development of targeted and effective management responses.

Predation by feral cats (*Felis catus*) has been identified as the most likely primary proximal cause of northern Australian mammal declines (Woinarski *et al.* 2015). The predatory impact of cats may have been exacerbated across northern Australia in recent decades by inappropriate fire regimes and habitat degradation caused by livestock, which reduce ground cover (McGregor *et al.* 2014; Leahy *et al.* 2016). However, cats are not the only predator in this system and a diversity of native species prey on small- and medium-sized mammals in northern Australia, including dingoes (*Canis familiaris*) (Corbett 1989) and raptors (Corbett *et al.* 2014). Recent ecological changes that may have increased vulnerability of mammals to predation by feral cats may have similarly promoted vulnerability to predators more generally.

There is ongoing debate regarding the role of dingoes in the conservation of Australian wildlife. While some authors propose that dingoes have a positive effect on threatened mammals by suppressing the predatory impacts of mesopredators (Brook *et al.* 2012; Johnson and Ritchie 2013), others advocate that the direct impacts of predation by dingoes are a threat to some native mammals (Allen *et al.* 2012). Two studies in northern Australian savanna demonstrated predation of small- and medium-sized native mammals by dingoes (Corbett 1989; Oakwood 2000), and other studies in Australia have found similar results (Paltridge 2002; Pavey *et al.* 2008; Allen *et al.* 2012). Dingoes have a flexible feeding strategy, and prey composition is variable depending on prey availability, habitat and their social organisation (Corbett and Newsome 1987).

Many studies have concurrently compared the diets of cats and dingoes in the same landscape during the same time period (Paltridge 2002; Pavey *et al.* 2008; Glen *et al.* 2011; Spencer *et al.* 2014;

Doherty 2015), but there are none that have evaluated temporal shifts in predator diets in relation to decadal-scale directional changes in native mammal populations. Given the severe depletion of components of the native mammal fauna over a ca. three decade period in Kakadu National Park, we evaluated how dingo and feral cat diets responded to this marked change in prey availability, and assessed whether predation may still be exerting some pressure on this declining mammal fauna.

We predicted that the frequency of small- and medium-sized mammal prey in predator scats would vary as a function of changes in prey availability, as measured by mammal trapping capture rates. We also predicted that dingo prey composition would be dominated by larger mammals whereas feral cat prey composition would be dominated by smaller mammals, as observed in comparable studies elsewhere (Corbett 2001; Doherty *et al.* 2015). We seek to use the results from these comparisons to draw implications for enhancing the management of declining and threatened mammals in this region.

Methods

Study area

The study was conducted in Kapalga, in the northern part of Kakadu National Park, Northern Territory (Fig. 1). The study area (12˚38.97'S, 132˚22.47'E) encompassed approximately 200 km^2 in lowland open forest dominated by *Eucalyptus miniata* and *E. tetrodonta* on flat topography, bounded to the east and the west by seasonally inundated floodplains.

Kakadu is situated in a region with high fire frequency. Approximately 50% of the lowlands burns annually with an average 3-year fire return interval within patches (Russell-Smith *et al.* 2017). Since the 1980s there has been a substantial increase in the extent of floodplain and lowland rainforest that burn annually (Russell-Smith *et al.* 2017). In addition, feral water buffalo (*Bubalis bubalis*) occur throughout Kakadu and have impacted ground-cover vegetation abundance and composition (Petty *et al.* 2007).

Mammal trapping data

Sampling of small- and medium-sized mammals commenced in the Kapalga region of Kakadu National Park in 1980-1982 (Braithwaite and Muller 1997a), and subsequent sampling provided some of the earliest indications of northern Australian mammal decline (Woinarski *et al.* 2010). An extensive dingo diet analysis was undertaken concurrent with the initial mammal studies in the early 1980s (Corbett 1989).

We report historical trapping data on small- and medium sized-mammals from Kapalga for 1980-1983 (Friend and Taylor 1985; Friend and Dudzinski 1988) (broadly equivalent to the initial predator scat sampling by Corbett), 1985-1987 and 1989-1995 (Braithwaite and Muller 1997b), 1999 (Woinarski et al. 2001), and 2002, 2008, 2013-2015 (NT Department of Environment and Natural Rsources, unpubl. data). All projects utilised comparable trapping techniques but varied in the ratio of wire cage traps to Elliott traps, grid configuration and sampling effort (see cited publications for specific methodologies). For this reason, we standardised each year of trapping for each mammal species, or species groups, as the mean number of captures per 100 trap-nights (trap success). Friend and Taylor (1985) and Friend and Dudzinski (1988) reported capture rates across sampling years for the 1980 to 1983 time period; thus we present a mean trap success for the three year sampling period. No relative abundance values were available for larger mammals (e.g. macropods), or for many other prey types (reptiles, most birds).

Diet analyses

Historical information on dingo and cat diet, from scat analysis, was sourced from Corbett (2001). Corbett (2001) does not describe the methods or provide details on the location of the study area within Kapalga; however such information is presented in Corbett (1995). Over the period 1980-1986, Corbett sampled for scats along 55 0.5-km road transects in Kapalga each month (Corbett 1995). For prey types that Corbett reported as occurring in < 0.1% of the scats, we assigned a value of 0.05% for the purpose of grouping prey into size categories. Corbett's publications do not report cat diet data to species, thus limiting comparisons to grouped data. Furthermore, Corbett classified native animals weighing from 500 g to 15 kg as medium-sized mammals, which included agile wallaby (*Notamacropus agilis*; mean adult body weight = 15 kg) and dingo (mean = 14 kg). Although cats do consume some large-bodied prey (Fancourt 2015), they are unlikely to be able to kill adult agile wallabies or dingoes, and we assume here that any such material in cat scats came from carrion.

In the present study, surveys to collect predator scats were undertaken on five occasions across three seasons from July 2014 to November 2015, providing a seasonal spread comparable with historical data. On each survey, 42 km of vehicle tracks, corresponding to those used by Corbett (Corbett 1995), were walked in Kapalga looking for scats of dingoes and cats. We suspect canids in the study area probably contain a mix of dingoes, feral dog and their hybrids (Stephens *et al.* 2015); herein we refer to the population in the Kapalga area collectively as dingoes. Each scat located was collected in a paper bag labelled with location coordinates and collection date. Scats were sun-dried and sent to one author (B. Triggs), an experienced analyst in the identification of prey from morphometric features of hair, bone and teeth (Brunner and Wallis 1986). Scat content results were reported at the genus level where there was ambiguity over positive species-level identification, or classified and clustered by taxonomic group.

We categorised native mammal species as small, medium or large, by taking the mean of the adult body weight range published in Van Dyck *et al.* (2013). Species with adult body mass < 500 g were classified as small mammals; those weighing from 500 g to 5500 g were classified as medium. All small- and medium-sized mammals in the study area (other than cat) were native, with no rabbits or exotic rodents known to occur in the area. Corbett classified native animals weighing from 500 g to 15 kg as medium-sized mammals, therefore we categorised our cat diet data in the same manner for this comparison only.

Frequency of occurrence (FO), defined as the proportion of scats containing a particular prey species or prey group, was used to assess the incidence of prey items in the diets of dingoes and cats. Although frequency methods provide no reliable conclusions about the importance of prey categories, they can be useful for understanding carnivores' roles as specialists or generalists and provide a useful and consistent measure for comparison between studies (Klare et al. 2011).

We compared contemporary prey frequencies in dingo scats with those reported historically by Corbett (2001). A Pearson's Chi-squared test of independence was undertaken to assess whether the observed frequency of prey groups in dingo scats differed between studies. Prey species were grouped as follows: feral herbivores, large native mammals, medium-sized native mammals, small-sized native mammals, and birds. Reptile and invertebrate prey items, which collectively made up < 3% frequency within scats, were excluded from the comparison. Standardised residuals were calculated to show where departures from expected values occurred (standardised residuals > 3 show lack of fit under the null hypothesis of no difference).

To test our hypothesis that dingo prey composition would be dominated by large mammals whereas feral cat prey composition would be dominated by small mammals, Fisher's exact test (for count data) was used to compare the frequency of contemporary prey items in feral cat scats and dingo scats, and p-values computed by Monte Carlo simulation. Due to low expected values for some prey species, prey items were pooled into three groups: large mammals (including feral herbivores), medium/small native mammals, and other prey items which included bird, reptile and invertebrate. A similar approach was undertaken to compare prey frequencies in cat scats between the current study and (Corbett 2001). For this comparison, data were pooled into the following three groups: medium-sized native mammals, small-sized native mammals and other prey which included bird, reptile, and invertebrate.

To compare similarity between the diets of dingoes and cats in the present study, we calculated dietary overlap (DO) at the species level (or higher taxonomic categories for prey types other than mammals) using Pianka's index (Pianka 1973):

$$DO = \sum P_{ij} P_{ik} \ / \sqrt{\sum P_{ij}^2 \sum P_{ik}^2} \ ,$$

where P_{ij} is the proportion of prey species *i* in the diet of predator *j* and P_{ik} is the proportion of prey species *i* in the diet of predator *k*. Pianka's coefficient was estimated using 1000 bootstraps and the 95 % CI computed on the empirical percentiles of the replicates. Dietary overlap values range from 0 to 1, with 0 indicating no overlap in diet and 1 indicating identical dietary composition for the dietary categories considered.

Results

Corbett (2001) collected 6722 dingo scats and 49 cat scats between 1980 and 1986. He identified six species of native small and medium-sized mammal, and six species of large mammal (four feral species) in dingo scats. In the 1980s sampling, small-sized native mammals were the prey item occurring at the highest frequency in scats for both dingoes (34 %) and cats (86 %) (Fig. 2).

Across the five sampling periods from 2014 to 2015, 84 cat and 1100 dingo scats were collected and analysed. Eleven species of native small and medium-sized mammal (11 in cat, 6 in dingo) were identified in the scats. Single prey species were identified in 97 % of dingo scats and 89 % of cat scats, two prey species in 3 % of dingo scats (0.1 % in same prey group) and 10 % of cat scats (4 % in same prey group), and three species in 1 % of cat scats. There was strong evidence for a difference in the frequency of occurrence of prey content in cat and dingo scats ($p = 0.0005$) (Fig. 2). Large mammals were the predominant prey group (69 %) in dingo scats; medium-sized native mammals were present in 7 %, and small-sized native mammals in 1 % of scats (Table 1). In comparison, 44 % of cat scats contained medium-sized mammals, and 24 % contained small-sized mammals, and only 8% contained large mammals. Pianka's index of dietary overlap was 0.27 (95 % CI: 0.005 – 0.54) suggesting there is slight overlap in species composition of the diets of dingoes and cats in the 2014-15 period in Kapalga.

There was strong evidence for a difference in prey frequencies found in dingo scats in the 2014-15 sampling compared to those reported in Corbett's study (*Chi-squared = 2021, df = 4, p = < 0.001*). Differences between the studies were driven by large changes in prey frequency in bird, macropod and small-sized mammal categories, with large Pearson's standardised residuals (> 3) indicating lack of fit of the null hypothesis of no difference in these categories. Macropod frequency increased from 17 % in the 1980s sampling to 67 % in 2014-2015 sampling; bird and small-mammal frequency decreased from 34 % each in the 1980s sampling to 4 % and 1 % in our re-sampling. Conversely, there was no evidence of a difference in the frequency of occurrence of medium-sized mammals in dingo diet between sampling periods (Pearson's standardised residuals < 3).

There was also strong evidence for a difference in prey frequency of occurrence in cat scats between sampling periods (*p = 0.0005*) (Fig. 2). Medium-sized native mammals increased in frequency in the diet from 12 % in Corbett's study to 52 % in the 2014-15 sampling (44 % excluding agile wallaby) (Table 2). The frequency of small-sized native mammals decreased from 86 % in Corbett's study to 24 % in 2014-15 sampling.

The relative abundance of small- and medium-sized mammals in Kapalga decreased by 95-98 % from the 1980-86 sampling period to 2013-15 (Fig. 3, Table 2).

Discussion

Consistent with our first hypothesis, the frequency of occurrence of small mammals in dingo diet declined in accordance with a decline in the relative abundance of small mammals. Similarly, the incidence of small mammals in cat scats declined substantially from the 1980s to our 2014-15 sampling. Small mammals were a major component of the diets of both dingoes and cats at Kapalga in the 1980s (Corbett 2001), when small mammals, such as the dusky rat (*Rattus colletti*), were much more abundant than at present. Notwithstanding their much lower relative abundance in our recent sampling, a diversity of small mammal species is still being preyed upon by cats. However, because we could not obtain species-level composition data for cat scats from the 1980s, we are unable to assess any species-level shifts that may have occurred in cat diets in response to changes in small mammal populations.

In comparison, the frequency of occurrence of medium-sized mammals did not decline in dingo scats, whilse a decline was observed in the relative abundance of medium-sized mammals (as estimated by trap success) over the same period. The frequency of occurrence of medium-sized mammals increased substantially in cat scats from the 1980s sampling to our 2014-15 sampling: northern brown bandicoot (*Isoodon macrourus*), in particular, was prevalent in cat and dingo scats in our 2014-15 sampling, ranking as the most frequently identified species in cat scats and the fourth most frequent in dingo scats. Furthermore, although bandicoot relative abundance (as estimated by trap success rates) declined substantially from the 1980s to 2010s (-95 % change) (Table 2), the frequency at which bandicoots occurred in dingo diets increased from the 1980s sampling to our re-sampling (1.4 % to 3.5 % respectively) (Table 2). In comparison, common brushtail possum (*Trichosurus vulpecula*) was well represented in dingo scats in the 1980s (9.6 %; Table 2), exceeding the frequency of occurrence of bandicoots. In the 1980s predation of possums by dingoes at times reached high frequencies (up to 25%) when other species were less available (Kerle 1998). Trap capture rates of possum have declined substantially from the 1980s to 2010s (- 96 % change; Table 2), but they were still represented in the diet of dingoes in 2014-15, albeit at a low frequency of occurrence (1.7 %; Table 1). Unfortunately, comparable data were unavailable for changes over time in occurrence of bandicoots or possums in cat scats, but notwithstanding their low trap success rates in recent sampling, bandicoots occurred in ca. 30 % and possums in ca. 12 % of cat scats in our 2010s sampling (Table 1).

Although both small- and medium-sized mammals declined to a comparable extent over the time period spanned here, the incidence of these prey groups in the diet of dingoes and cats did not follow the same pattern. This either indicates that the actual abundance of small mammals in the study area is lower than that of medium-sized mammals despite similar capture rates, or alternatively that there is higher selectivity, or predation success, for medium-sized mammals over smaller-sized mammals by both predators. Corbett and Newsome (1987) suggested that individual dingoes preferred particular prey and that their diets are heavily influenced by prey catchability and accessibility. When small mammals were in greater abundance in Kapalga in the 1980s, they made up the greatest proportion of the diet of both dingoes and cats. Corbett (1989) found that the abundance of prey in dingo scats fluctuated with the wet and dry seasons in response to species availability. He observed that dusky rats and magpie geese (*Anseranas semipalmata*) were staple prey in the dry season, especially in years of high abundance, and that agile wallaby was a consistently available prey that dingoes switched back to in the wet season.

Dusky rat populations are irruptive, experiencing breeding booms during years with optimal rainfall late in the wet season, followed by periods of relative rarity (Madsen *et al.* 2006a; Madsen *et al.* 2006b). Friend and Dudzinski (1988) observed declines in the abundance of dusky rat over the 1981-82 sampling period due to extreme wet season rainfall resulting in extensive flooding of low-lying areas; abundance appeared to have then peaked in 1984 after a series of wet seasons with lower rainfall. Capture rates for dusky rat declined by almost 100% between the 1980s and 2015 (Table 2).

Wet season rainfall in the 2010s has been marked by large inter-annual differences with rainfall well above average in some years (Fig. 3) and rainfall continuing into the late wet season (April – May). Timing and magnitude of rainfall have important biological influences on dusky rat breeding success and subsequent population irruptions (Redhead 1979; Madsen *et al.* 2006b). Changes in the pattern of wet season rainfall may have resulted in poor breeding success in dusky rats, leading to reduced availability of this species to predators in the 2010s. Furthermore, current and historic wet season population data for magpie geese are highly variable due to marked, rainfall-driven, fluctuations of recruitment rates (Delaney *et al.* 2009). Anecdotally, reports suggest that the South Alligator floodplain region (an area adjacent to Kapalga) is no longer an important dry season residence for geese as it was in the late 1980s (Keith Saalfeld, Department of Environment and Natural Resources, pers. comm.). The change in frequency of small mammals and birds in dingo scats may therefore be attributed to the reduction in dry season availability of magpie geese and dusky rats. Note also that the incidence of birds in the diet of cats increased from the 1980s to 2010s sampling (Fig. 2); given cats are unlikely to prey on magpie geese, this further suggests that the decline in birds in the diet of dingoes over the 1980s to 2010s period may be mostly driven by decline in local abundance of magpie geese, rather than decline in bird abundance more generally.

Trap success rate is a coarse index of relative abundance and does not account for imperfect detection; therefore it is possible that despite similar declines in capture rate, small mammals were less abundant than medium-sized mammals during the 2010s period. Species detected in predator scats represent a sample from a suite of species available to the predator in a particular time and place. In the Simpson Desert, Pavey *et al.* (2008) observed that both dingoes and cats exploited prey resources that were in greatest abundance and that diets shifted as the resource abundance changed. In a review of dingo diet across bioregions, (Corbett 2001) reported that more than 60 % of the dingo diet comprised small- and medium-sized mammals (defined as species < 15 kg) and that large prey only predominated in the diet when there was a paucity of available small- and medium-sized mammals available. Paltridge *et al.* (1997) and Kutt (2012) observed that mammals were the most important prey group for feral cats and concluded that they selectively preyed on small-sized prey (< 350 g). Likewise, Doherty *et al.* (2015) reported that the frequency of occurrence of medium-sized mammals (there defined as 500-6999 g) in feral cat diets across the continent is generally low (typically <10 %). Therefore, our diet results suggest that in Kapalga, small-mammal populations may be more depleted than medium-sized mammals, with cats now focussed on medium-sized mammals as their predominant prey.

We also predicted that prey composition of dingoes would be dominated by large mammals whereas that of feral cats would be dominated by small mammals. Dietary overlap in the 2010s sampling was relatively low; dingoes preyed more often on macropods, whereas medium-sized mammals dominated the prey of feral cats. Cats also took a greater diversity of small-sized prey including birds, reptiles, insects and small mammals; findings broadly consistent with other dietary studies of feral cats (Doherty *et al.* 2015). However, there was notable dietary overlap in the predation of bandicoots, with this prey ranking in the top four most frequently occurring species in both dingo and cat scats. The frequency of macropods in the diet of dingoes increased significantly from the 1980s to 2010s. This pattern is either attributable to a decline in the proportional availability of small mammals and geese, indicative of a greater availability and abundance of macropods, or a combination of the two. Unfortunately, data concerning changes in abundance are not available for most birds, reptiles or large mammals, thus limiting our interpretation.

We recognise that the impact of predation on native mammal populations is related not only to the incidence of a species in a predator's diet, but also to the relative densities of those predators and prey in the system (and prey life history characteristics). We were unable to assess the relative densities of cats and dingoes, or any changes in such densities from the 1980s to 2010s in this study. Feral cat remains were infrequently present in dingo scats, both historically and in this study (< 1 % of scats, Fig. 2), consistent with Schroeder *et al.* (2015), who concluded that dingoes do not actively hunt cats but will opportunistically kill them. There is still little known about the ecological interactions between dingoes and cats in northern Australia; it is recommended that comparable future studies include sampling to monitor changes in density of these predators.

Spanning the same period as the observed mammal declines, Kakadu has experienced changes in environmental condition. High frequency of extensive fires, which reduces the structural complexity and floristic composition of savanna landscapes (Williams *et al.* 1999), has been shown to adversely affect small and medium-sized mammal diversity (Griffiths *et al.* 2015; Lawes *et al.* 2015). Furthermore, the hunting efficiency of feral cats increases substantially in habitats that have been structurally simplified through intense fire and grazing by introduced herbivores (McGregor *et al.* 2014; McGregor *et al.* 2015). These findings have contributed significantly to our understanding of the potential role of feral cats in northern Australian mammal declines (Ziembicki *et al.* 2015). However, our findings demonstrate that dingoes may also be an important predator of small- and medium-sized native mammals. It is plausible that hunting behaviour and efficiency of dingoes are also enhanced in landscapes that have been simplified.

Conclusions

Our results support the findings of other studies that show cats are highly effective predators of small and medium-sized mammals and are able to seek out and prey on them even when their population densities are very low (Kutt 2011; Spencer *et al.* 2014; Moseby *et al.* 2015). Our findings also provide further evidence that dingoes may be able to exert predatory pressure on some declining species (Jolly 2017 *et al.* 2017, Cremona *et al.* 2017), and may limit the recovery of those affected by other threatening processes (Kerle *et al.* 1992; Moseby *et al.* 2011; Allen and Fleming 2012). Consequently the predatory role of both feral cats and dingoes should to be considered in the conservation management of native mammal species in northern Australia.

The role of feral cats in the declines of northern Australian mammals, either singularly or in concert with other environmental processes such as fire and livestock, has received considerable research, policy and management attention in recent years (McGregor *et al.* 2014; Ziembicki *et al.* 2015). The ecologies of cats and dingoes in savanna ecosystems, and the interactions between these predators and native mammal populations, are likely to be complex (Ziembicki et al. 2015). Current knowledge of population dynamics of dingoes and feral cats and their interactive effects in Kakadu and similar ecosystems remains extremely poor. A greater understanding is required of these predator interactions and how these broadly manifest into top-down impacts on small and medium-sized mammals.

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References

Allen, B. L. and Fleming, P. J. S. (2012). Reintroducing the dingo: the risk of dingo predation to threatened vertebrates of western New South Wales. *Wildlife Research* **39**, 35-50. doi: 10.1071/wr11128.

Allen, L. R., Goullet, M., and Palmer, R. (2012). The diet of the dingo (*Canis lupus dingo* and hybrids) in north-eastern Australia: a supplement to the paper of Brook and Kutt (2011). *The Rangeland Journal* **34**, 211-217. doi: 10.1071/rj11092.

Braithwaite, R. W. and Muller, W. J. (1997a). Rainfall, groundwater and refuges: Predicting extinctions of Australian tropical mammal species. *Australian Journal of Ecology* **22**, 57-67.

Braithwaite, R. W. and Muller, W. J. (1997b). Rainfall, groundwater and refuges: predicting extinctions of Australian tropical mammal species. *Australian Journal of Ecology* **22**, 57-67.

Brook, L. A., Johnson, C. N., Ritchie, E. G., and Dickman, C. (2012). Effects of predator control on behaviour of an apex predator and indirect consequences for mesopredator suppression. *Journal of Applied Ecology* **49**, 1278-1286. doi: 10.1111/j.1365-2664.2012.02207.x.

Brunner, H. and Wallis, R. L. (1986). Roles of predator scat analysis in Australian mammal research. *Victorian Field Naturalist* **103**.

Bureau of Meteorology (2017). Climate statistics for Australian locations. Retrieved 27/09/2017. (Commonwealth of Australia: http://www.bom.gov.au/climate/averages/tables/cw_014198.)

Corbett, L. (1989). Assessing the diet of dingoes from feces: A comparison of 3 methods. *The Journal of Wildlife Management* **53**, 343-346.

Corbett, L. (1995). Does Dingo Predation or Buffalo Competition Regulate Feral Pig Populations in the Australian Wet-Dry Tropics? An Experimental Study. *Wildlife Research* **22**, 65-74. doi: 10.1071/WR9950065.

Corbett, L. (2001) 'The dingo in Australia and Asia.' 2nd edn. (J. B. Books: Marleston, S. Aust.)

Corbett, L., Hertog, T., and Estbergs, J. (2014). Diet of 25 sympatric raptors at Kapalga, Northern Territory, Australia 1979–89, with data on prey availability. *Corella* **38**, 81-94.

Corbett, L. and Newsome, A. E. (1987). The feeding ecology of the Dingo. III. Dietary relationships with widely fluctuating prey populations in arid Australia: An hypothesis of alternation of predation. *Oecologia* **74**, 215-227.

Delaney, R., Fukuda, Y., and Saalfeld, K. (2009). Management program for the Magpie Goose (*Anseranas semipalmata*) in the Northern Territory of Australia, 2009–2014. Department of Natural Resources, Environment, the Arts and Sport. (N. T. Government.: Darwin.)

Doherty, T. S. (2015). Dietary overlap between sympatric dingoes and feral cats at a semiarid rangeland site in Western Australia. *Australian Mammalogy* **37**, 219-224. doi: 10.1071/AM14038.

Doherty, T. S., Davis, R. A., van Etten, E. J. B., Algar, D., Collier, N., Dickman, C. R., Edwards, G., Masters, P., Palmer, R., Robinson, S., and McGeoch, M. (2015). A continental-scale analysis of feral cat diet in Australia. *Journal of Biogeography* **42**, 964-975. doi: 10.1111/jbi.12469.

Fancourt, B. A. (2015). Making a killing: photographic evidence of predation of a Tasmanian pademelon (*Thylogale billardierii*) by a feral cat (*Felis catus*). *Australian Mammalogy* **37**, 120-124.

Fisher, D. O., Blomberg, S. P., and Owens, I. P. (2003). Extrinsic versus intrinsic factors in the decline and extinction of Australian marsupials. *Proceedings of the Royal Society of London B: Biological Sciences* **270**, 1801-1808.

Friend, G. R. and Dudzinski, M. L. (1988). *Rattus colletti* (Rodentia: Muridae) in the Australian wet-dry tropics: Seasonal habitat preferences, population dynamics and the effects of buffalo (*Bubalus bubalis*). *Australian Journal of Ecology* **13**, 51-66.

Friend, G. R. and Taylor, J. A. (1985). Habitat preferences of small mammals in tropical open-forest of the Northern Territory. *Australian Journal of Ecology* **10**, 173-185.

Glen, A. S., Pennay, M., Dickman, C. R., Wintle, B. A., and Firestone, K. B. (2011). Diets of sympatric native and introduced carnivores in the Barrington Tops, eastern Australia. *Austral Ecology* **36**, 290-296. doi: 10.1111/j.1442-9993.2010.02149.x.

Griffiths, A. D., Garnett, S. T., and Brook, B. W. (2015). Fire frequency matters more than fire size: Testing the pyrodiversity–biodiversity paradigm for at-risk small mammals in an Australian tropical savanna. *Biological Conservation* **186**, 337-346. doi: 10.1016/j.biocon.2015.03.021.

Johnson, C. N. and Isaac, J. L. (2009). Body mass and extinction risk in Australian marsupials: The ‘Critical Weight Range’ revisited. *Austral Ecology* **34**, 35-40. doi: 10.1111/j.1442-9993.2008.01878.x.

Johnson, C. N. and Ritchie, E. G. (2013). The dingo and biodiversity conservation: response to Fleming et al. (2012). *Australian Mammalogy* **35**, 8-14. doi: 10.1071/am12005.

Kerle, J. A. (1998). The population dynamics of a tropical possum, *Trichosurus vulpecula arnhemensis* Collett. *Wildlife Research* **25**, 171-181.

Kerle, J. A., Foulkes, J. N., Kimber, R. J., and Papenfus, D. (1992). The decline of the brushtail possum, *Trichosurus vulpecula* (Kerr 1798), in arid Australia. *The Rangeland Journal* **14**, 107-127.

Klare, U., Kamler, J. F., and Macdonald, D. W. (2011). A comparison and critique of different scat-analysis methods for determining carnivore diet. *Mammal Review* **41**, 294-312. doi: 10.1111/j.1365-2907.2011.00183.x.

Kutt, A. S. (2011). The diet of the feral cat (Felis catus) in north-eastern Australia. *Acta Theriologica* **56**, 157–169. doi: DOI 10.1007/s13364-010-0016-7.

Kutt, A. S. (2012). Feral cat (*Felis catus*) prey size and selectivity in north-eastern Australia: Implications for mammal conservation. *Journal of Zoology* **287**, 292-300. doi: 10.1111/j.1469-7998.2012.00915.x.

Lawes, M. J., Murphy, B. P., Fisher, A., Woinarski, J. C. Z., Edwards, A. C., and Russell-Smith, J. (2015). Small mammals decline with increasing fire extent in northern Australia: Evidence from long-term monitoring in Kakadu National Park. *International Journal of Wildland Fire* **24**, 712-722. doi: 10.1071/wf14163.

Leahy, L., Legge, S. M., Tuft, K., McGregor, H. W., Barmuta, L. A., Jones, M. E., and Johnson, C. N. (2016). Amplified predation after fire suppresses rodent populations in Australia's tropical savannas. *Wildlife Research* **42**, 705-716. doi: http://dx.doi.org/10.1071/WR15011.

Madsen, T., Ujvari, B., Shine, R., Buttemer, W., and Olsson, M. (2006a). Size matters: extraordinary rodent abundance on an Australian tropical flood plain. *Austral Ecology* **31**, 361-365. doi: 10.1111/j.1442-9993.2006.01564.x.

Madsen, T., Ujvari, B., Shine, R., and Olsson, M. (2006b). Rain, rats and pythons: Climate-driven population dynamics of predators and prey in tropical Australia. *Austral Ecology* **31**, 30-37. doi: 10.1111/j.1442-9993.2006.01540.x.

McGregor, H., Legge, S., Jones, M. E., and Johnson, C. N. (2015). Feral cats are better killers in open habitats, revealed by animal-borne video. *PLoS ONE* **10**, e0133915. doi: DOI:10.1371/journal.pone.0133915.

McGregor, H. W., Legge, S., Jones, M. E., and Johnson, C. N. (2014). Landscape management of fire and grazing regimes alters the fine-scale habitat utilisation by feral cats. *PLoS ONE* **9**, e109097. doi: 10.1371/journal.pone.0109097.

Moseby, K., Peacock, D. E., and Read, J. L. (2015). Catastrophic cat predation: A call for predator profiling in wildlife protection programs. *Biological Conservation* **191**, 331-340. doi: 10.1016/j.biocon.2015.07.026.

Moseby, K. E., Read, J. L., Paton, D. C., Copley, P., Hill, B. M., and Crisp, H. A. (2011). Predation determines the outcome of 10 reintroduction attempts in arid South Australia. *Biological Conservation* **144**, 2863-2872. doi: 10.1016/j.biocon.2011.08.003.

Oakwood, M. (2000). Reproduction and demography of the northern quoll, *Dasyurus hallucatus*, in the lowland savanna of northern Australia. *Australian Journal of Zoology* **48**, 519-539.

Paltridge, R. (2002). The diet of cats, foxes and dingoes in relation to prey availability in the Tanami Desert, Northern Territory. *Wildlife Research* **29**, 389-403.

Paltridge, R. M., Gibson, D., and Edwards, G. P. (1997). Diet of the feral cat (*Felis catus*) in central Australia. *Wildlife Research* **24**, 67-76.

Pavey, C. R., Eldridge, S. R., and Heywood, M. (2008). Population dynamics and prey selection of native and introduced predators during a rodent outbreak in arid Australia. *Journal of Mammalogy* **89**, 674-683. doi: 10.1644/07-mamm-a-168r.1.

Petty, A. M., Werner, P. A., Lehmann, C. E. R., Riley, J. E., Banfai, D. S., and Elliott, L. P. (2007). Savanna responses to feral buffalo in Kakadu national park, Australia. *Ecological Monographs* **77**, 441-463. doi: 10.1890/06-1599.1.

Pianka, E. R. (1973). The structure of lizard communities. *Annual Review of Ecology and Systematics* **4**, 53-74.

Redhead, T. D. (1979). On the demography of *Rattus sordidus colletti* in monsoonal Australia. *Australian Journal of Ecology* **4**, 115-136.

Russell-Smith, J., Evans, J., Edwards, A. C., and Simms, A. (2017). Assessing ecological performance thresholds in fire-prone Kakadu National Park, northern Australia. *Ecosphere* **8**, e01856. doi: 10.1002/ecs2.1856.

Schroeder, T., Lewis, M. M., Kilpatrick, A. D., and Moseby, K. E. (2015). Dingo interactions with exotic mesopredators: Spatiotemporal dynamics in an Australian arid-zone study. *Wildlife Research* **42**, 529-539. doi: 10.1071/wr15104.

Spencer, E. E., Crowther, M. S., and Dickman, C. R. (2014). Diet and prey selectivity of three species of sympatric mammalian predators in central Australia. *Journal of Mammalogy* **95**, 1278-1288. doi: 10.1644/13-mamm-a-300.

Stephens, D., Wilton, A. N., Fleming, P. J., and Berry, O. (2015). Death by sex in an Australian icon: A continent-wide survey reveals extensive hybridization between dingoes and domestic dogs. *Mol Ecol* **24**, 5643-5656. doi: 10.1111/mec.13416.

Van Dyck, S., Gynther, I., and Baker, A. (2013) 'Field companion to the mammals of Australia.' (New Holland Publishers: Sydney.)

Williams, R. J., Cook, G. D., Gill, M. A., and Moore, P. H. R. (1999). Fire regime, fire intensity and tree survival in a tropical savanna in northern Australia. *Australian Journal of Ecology* **24**, 50-59.

Woinarski, J. C., Burbidge, A. A., and Harrison, P. L. (2015). Ongoing unraveling of a continental fauna: Decline and extinction of Australian mammals since European settlement. *PNAS* **112**, 4531-4540. doi: 10.1073/pnas.1417301112.

Woinarski, J. C. Z., Armstrong, M., Brennan, K., Fisher, A., Griffiths, A. D., Hill, B., Milne, D. J., Palmer, C., Ward, S., Watson, M., Winderlich, S., and Young, S. (2010). Monitoring indicates rapid and severe decline of native small mammals in Kakadu National Park, northern Australia. *Wildlife Research* **37**, 116–126.

Woinarski, J. C. Z., Burbidge, A. A., and Harrison, P. (2014) 'The action plan for Australian mammals.' (CSIRO Publishing: Melbourne.)

Woinarski, J. C. Z., Milne, D. J., and Wanganeen, G. (2001). Changes in mammal populations in relatively intact landscapes of Kakadu National Park, Northern Territory, Australia. *Austral Ecology* **26**, 360-370. doi: 10.1046/j.1442-9993.2001.01121.x.

Ziembicki, M. R., Woinarski, J. C., Webb, J. K., Vanderduys, E., Tuft, K., Smith, J., Ritchie, E. G., Reardon, T. B., Radford, I. J., Preece, N., Perry, J., Murphy, B. P., McGregor, H. W., Legge, S., Leahy, L., Lawes, M. J., Kanowski, J., Johnson, C. N., James, A., Griffiths, A. D., Gillespie, G. R., Frank, A. S. K., Fisher, A., and Burbridge, A. A. (2015). Stemming the tide: progress towards resolving the causes of decline and implementing. *THERYA* **6**, 169-226. doi: 10.12933/therya-15-236.

Figure 1. Kapalga study location within Kakadu National Park.

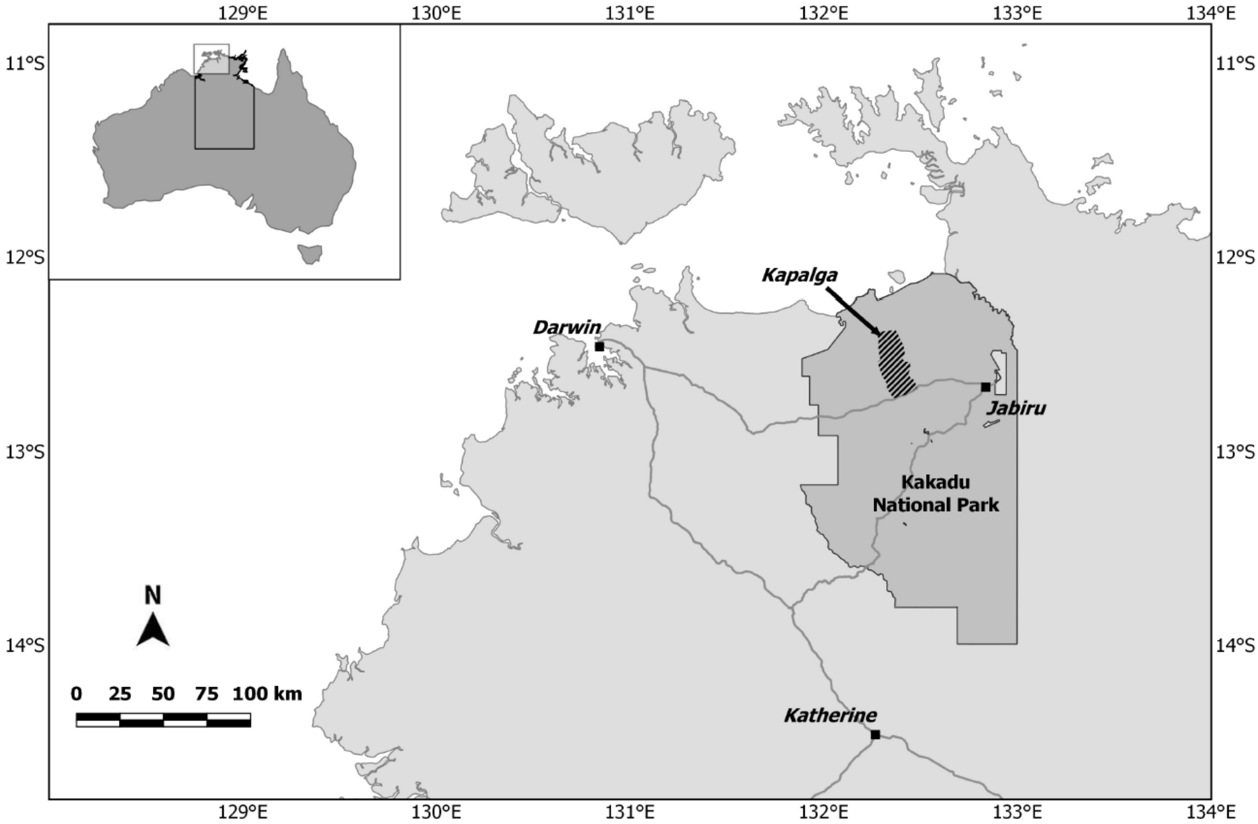
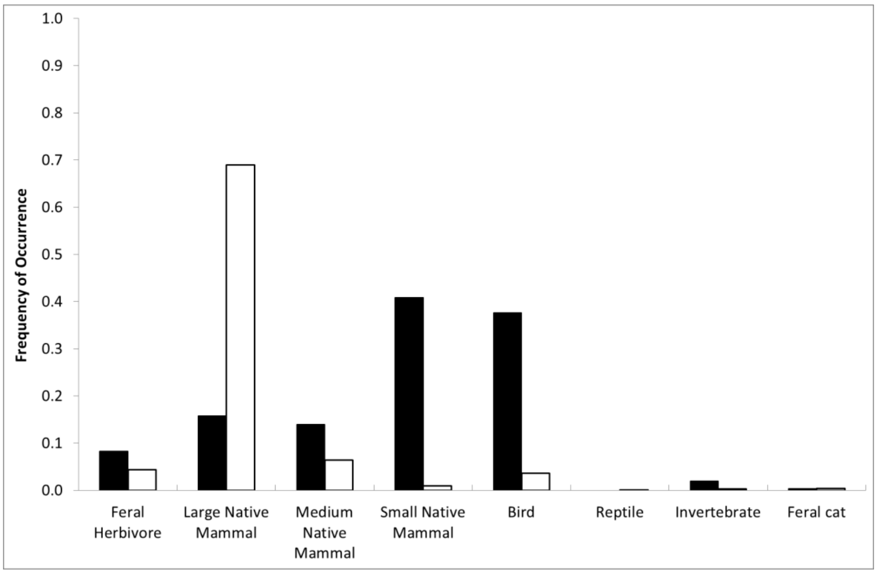


Figure 2. Frequency of occurrence of prey, by category, present in dingo scats (a) collected at Kapalga by Corbett (2001) (black bars, n = 6722) and in the present study (open bars, n = 1100). Frequency of occurrence of prey, by category, present in cat scats (b) by Corbett (2001) (black bars, n = 49) and in the present study (open bars, n = 84). Note agile wallaby is classified as a medium-sized native mammal in prey groups for cat scats only, black dot represents prey frequency of medium-sized native mammals excluding agile wallabies in the present study. Note also that frequency of occurrences across categories do not sum to 1.

a)



b)

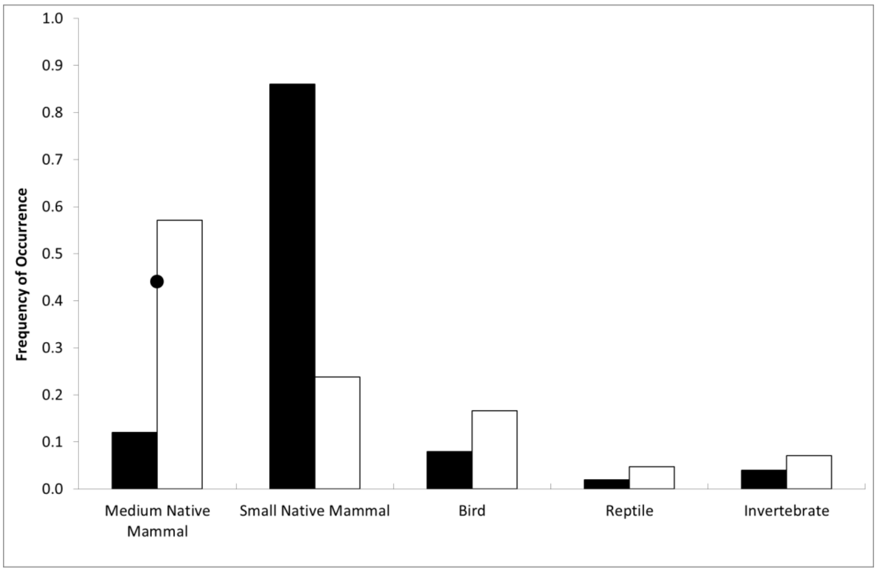


Table 1. Frequency of occurrence (as a percentage of scats) of prey species, and prey groups, identified in dingo and cat scats collected between June 2014 and November 2015 at Kapalga. Note frequency occurrence of prey groups accounts for multiple prey occurring within scats.

Prey item	Cat	Dingo
Small Native Mammal (< 500 g)	**23.8**	**0.9**
Leggadina lakedownensis	1.2	0
Melomys burtoni	3.6	0.4
Petaurus breviceps	13.1	0.5
Pseudomys calabyi	1.2	0
Pseudomys sp.	1.2	0
Sminthopsis bindi[#]	1.2	0
Zyzomys sp.[#]	1.2	0
Rodent, unidentified	1.2	0.1
Medium Native Mammal (500 - 5500 g)	**44.0**	**6.5**
*Dasyurus hallucatus**	3.6	0
Isoodon macrourus	29.8	3.5
*Mesembriomys gouldii**	3.6	0
Pteropus alecto	0.0	0.3
Tachyglossus aculeatus	0.0	0.9
Trichosurus vulpecula	11.9	1.7
Mammal, unidentified	0	0.1
Large native mammals (> 5500 g)	**8.3**	**68.9**
Notamacropus agilis	7.1	37.5
Osphranter antilopinus	0.0	16.8
Osphanter bernardus[#]	0	0.4
Osphranter robustus	0	8.2
Large Macropod, unidentified	1.2	4.6
Canis familiaris	0	1.5
Feral herbivores	**0**	**4.4**
Bubalus bubalis	0	0.2
Bos taurus	0	1.9
Sus scrofa	0	2.3
Other		
Felis catus	0	0.4
Birds, unidentified	16.7	3.6
Invertebrates, unidentified	7.1	0.3
Reptiles, unidentified	4.8	0.1
Human	0	0.1

[#]Species which have not historically been detected in the Kapalga area
* Endangered, *EPBC* Act

Table 2. Percent change in mean capture rate (per 100 trap-nights) and frequency of occurrence in scats of small- and medium-sized mammals, northern brown bandicoot and brushtail possum, between 1980-1983 and 2013-2015 study periods. Note scat sampling occurred over the 2014-2015 period. Frequency of occurrence of individual prey items was not available for cats in the 1980s sampling. Corbett 1995 categorised agile wallaby as a medium-sized native mammal in cat scats.

	1980-1986	**2013-2015**	**% Change**
Medium-sized native mammals			
Mean capture rate and number of species	5.7 (4 spp.)	0.26 (3 spp.)	-95
Frequency occurrence in cat scats (includes Agile wallaby)	12	52.4	+336
Frequency occurrence in dingo scats	11.4	6.5	-43
Mean capture rate: Bandicoot	0.2	0.01	-95
Frequency occurrence in dingo scats: Bandicoot	1.4	3.5	+150
Mean capture rate: Possum	0.28	0.01	-96
Frequency occurrence in dingo scats: Possum	9.7	1.7	-82
Small-sized native mammals			
Mean capture rate and number of species	13.1 (4 spp.)	0.21 (2 spp.)	-98
Frequency occurrence in cat scats	86	23.8	-72
Frequency occurrence in dingo scats	34.3	0.9	-97
Mean capture rate: Dusky rat	9.7	0.10	-99
Frequency occurrence in dingo scats: Dusky rat	33.9	0	-100

Figure 3. Change over time in capture rate (per 100 trap-nights) in small-sized mammals (solid bars) and medium-sized mammals (open bars). Asterisk indicates no captures were obtained within the year of sampling, and there was no sampling in the years with no bars or asterisk. The spikes in small mammal capture rates in 1981 and 2002 are associated with high incidences of dusky rat captures adjacent to the floodplains. Note: capture rate presented for 1981 represents a mean capture rate obtained across 1980 – 1983 sampling periods. Grey squares - rainfall from 1 July in the preceding year to 30 June; Grey line - 35 year (1971 – 2017) long-term average annual rainfall obtained from Jabiru Airport (12.66°S, 132.89°E) (Source: Bureau of Meteorology 2017).