Diet of dingoes and cats in central Australia: does trophic competition underpin a rare mammal refuge?

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We investigated the hypothesis that trophic competition between a top predator and a smaller predator can create refuge from predation for small mammalian prey, using the dingo (*Canis lupus dingo*) and feral cat (*Felis catus*) in the MacDonnell Ranges of dryland Australia as a case study. We analyzed the diets of the 2 predator species for evidence of potential competition. There was no evidence of exploitation competition between the 2 carnivores—cats consumed mostly small mammals and particularly larger rodents, whereas the diet of dingoes was dominated by 1 species of large macropod. There was also no evidence of a shift in diet of cats, as their diets in refuges and non-refuges were highly overlapping. Consistent with interference competition, cats were the third most frequently consumed mammal species by dingoes. Although predation by dingoes could limit densities of cats across the MacDonnell Ranges, this alone does not explain why the most rugged habitats in the region are a refuge for rare mammals. We conclude that habitat complexity most likely underpins the refuge and that possible effects of dingo predation on the cat population would be of secondary importance.

Key words: activity, arid, *Canis lupus dingo*, competition, diet, *Felis catus*, mesopredator

Australia has a highly distinctive mammal fauna that has been severely impacted since European colonization in 1788. At least 30 endemic mammal species (> 10% of the original mammal fauna) became extinct in this period and a further 56 species meet the IUCN criteria for listing under one of the threatened categories (Woinarski et al. 2015). In contrast to the global situation, where habitat loss and hunting are the main factors threatening mammals (Hoffman et al. 2011), Australia's mammal extinctions and declines have probably been driven primarily by predation from 2 introduced mesopredators: the feral cat (*Felis catus*; hereafter referred to as "cat") and red fox (*Vulpes vulpes*—Woinarski et al. 2015).

While Australia's mammal extinctions and declines have been exceptional on a global scale, declines have not been geographically uniform. For example, 3 species of native mammal that once occurred widely on mainland Australia are now confined to Australia's largest fox-free island, Tasmania (Woinarski et al. 2015). Variation in mesopredator-driven mammal decline

on the Australian mainland has also been linked to variation in habitat complexity. For example, habitat refuges for threatened mammals are typically associated with complex terrain or vegetation (Hernandez-Santin et al. 2016; Davies et al. 2017; McDonald et al. 2017).

The quartzite mountains of the MacDonnell Ranges in central Australia have been identified as an important refuge for small to medium-sized threatened mammals (McDonald et al. 2015, 2017). These mountains support the most intact mammal fauna in central Australia and several species are now regionally or globally restricted to this refuge. In contrast to the quartzite mountains, the surrounding landforms (including lower-elevation rocky hills, valleys, and alluvial plains) are characterized by relatively simple topography (McDonald et al. 2017). McDonald et al. (2017) hypothesized that the rugged and structurally complex quartzite geology mediates predation from cats by affecting their foraging efficiency and density. While ruggedness was found to be a more important driver

of mammal assemblages than productivity in the MacDonnell Ranges (McDonald et al. 2017), there remains an additional possible explanation for why this region is a refuge for rare mammals—top-down suppression of cats by dingoes (*Canis lupus dingo*).

Dingoes and cats are the 2 largest mammalian predators resident in the MacDonnell Ranges. Red foxes are infrequently recorded in the region and are absent from the core area of upland terrain (see McDonald et al. 2017). While cats are ubiquitous throughout dryland Australia, available data suggest that densities of cats are lower in the quartzite refuge than in nearby topographically simple habitats (Legge et al. 2017). The dingo, Australia's apex mammalian predator, occurs throughout the MacDonnell Ranges probably as a consequence of the presence of extensive protected areas with abundant surface water and the absence of lethal control. Given the widespread reporting of suppression of cats by dingoes (e.g., Kennedy et al. 2012; Moseby et al. 2012; Greenville et al. 2014), there could be important interactions between the 2 predators in this system.

The theoretical mechanisms for suppression of cats by dingoes are exploitation and interference competition. Exploitation competition occurs between 2 species when there is high niche overlap (Wiens 1993). For example, when there is high dietary overlap between a pair of species, one species will outcompete the other in times of food shortage (Korpimäki 1987). Exploitation competition may also drive niche shift in one species, forcing its increased use of a suboptimal niche (Bonesi et al. 2004; Harrington et al. 2009). Interference competition occurs when one species limits another's use of resources (Wiens 1993). In carnivores, this process includes intraguild predation and a fear of predation that drives spatial and temporal avoidance of a larger carnivore (Fedriani et al. 2000; Linnell and Strand 2000). These phenomena are demonstrably important in intraguild relationships among carnivores, often with consequences for conservation (e.g., Herteinsson and Macdonald 1992; Sidorovich et al. 1999).

Understanding the trophic ecology of dingoes and cats is a prerequisite to uncovering potentially important competitive interactions between the 2 predators that help to maintain the mammal refuge. While studies from Australia's sandy desert systems have found moderate to high dietary overlap between dingoes and cats (Paltridge 2002; Pavey et al. 2008; Spencer et al. 2014), no dietary research has been undertaken in the biologically distinct central Australian uplands. The MacDonnell Ranges differ from the sandy deserts in their complex topography (McDonald et al. 2015), variegated and well-defined vegetation communities (Nano and Clarke 2008), and abundant natural surface water (Box et al. 2008). This environment supports a substantial population of a large macropod, the euro or hill kangaroo (*Osphranter robustus*—McDonald et al. 2017), which thrives here because of access to abundant areas of shade (afforded by caves, overhangs, and vegetation) used as shelter during the day and surface water (Ealey et al. 1965). Unlike cats, dingoes are large enough to capture and subdue large mammal prey, particularly when hunting in packs (Corbett 1995). If euros dominate the diet of dingoes in the MacDonnell Ranges, this would suggest that dingoes and cats have highly divergent dietary ecologies and render competition between the 2 predators less likely (Keddy 2001).

Here, we investigated the hypothesis that dingoes are an important trophic regulator that suppress cats, and thus help to sustain a refuge for rare mammals, in the MacDonnell Ranges. We examined the diets of both predators from scats collected inside and outside the refuge. Based on a scenario of exploitation competition, if dingoes outcompete cats for prey, we predicted either: 1) high overall dietary overlap between the 2 predators and thus the potential for fitness impacts on the subordinate predator during times of food shortage, or 2) competition with dingoes would force cats to consume increased quantities of suboptimal prey in the refuge (dietary niche shift). However, if dingoes consumed mostly large mammals, we expected low dietary overlap between the 2 predators and thus low potential for exploitation competition. Based on a scenario of interference competition, we expected evidence of intraguild predation with a high proportion of cats in dingo scats.

MATERIALS AND METHODS

Study region.—We conducted our study in the 2,592-km² Tjoritja–West MacDonnell National Park (referred to hereafter as "Tjoritja NP") in the MacDonnell Ranges Bioregion (Thackway and Cresswell 1995), southern Northern Territory, Australia (Fig. 1). Climate is typical of semiarid Australia, with
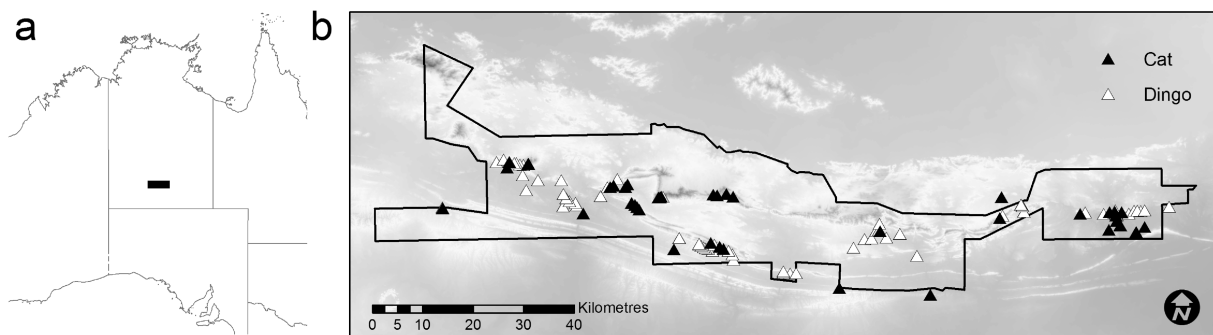

Fig. 1.—a) Location of the study area in the Northern Territory, Australia. b) Study area enlarged with the locations of cat (*Felis catus*; $n = 74$) and dingo (*Canis lupus dingo*; $n = 98$) scats collected in Tjoritja National Park (park boundary indicated by black line). Maps generated in ArcMap 10.2 (www.esri.com). Background imagery courtesy of Geoscience Australia (www.ga.gov.au).

highly irregular rainfall (mean annual rainfall at Alice Springs Airport = 283.7 mm) and temperatures ranging from hot in summer (daytime maxima frequently > 40°C) to cool in winter (overnight minima frequently < 0°C) (Australian Bureau of Meteorology Climate Data, http://www.bom.gov.au/climate/data/). The main landforms in the park are rugged quartzite mountains and ridges (to 1,389 m elevation), lower rocky hills and flats of varying geology, and ephemeral rivers and alluvial plains. Vegetation communities are generally well defined, with hummock grasslands (*Triodia* spp.) and *Acacia* (e.g., *Acacia aneura*) shrublands dominating the rocky landforms, while rivers and alluvial plains support river red gum (*Eucalyptus camaldulensis*) and ironwood (*Acacia estrophiolata*) woodlands. We defined the rugged quartzite mountain ranges as a refuge because they support several species of mammals that no longer occur, or are very rare, outside of this landform (McDonald et al. 2017).

Collection and analysis of fecal remains.—Cat and dingo fecal remains (hereafter "scats") were collected opportunistically throughout the study area (Fig. 1b). Cat and dingo scats were collected between 2011 and 2013 and cat scats were also collected in 2015–2016. Only intact scats judged to be < 6 months old were used for analysis. We identified scats as cat or dingo according to size, shape, and smell (Triggs 1996). We placed scats individually into paper bags and then into an oven at 70°C for > 10 h to kill parasites. We then washed samples through a series of sieves that left only indigestible fragments of prey. We placed fragments into sorting trays divided into 4 equal sections for inspection and visual estimation of percentage volume of prey categories. Mammals were identified to the lowest possible taxonomic level by inspection of hair remains using cross-section and whole-mount techniques, and jaw and skull fragments (Archer 1981; Watts and Aslin 1981; Brunner and Triggs 2002). Mammals were classified into size categories of small (< 500 g), medium (500–6,999 g), and large (≥ 7,000 g). All other prey items were categorized as arthropod, reptile or frog, bird, vegetation, or rubbish.

Analysis.—To determine whether our scat sample sizes were sufficient for capturing mammal species and dietary diversity, we plotted the cumulative diversity of all mammal species and the other food categories against the number of scats examined for both cats and dingoes. We calculated diversity with the Brillouin index:

$$H = \frac{\ln N! - \sum \ln n_i!}{N}$$

where H is the dietary diversity of the predator, N is the total number of individual prey recorded, and n_i is the number of individual prey items of the ith type (Brillouin 1956). To test for dietary overlap or partitioning between cats and dingoes, we constructed a scat by food category matrix that was based on the untransformed volumetric contribution of each category (Klare et al. 2011). For this, we used 172 scats and the 8 food categories.

We used a range of multivariate techniques available in the PRIMER 7 software package with PERMANOVA + add-on (Plymouth Marine Laboratory—Anderson et al. 2008; Clarke and Gorley 2015) to explore dietary differences between the 2 species. We first used the similarity percentage (SIMPER) analysis procedure to determine within- and between-group diagnostic food categories for each species. We then used distance-based linear models (DISTLMs) to analyze and model the relationship between the adjusted Bray–Curtis similarity resemblance matrix of untransformed food category data and 6 categorical and continuous predictor variables. We sought to determine the effect of species versus a range of environmental parameters (refuge versus non-refuge, rainfall, and season of collection) on food content. We used the Draftsman Plot tool to test for a skewed distribution in the explanatory variables (indicating a requirement for transformation) and for collinearity among the variables. Redundant variables, those strongly correlated with other variables ($r > 0.95$), were removed from the analysis. Following this, we used the *Forward Selection* procedure on the basis of the adjusted R^2 selection criterion and then carried out constrained ordination using distance-based redundancy analysis (dbRDA).

Because dietary overlap is frequently reported using Pianka's index, we also calculated this for prey frequency occurrence and volume using the equation:

$$O_{jk} = \sum p_{ij} p_{ik} \Big/ \left(\sum p_{ij^2} \sum p_{ik^2} \right)^{0.5}$$

where j and k are the 2 species being compared, and p_i is the frequency of occurrence (or volume) of the ith food type. Overlap ranges from 0 (no overlap) to 1 (complete overlap). We computed Pianka's index for cats and dingoes from all scats. Because cats have smaller home ranges than dingoes in dryland Australia (Corbett 1995; Edwards et al. 2001), we expected their scats deposited in the refuge were more likely to include prey consumed in the refuge, so we also calculated Pianka's index for cats separately for refuge and non-refuge locations. We compared Pianka's index values to linear null models, using the randomization algorithm RA3 with 10,000 runs in EcoSim Professional Version 1 (Entsminger 2014).

RESULTS

Diet.—We collected and analyzed 98 dingo and 74 cat scats from across the study area (Fig. 1; Supplementary Data SD1). Cumulative diversity of mammal species and other prey categories reached asymptote for dingoes and cats, indicating that sampling was sufficient to reliably describe the diets of the predators (Supplementary Data SD2).

Similarity percentage analysis revealed that diets of dingoes and cats were highly divergent in their primary prey consumption. The diet of cats was characterized primarily by small mammals (80.4% within-group similarity), while the diet of dingoes was characterized by large mammals (78.4% within-group similarity). Birds and arthropods were 2nd- and 3rd-order contributors for cats, followed by reptiles or frogs and medium-sized mammals. Vegetation (mostly masticated grass

likely consumed by euros and other large mammal prey) and medium-sized mammals were 2nd- and 3rd-order contributors for dingoes. Between-group dissimilarity analysis showed that diets of cats and dingoes were distinguishable primarily on the basis of the 3 mammal size classes (Table 1). A high proportion

Table 1.—Similarity percentage (SIMPER) results showing the average abundance (Av ab), average dissimilarity (Av diss), percentage contribution to overall dissimilarity (% cont), and cumulative percentage (Cum %) for cat (*Felis catus*) and dingo (*Canis lupus dingo*) dietary comparison in the MacDonnell Ranges, Northern Territory, central Australia.

Food category	Av ab cat	Av ab dingo	Av diss	% cont	Cum %
Small mammal	54.66	2.8	26.93	28.57	28.57
Large mammal	0	49.74	24.87	26.39	54.95
Medium mammal	8.45	15.36	10.53	11.17	66.12
Vegetation	1.08	18.29	9.37	9.94	76.06
Bird	15.47	5.51	9.32	9.89	85.96
Reptile	8.18	6.63	6.64	7.04	93
Arthropod	12.16	0.87	6.2	6.57	99.57
Rubbish	0	0.81	0.4	0.43	100

of small mammals distinguished the diet of cats from that of dingoes; large mammals distinguished the diet of dingoes from that of cats; and while medium-sized mammals were present in the diet of both species, they were more prevalent in the diet of dingoes. Vegetation and rubbish were more closely associated with the diet of dingoes, while a higher content of birds, reptiles, and arthropods distinguished the diet of cats from that of dingoes (Table 1).

The patterns in the SIMPER analysis were supported by the DISTLM and the dbRDA (Fig. 2; Table 1). The Draftsman Plot tool revealed that *past annual rainfall* and *past winter rainfall* were collinear and we removed the latter from the model. The marginal tests showed that 2 explanatory variables had a highly significant relationship ($P < 0.001$, *species* and *past annual rainfall*), and 1 variable had a significant relationship ($P < 0.01$, *position*) with the multivariate dietary data cloud. These 3 variables produced the most parsimonious model; *species* (i.e., cat versus dingo) explained most of the variation in scat composition (adjusted $R^2 = 0.247$) and the addition of *position* and then *past annual rainfall* resulted in a marginal increase in explanatory power (adjusted $R^2 = 0.253$). The first 2 dbRDA axes captured 99.4% of the variability in the fitted model, but
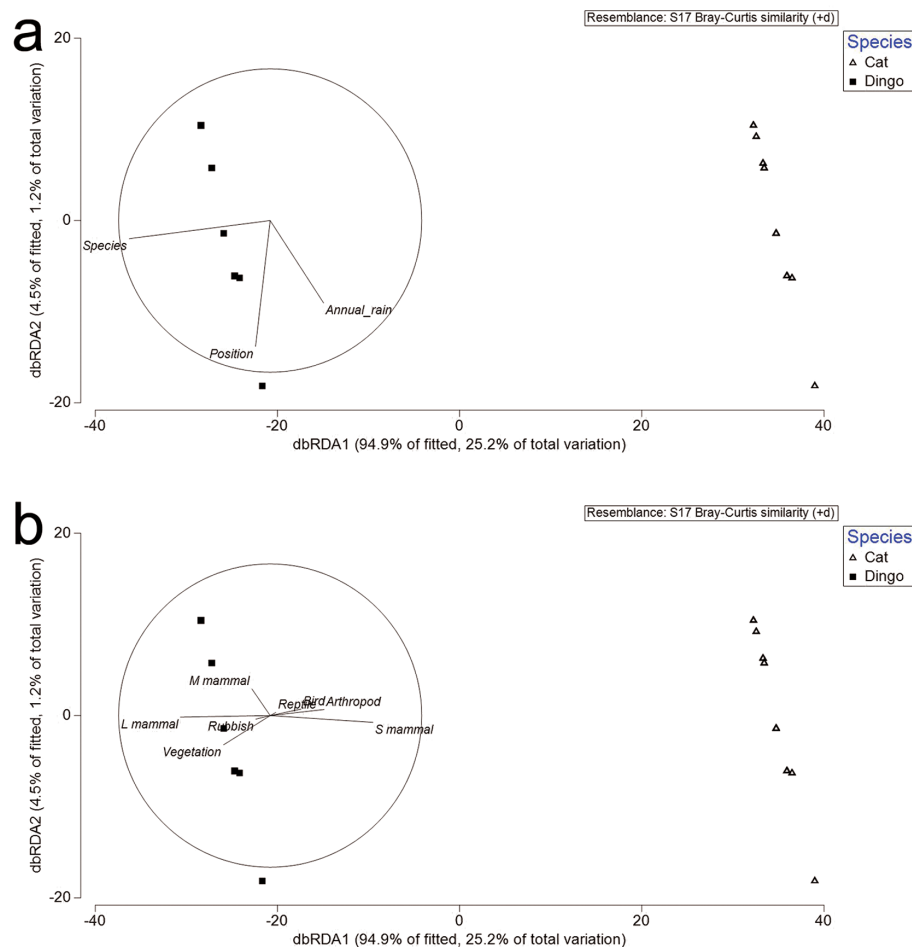
Fig. 2.—a) Distance-based redundancy analysis (dbRDA) of food category volume data from the most parsimonious model with 3 explanatory variables, and b) the same dbRDA model with a vector overlay of food category abundance Pearson correlations with the dbRDA axes. *L mammal* = large mammal; *M mammal* = medium-sized mammal; *S mammal* = small mammal; *Annual_rain* = rainfall (mm) in 12 months prior to scat collection.

Table 2.—Observed (*O*) and expected (*E*, simulated mean) Pianka's index for temporal, spatial, and dietary overlap. One-tailed *P*-values are based on 10,000 randomizations, and a priori predictions were based on competition theory. Frequency = % frequency occurrence of prey items in diet; Volume = % volumetric representation of prey items in diet.

Species	Overlap type	Location	Predicted overlap	Observed	Expected	*P*-value
Dingo/cat	Frequency	All	High	0.343	0.549	0.899
Dingo/cat	Volume	All	High	0.133	0.376	0.933
Cat/cat	Frequency	Refuge/non-refuge	Low	0.962	0.542	0.002
Cat/cat	Volume	Refuge/non-refuge	Low	0.993	0.356	0.000

only 26.4% of the total variation in the data cloud (Fig. 2). Axis 1 explained most of the variation in scat composition and it was most strongly related to *species* and to a lesser extent *past annual rainfall* (multiple partial correlations = −0.931 and 0.353, respectively). The 2nd axis was most strongly related to *landscape position* and then to *past annual rainfall* (multiple partial correlations = −0.831 and −0.544, respectively). The vector overlay of food categories showed that large mammal and small mammal components were most strongly dissociated along axis 1, aligning with dingo and cat, respectively. The same relationship was apparent with vegetation and medium-sized mammals (less so) versus arthropods and birds (less so), though the correlation was not as strong. Small mammals, arthropods, and birds (less so) were also weakly positively associated with *past annual rainfall* along axis 1. Along axis 2, medium-sized mammals were weakly associated with high landscape position.

Consistent with the SIMPER and dbRDA analyses, dietary overlap between cats and dingoes was not higher than expected by chance (Table 2). Dietary overlap for cats between the refuge and non-refuge was significantly higher than expected by chance based on the broad food categories (Table 2). However, there were substantial differences in the proportions of mammalian prey consumed by cats between the refuge and non-refuge. Within the refuge, the critically endangered central rock-rat (*Zyzomys pedunculatus*) was the dominant diet item (22.8% of total scat volume; 25% by frequency of occurrence), followed by the fat-tailed antechinus (*Pseudantechinus macdonnellensis*; 19.0% vol.; 25% freq.), and house mouse (*Mus musculus*; 2.8% vol.; 5.6% freq.; Fig. 3). Outside the refuge, the desert mouse (*Pseudomys desertor*) was the dominant diet item (26.2% vol.; 42.1% freq.), followed by the house mouse (7.6% vol.; 10.5% freq.), fat-tailed pseudantechinus (4.2% vol.; 10.5% freq.), and long-haired rat (*Rattus villosissimus*; 2.6% vol.; 2.6% freq.; Fig. 3).

Within the large and medium-sized mammal prey categories for dingoes, the euro dominated (30.2% vol.; 49.0% freq.), followed by cattle (*Bos taurus*; 8.1% vol.; 10.2% freq.), cat (6.7% vol.; 9.2% freq.), short-beaked echidna (*Tachyglossus aculeatus*; 5.7% vol.; 7.1% freq.), horse (5.3% vol.; 8.2% freq.), red kangaroo (*Macropus rufus*; 4.8% vol.; 5.1% freq.), rabbit (2.0% vol.; 2% freq.), common brushtail possum (*Trichosurus vulpecula vulpecula*; 0.9% vol.; 1.0% freq.), and dingo (0.2% vol.; 1.0% freq.; Fig. 4). We found no incidence of dingo predation on the central rock-rat or fat-tailed pseudantechinus and only 1 incidence of predation on the desert mouse (0.0% vol.; 1% freq.).
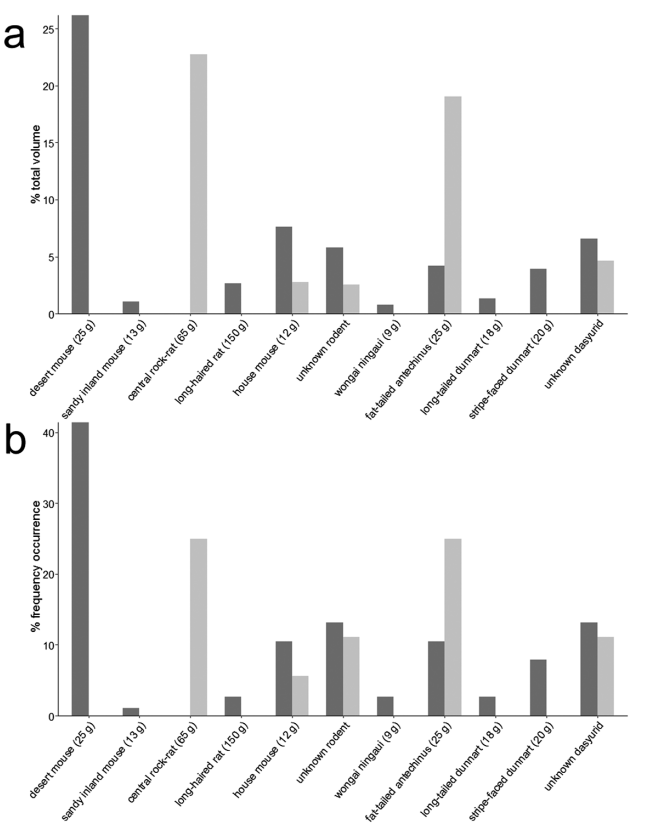

Fig. 3.—a) % volume of small mammal species in cat (*Felis catus*) scats in non-refuge (dark gray) and refuge habitats (light gray), and b) % frequency of occurrence of small mammal species identified from cat scats collected in non-refuge (dark gray) and refuge habitats (light gray) in the MacDonnell Ranges, Northern Territory, central Australia.

DISCUSSION

We investigated the hypothesis that dingoes suppress cats through trophic competition mechanisms and that this suppression helps to sustain a refuge for rare mammals in the MacDonnell Ranges. We found no evidence consistent with exploitation competition between the 2 predators and some evidence consistent with interference competition. Although predation by dingoes could limit densities of cats across the region, it is hard to see how this could explain why the most rugged habitats in the region are a refuge for rare mammals.

Cats and dingoes had highly divergent diets in the MacDonnell Ranges, suggesting limited potential for exploitation competition during periods of food shortage (Wiens 1993). We found that cats fed mostly on small mammals and particularly rodents. Globally, cats are exceptional hunters of rodents
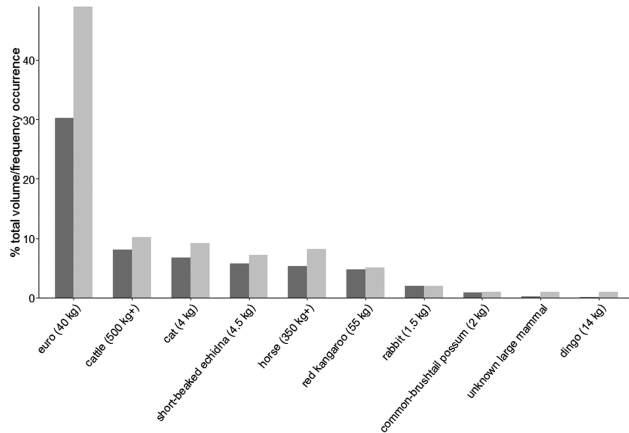
Fig. 4.—% volume (dark gray) and frequency occurrence (light gray) of medium and large mammal species identified from dingo (*Canis lupus dingo*) scats in the MacDonnell Ranges, Northern Territory, central Australia.

and rabbits (Pearre and Maass 1998), which is also consistent with most studies from dryland Australia (Pavey et al. 2008; Spencer et al. 2014; Doherty 2015). In contrast, dingoes are highly flexible predators capable of consuming small, medium-sized, and large mammal prey (Corbett 1995). This flexibility relates to body size and sociality—dingoes (~13–15 kg) are large enough to capture and subdue large mammals, particularly when hunting in packs (Corbett 1995), but small enough that they are not constrained by the energy requirements for large prey imposed on large carnivores (> 21.5 kg—Carbone et al. 1999). The diet of dingoes in the MacDonnell Ranges was dominated by 1 species of large kangaroo, the euro, which was also the most widely detected mammal species in our study area in 2011–2013 (McDonald et al. 2017). Therefore, the availability of a stable population of large kangaroos probably underpins the low likelihood of exploitation competition between cats and dingoes in the MacDonnell Ranges.

We found no evidence that competition with dingoes has driven a dietary niche shift in the refuge—there was high overlap between the refuge and non-refuge diets of cats. The high incidence of central rock-rat and fat-tailed pseudantechinus remains in cat scats collected in the refuge supported our a priori split of cat scats into refuge and non-refuge categories; these small mammal species are restricted to or more widespread within the refuge, respectively (McDonald et al. 2015; McDonald et al. 2017). Our dietary data, together with previous data on the occurrence of small mammals in the study area, suggest that cats preferentially hunt larger rodents. Specifically, in non-refuge habitats the desert mouse (25 g), a specialist inhabitant of dense spinifex grasslands (Letnic and Dickman 2005; McDonald et al. 2016), was the dominant small mammal prey, yet its occurrence is highly restricted compared with the smaller (12 g), habitat-generalist house mouse (McDonald et al. 2017). The house mouse was rarely consumed by cats. Similarly, in the refuge, the central rock-rat (65 g) was dominant in the diet of cats despite having a more restricted occupancy than both the fat-tailed pseudantechinus (25 g) and house

mouse (McDonald et al. 2015, 2016). The preference for larger rodents presumably confers an energetic advantage for cats targeting these species (MacArthur and Pianka 1966) and provides some support to the idea that predation by feral cats is an important factor in the ongoing declines of the central rock-rat and other critical weight range rodent species (McDonald et al. 2015, 2017; Davies et al. 2017). In the face of targeted predation by cats, the persistence of the central rock-rat and desert mouse could be facilitated by the fine-scale protection afforded by rockiness and dense spinifex grass, respectively (McGregor et al. 2015; McDonald et al. 2016).

Consistent with interference competition, cats were the third most frequently consumed mammal species by dingoes (6.7% vol.; 9.2% freq.). To our knowledge, this is the highest incidence of cat consumption by dingoes thus far recorded for dryland Australia (Paltridge 2002; Pavey et al. 2008; Doherty 2015) and possibly the highest incidence of canid consumption of a felid globally (Macdonald and Sillero-Zubiri 2004). While this suggests that predation by dingoes could maintain lower densities of cats in the MacDonnell Ranges, even a high incidence of intraguild predation may not have population-level impacts. For example, in Tanzania, predation by African lions (*Panthera leo*) was the leading cause of juvenile mortality in cheetahs (*Acinonyx jubatus*—Laurenson 1994). However, despite a tripling of the lion population over 3 decades, the cheetah population remained relatively stable in the study area (Swanson et al. 2014). Similarly, in South Africa, lions accounted for > 20% of leopard (*Panthera pardus*) mortality but did not suppress their population or distribution (Balme et al. 2017). Determining whether dingo predation on cats is compensatory or additive will require manipulation of densities of dingoes (Newsome et al. 2015). Previous experimental studies (Allen et al. 2013, 2018) have been unable to address this question because they could not effectively or consistently reduce dingo populations (Johnson et al. 2014).

We were unable to evaluate evidence for an additional potential mechanism for suppression of cats by dingoes, that foraging behavior or densities of cats are influenced by a "landscape of fear" associated with avoidance of dingoes (Kennedy et al. 2012; Greenville et al. 2014). For a "landscape of fear" to negatively influence cats at the population level, avoidance of dingoes by cats must have an energetic cost. However, in the MacDonnell Ranges, even if cat activity was influenced by dingoes, our data demonstrating that cats consumed their preferred rodent prey throughout the study area suggest that foraging strategies of cats are not strongly influenced by dingoes in refuge or non-refuge locations.

In summary, we found no evidence that dingoes affect cats through exploitative trophic competition in the MacDonnell Ranges; diets of cats and dingoes were highly divergent and cats targeted their preferred small mammal prey in refuge and non-refuge habitats. While we found a relatively high incidence of dingo predation on cats, we do not know whether predation was compensatory or additive. Regardless of whether dingo predation influences densities of cats in the MacDonnell Ranges, predation does not explain why the most rugged

habitats in the region are a refuge for rare mammals. We therefore conclude that habitat complexity, and its effect on foraging efficiency of mammalian predators, remains the most likely mechanism underpinning the refuge (McDonald et al. 2017). Dingo predation of cats is either of secondary importance (if predation is additive) or is not a factor (if predation is compensatory) in contributing to the maintenance of the refuge for rare small mammals.

SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Percent occurrence (% occurrence) and percent volumetric (% volume) composition of prey types in dingo (*Canis lupus dingo*) and cat (*Felis catus*) scats collected in the MacDonnell Ranges, central Australia. The dingo data include all scats collected across the study area, whereas the cat data are separated into refuge and non-refuge locations. See "Materials and Methods" section for more information.

Supplementary Data SD2.—Accumulation of prey diversity with increasing scat sample size for the dingo (*Canis lupus dingo*) and feral cat (*Felis catus*) in the MacDonnell Ranges, Northern Territory, central Australia.

LITERATURE CITED

ALLEN, B. L., L. R. ALLEN, R. M. ENGEMAN, AND L. K. LEUNG. 2013. Intraguild relationships between sympatric predators exposed to lethal control: predator manipulation experiments. Frontiers in Zoology 10:39.

ALLEN, B. L., A. FAWCETT, A. ANKER, R. M. ENGEMAN, A. LISLE, AND L. K. LEUNG. 2018. Environmental effects are stronger than human effects on mammalian predator-prey relationships in arid Australian ecosystems. The Science of the Total Environment 610:451–461.

ANDERSON, M., R. N. GORLEY, AND R. K. CLARKE. 2008. Permanova+ for Primer: Guide to Software and Statistical Methods. Primer-E Limited, Plymouth.

ARCHER, M. 1981. Results of the Archbold Expeditions. No. 104. Systematic revision of the marsupial dasyurid genus *Sminthopsis* Thomas. Bulletin of the American Museum of Natural History 168:61–224.

BALME, G. A., T. PITMAN, H. S. ROBINSON, J. R. MILLER, P. J. FUNSTON, AND L. T. HUNTER. 2017. Leopard distribution and abundance is unaffected by interference competition with lions. Behavioral Ecology 28:1348–1358.

BONESI, L., P. CHANIN, AND D. W. MACDONALD. 2004. Competition between Eurasian otter *Lutra lutra* and American mink *Mustela vison* probed by niche shift. Oikos 106:19–26.

BOX, J. B., ET AL. 2008. Central Australian waterbodies: the importance of permanence in a desert landscape. Journal of Arid Environments 72:1395–1413.

BRILLOUIN, L. 1956. Science and information theory. Academic Press, New York.

BRUNNER, H., AND B. TRIGGS. 2002. Hair ID: an interactive tool for identifying Australian mammalian hair. CSIRO Publishing, Collingwood, Victoria, Australia.

CARBONE, C., G. M. MACE, S. C. ROBERTS, AND D. W. MACDONALD. 1999. Energetic constraints on the diet of terrestrial carnivores. Nature 402:286–288.

CLARKE, K. R., AND R. N. GORLEY. 2015. Getting started with PRIMER v7. PRIMER-E, Plymouth, United Kingdom.

CORBETT, L. K. 1995. The dingo in Australia and Asia. UNSW Press, Sydney, New South Wales, Australia.

DAVIES, H. H., ET AL. 2017. Top-down control of species distributions: feral cats driving the regional extinction of a threatened rodent in northern Australia. Diversity and Distributions 23:272–283.

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.

EALEY, E. H. M., P. J. BENTLEY, AND A. R. MAIN. 1965. Studies on water metabolism of the hill kangaroo, *Macropus robustus* (Gould), in northwest Australia. Ecology 46:473–479.

EDWARDS, G. P., N. DE PREU, B. J. SHAKESHAFT, I. V. CREALY, AND R. M. PALTRIDGE. 2001. Home range and movements of male feral cats (*Felis catus*) in a semiarid woodland environment in central Australia. Austral Ecology 26:93–101.

ENTSMINGER, G. L. 2014. EcoSim Professional: null modeling software for ecologists, version 1. Acquired Intelligence Inc., Kesey-Bear, and Pinyon Publishing, Montrose, Colorado.

FEDRIANI, J. M., T. K. FULLER, R. M. SAUVAJOT, AND E. C. YORK. 2000. Competition and intraguild predation among three sympatric carnivores. Oecologia 125:258–270.

GREENVILLE, A. C., G. M. WARDLE, B. TAMAYO, AND C. R. DICKMAN. 2014. Bottom-up and top-down processes interact to modify intraguild interactions in resource-pulse environments. Oecologia 175:1349–1358.

HARRINGTON, L. A., ET AL. 2009. The impact of native competitors on an alien invasive: temporal niche shifts to avoid interspecific aggression. Ecology 90:1207–1216.

HERNANDEZ-SANTIN, L., GOLDIZEN, A. W., AND D. O. FISHER. 2016. Introduced predators and habitat structure influence range contraction of an endangered native predator, the northern quoll. Biological Conservation 203:160–167.

HERTEINSSON, P., AND D. W. MACDONALD. 1992. Interspecific competition and the geographical distribution of red and arctic foxes *Vulpes vulpes* and *Alopex lagopus*. Oikos 1992:505–515.

HOFFMAN, M., ET AL. 2011. The changing fates of the world's mammals. Philosophical Transactions of the Royal Society of London B: Biological Sciences 366:2598–2610.

JOHNSON, C. N., ET AL. 2014. Experiments in no-impact control of dingoes: comment on Allen *et al*. 2013. Frontiers in Zoology 11:17.

KEDDY, P. A. 2001. Competition. Springer, Dordrecht.

KENNEDY, M., B. L. PHILLIPS, S. LEGGE, S. A. MURPHY, AND R. A. FAULKNER. 2012. Do dingoes suppress the activity of feral cats in northern Australia? Austral Ecology 37:134–139.

KLARE, U., J. F. KAMLER, AND D. W. MACDONALD. 2011. A comparison and critique of different scat-analysis methods for determining carnivore diet. Mammal Review 41:294–312.

KORPIMÄKI, E. 1987. Dietary shifts, niche relationships and reproductive output of coexisting kestrels and long-eared owls. Oecologia 74:277–285.

Laurenson, M. K. 1994. High juvenile mortality in cheetahs (*Acinonyx jubatus*) and its consequences for maternal care. Journal of Zoology 234:387–408.

Legge, S., et al. 2017. Enumerating a continental-scale threat: how many feral cats are in Australia? Biological Conservation 206:293–303.

Letnic, M., and C. R. Dickman. 2005. The responses of small mammals to patches regenerating after fire and rainfall in the Simpson Desert, Australia. Austral Ecology 30:24–39.

Linnell, J. D. C., and O. Strand. 2000. Interference interactions, co-existence and conservation of mammalian carnivores. Diversity and Distributions 6:169–176.

MacArthur, R. H., and E. R. Pianka. 1966. On optimal use of a patchy environment. The American Naturalist 100:603–609.

Macdonald, D. W., and C. Sillero-Zubiri. 2004. Wild canids—an introduction and dramatis personae. Pp. 3–36 in Biology and conservation of wild canids (D. W. Macdonald and S. Sillero-Zubiri, eds.). Oxford University Press, Oxford, United Kingdom.

McDonald, P. J., et al. 2017. Habitat as a mediator of mesopredator-driven mammal extinction. Conservation Biology 31:1183–1191.

McDonald, P. J., A. D. Griffiths, C. E. M. Nano, C. R. Dickman, S. J. Ward, and G. W. Luck. 2015. Landscape-scale factors determine occupancy of the critically endangered central rock-rat in arid Australia: the utility of camera trapping. Biological Conservation 191:93–100.

McDonald, P. J., A. Stewart, and C. R. Dickman. 2018. Applying the niche reduction hypothesis to modelling distributions: a case study of a critically endangered rodent. Biological Conservation 217C:207–212.

McDonald, P. J., A. Stewart, A. T. Schubert, C. E. M. Nano, C. R. Dickman, and G. W. Luck. 2016. Fire and grass cover influence occupancy patterns of rare rodents and feral cats in a mountain refuge: implications for management. Wildlife Research 43:121–129.

McGregor, H., S. Legge, M. E. Jones, and C. N. Johnson. 2015. Feral cats are better killers in open habitats, revealed by animal-borne video. PLoS One 10:e0133915.

Moseby, K. E., H. Neilly, J. L. Read, and H. A. Crisp. 2012. Interactions between a top order predator and exotic mesopredators in the Australian rangelands. International Journal of Ecology 2012:250352.

Nano, C. E. M., and P. J. Clarke. 2008. Variegated desert vegetation: covariation of edaphic and fire variables provides a framework for understanding mulga-spinifex coexistence. Austral Ecology 33:848–862.

Newsome, T. M., et al. 2015. Resolving the value of the dingo in ecological restoration. Restoration Ecology 23:201–208.

Paltridge, R. 2002. The diets of cats, foxes and dingoes in relation to prey availability in theTanami Desert, Northern Territory. Wildlife Research 29:389–403.

Pavey, C. R., S. R. Eldridge, and M. Heywood. 2008. Native and introduced predator population dynamics and prey selection during a rodent outbreak in arid Australia. Journal of Mammalogy 89:674–683.

Pearre, S., and R. Maass. 1998. Trends in the prey size-based trophic niches of feral and house cats *Felis catus* L. Mammal Review 28:125–39.

Sidorovich, V. E., H. Kruuk, and D. W. Macdonald. 1999. Body size, and interactions between European and American mink (*Mustela lutreola* and *M. vison*) in Eastern Europe. Journal of Zoology 248:521–527.

Spencer, E. E., M. S. Crowther, and C. R. Dickman. 2014. Diet and prey selectivity o three species of sympatric mammalian predators in central Australia. Journal of Mammalogy 95:1278–1288.

Swanson, A., et al. 2014. Cheetahs and wild dogs show contrasting patterns of suppression by lions. The Journal of Animal Ecology 83:1418–1427.

Thackway, R., and I. D. Creswell.1995. An interim bioregionalisation for Australia. Australian Nature Conservation Agency, Canberra, Australian Capital Territory, Australia.

Triggs, B. E. 1996. Tracks, scats and other traces: a field guide to Australian mammals. Oxford University Press, Melbourne, Victoria, Australia.

Watts, C. H. S., and H. J. Aslin. 1981. The rodents of Australia. Angus and Robertson, Sydney, New South Wales, Australia.

Wiens, J. A. 1993. The ecology of bird communities: processes and variations. Cambridge University Press, Cambridge, United Kingdom.

Woinarski, J. C. Z., A. A. Burbidge, and P. L. Harrison. 2015. Ongoing unraveling of a continental fauna: decline and extinction of Australian mammals since European settlement. Proceedings of the National Academy of Sciences of the United States of America 112:4531–4540.