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Running header: Cat and dingo competition

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 analysed 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

1 in diet of cats, as their diets in refuges and non-refuges were highly overlapping. Consistent
2 with interference competition, cats were the third most frequently consumed mammal species
3 by dingoes. Although predation by dingoes could limit densities of cats across the
4 MacDonnell Ranges, this alone does not explain why the most rugged habitats in the region
5 are a refuge for rare mammals. We conclude that habitat complexity most likely underpins
6 the refuge and that possible effects of dingo predation on the cat population would be of
7 secondary importance.

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

19 While Australia's mammal extinctions and declines have been exceptional on a global
20 scale, declines have not been geographically uniform. For example, 3 species of native
21 mammal that once occurred widely on mainland Australia are now confined to Australia's
22 largest fox-free island, Tasmania (Woinarski et al. 2015). Variation in mesopredator-driven
23 mammal decline on the Australian mainland has also been linked to variation in habitat
24 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.

1 The theoretical mechanisms for suppression of cats by dingoes are exploitation and
2 interference competition. Exploitation competition occurs between 2 species when there is
3 high niche overlap (Wiens 1989). For example, when there is high dietary overlap between a
4 pair of species, one species will outcompete the other in times of food shortage (Korpimäki
5 1987). Exploitation competition may also drive niche shift in one species, forcing its
6 increased use of a sub-optimal niche (Bonesi et al. 2004; Harrington et al. 2009). Interference
7 competition occurs when one species limits another's use of resources (Wiens 1993). In
8 carnivores, this process includes intraguild predation and a fear of predation that drives
9 spatial and temporal avoidance of a larger carnivore (Fedriani et al. 2000; Linnell and Strand
10 2000). These phenomena are demonstrably important in intraguild relationships among
11 carnivores, often with consequences for conservation (e.g., Hersteinsson and Macdonald
12 1992; Sidorovich et al. 1999; Moehrenschrager et al. 2007).

13 Understanding the trophic ecology of dingoes and cats is a prerequisite to uncovering
14 potentially important competitive interactions between the 2 predators that help to maintain
15 the mammal refuge. While studies from Australia's sandy desert systems have found
16 moderate to high dietary overlap between dingoes and cats (Paltridge 2002; Pavey et al.
17 2008; Spencer et al. 2014), no dietary research has been undertaken in the biologically distinct
18 central Australian uplands. The MacDonnell Ranges differ from the sandy deserts in their
19 complex topography (McDonald et al. 2015), variegated and well-defined vegetation
20 communities (Nano and Clarke 2008), and abundant natural surface water (Box et al. 2008).
21 This environment supports a substantial population of a large macropod, the euro or hill
22 kangaroo (*Osphranter robustus*; McDonald et al. 2017), which thrives here because of access
23 to abundant areas of shade (afforded by caves, overhangs, and vegetation) used as shelter
24 during the day and surface water (Ealey et al. 1965). Unlike cats, dingoes are large enough to
25 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 sub-optimal 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 semi-arid Australia, with 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.)

1 and *Acacia* (e.g., *Acacia aneura*) shrublands dominating the rocky landforms, while rivers
2 and alluvial plains support river red gum (*Eucalyptus camaldulensis*) and ironwood (*Acacia*
3 *estrophiolata*) woodlands. We defined the rugged quartzite mountain ranges as a refuge
4 because they support several species of mammals that no longer occur, or are very rare,
5 outside of this landform (McDonald et al. 2017).

6 *Collection and analysis of fecal remains.*— Cat and dingo fecal remains (hereafter
7 ‘scats’) were collected opportunistically throughout the study area (Fig. 1b). Cat and dingo
8 scats were collected between 2011-13 and cat scats were also collected in 2015-16. Only
9 intact scats judged to be <6 months old were used for analysis. We identified scats as cat or
10 dingo according to size, shape, and smell (Triggs 1996). We placed scats individually into
11 paper bags and then into an oven at 70°C for >10 hours to kill parasites. We then washed
12 samples through a series of sieves that left only indigestible fragments of prey. We placed
13 fragments into sorting trays divided into 4 equal sections for inspection and visual estimation
14 of percentage volume of prey categories. Mammals were identified to the lowest possible
15 taxonomic level by inspection of hair remains using cross-section and whole-mount
16 techniques, and jaw and skull fragments (Archer et al. 1981; Watts and Aslin 1981; Brunner
17 and Triggs 2002). Mammals were classified into size categories of small (<500 g), medium
18 (500-6,999 g) and large ($\geq 7,000$ g). All other prey items were categorized as arthropod,
19 reptile or frog, bird, vegetation, or rubbish.

20 *Analysis.*— To determine whether our scat sample sizes were sufficient for capturing
21 mammal species and dietary diversity, we plotted the cumulative diversity of all mammal
22 species and the other food categories against the number of scats examined for both cats and
23 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 i th 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 analysis procedure (SIMPER) to determine within- and between-group diagnostic food categories for each species. We then used distance-based linear models (DISTLM) 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:

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

where j and k are the 2 species being compared, and p_i is the frequency of occurrence (or volume) of the i th 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).

SIMPER 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 second- and third-order contributors for cats, followed by reptiles or frogs and medium-size mammals. Vegetation (mostly masticated grass likely consumed by euros and other large mammal prey) and medium-size mammals were second- and third-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 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-size 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 distance-based linear model and the distance-based redundancy analysis (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 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 second 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-size 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-size 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 (*Zyomys 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. 4a).

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. 4b). 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.).

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

1 how this could explain why the most rugged habitats in the region are a refuge for rare
2 mammals.

3 Cats and dingoes had highly divergent diets in the MacDonnell Ranges, suggesting
4 limited potential for exploitation competition during periods of food shortage (Wiens 1993).
5 We found that cats fed mostly on small mammals and particularly rodents. Globally, cats are
6 exceptional hunters of rodents and rabbits (Pearre and Maass 1998), which is also consistent
7 with most studies from dryland Australia (Pavey et al. 2008; Spencer et al. 2014; Doherty
8 2015). In contrast, dingoes are highly flexible predators capable of consuming small,
9 medium-sized, and large mammal prey (Corbett 1995). This flexibility relates to body size
10 and sociality – dingoes (~13-15 kg) are large enough to capture and subdue large mammals,
11 particularly when hunting in packs (Corbett 1995), but small enough that they are not
12 constrained by the energy requirements for large prey imposed on large carnivores (>21.5 kg;
13 Carbone et al. 1999). The diet of dingoes in the MacDonnell Ranges was dominated by 1
14 species of large kangaroo, the euro, which was also the most widely detected mammal
15 species in our study area in 2011-2013 (McDonald et al. 2017). Therefore, the availability of
16 a stable population of large kangaroos probably underpins the low likelihood of exploitation
17 competition between cats and dingoes in the MacDonnell Ranges.

18 We found no evidence that competition with dingoes has driven a dietary niche shift
19 in the refuge – there was high overlap in cat's refuge and non-refuge diets. The high
20 incidence of central rock-rat and fat-tailed pseudantechinus remains in cat scats collected in
21 the refuge supported our *a priori* split of cat scats into refuge and non-refuge categories;
22 these small mammal species are restricted to or more widespread within the refuge,
23 respectively (McDonald et al. 2015; McDonald et al. 2017). Our dietary data, together with
24 previous data on the occurrence of small mammals in the study area, suggest that cats
25 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 feral cat predation 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. 2016). 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).

In this study, we were unable to evaluate evidence for an additional potential mechanism for suppression of cats by dingoes, that cat foraging behavior or densities 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 exploit cats through 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.

ACKNOWLEDGMENTS

We thank the traditional owners of Tjoritja/West MacDonnell NP for allowing access to the survey locations. Park rangers from the NT Parks and Wildlife Commission assisted with the collection of predator scats, particularly C. Stenhouse. G. Story analyzed the dingo scat remains. E. Connellan from Mengel's Heli Services flew us into all remote sites.

SUPPLEMENTARY DATA

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 methods section for more information.

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

LITERATURE CITED

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

- 1 ALLEN, B. L., L. R. ALLEN, L. K. LEUNG, AND ENGEMAN, R. M. 2013. Intraguild relationships
2 between sympatric predators exposed to lethal control: predator manipulation experiments.
3 *Frontiers in Zoology* 10:39.
- 4 ARCHER, M. 1981. Results of the Archbold Expeditions. No. 104. Systematic revision of the
5 marsupial dasyurid genus *Sminthopsis* Thomas. *Bulletin of the American Museum of Natural*
6 *History* 168:61–224.
- 7 BALME, G. A., T. PITMAN, H. S. ROBINSON, J. R. MILLER, P. J. FUNSTON, AND L. T. HUNTER.
8 2017. Leopard distribution and abundance is unaffected by interference competition with
9 lions. *Behavioral Ecology* 28:1348–1358.
- 10 BATES, D., ET AL. 2014. Package ‘lme4’. R foundation for statistical computing, Vienna.
- 11 BIRCH, L.C. 1957. The meanings of competition. *The American Naturalist* 91:5–18.
- 12 BONESI, L., P. CHANIN, AND D. W. MACDONALD. 2004. Competition between Eurasian otter
13 *Lutra lutra* and American mink *Mustela vison* probed by niche shift. *Oikos* 106:19-26.
- 14 BRILLOUIN, L. 1956. Science and information theory. Academic Press, Michigan.
- 15 BOX, J. B., ET AL. 2008. Central Australian waterbodies: the importance of permanence in a
16 desert landscape. *Journal of Arid Environments* 72:1395–1413.
- 17 BRUNNER, H., AND B. TRIGGS. 2002. Hair ID: an interactive tool for identifying Australian
18 mammalian hair. CSIRO Publishing, Collingwood, Australia.
- 19 BURNHAM, K. P, AND D. R. ANDERSON. 2003. Model selection and multimodel inference: a
20 practical information-theoretic approach. Springer Science and Business Media, Colorado
21 State University.
- 22 CARBONE, C., G. M. MACE, S. C. ROBERTS, AND D. W. MACDONALD. 1999. Energetic
23 constraints on the diet of terrestrial carnivores. *Nature* 402:286–288.

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

3 CORBETT, L. K. 1995. The dingo in Australia and Asia. UNSW Press, Sydney.

4 COZZI, G., F. BROEKHUIS, J. W. MCNUTT, L. A. TURNBULL, D. W. MACDONALD, AND B.
5 SCHMID. 2012. Fear of the dark or dinner by moonlight? Reduced temporal partitioning
6 among Africa's large carnivores. *Ecology* 93:2590-2599.

7 DAVIES, H. H., ET AL. 2017. Top - down control of species distributions: feral cats driving the
8 regional extinction of a threatened rodent in northern Australia. *Diversity and Distributions*
9 23:272-283.

10 DOHERTY, T. S. 2015. Dietary overlap between sympatric dingoes and feral cats at a semiarid
11 rangeland site in Western Australia. *Australian Mammalogy* 37:219-224.

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

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

17 ENTSMINGER, G. L. 2014. EcoSim Professional: null modeling software for ecologists,
18 Version 1. Acquired Intelligence Inc., Kesey-Bear, and Pinyon Publishing. Montrose,
19 Colorado. www.garyentsminger.com/ecosim/index.htm.

20 FEDRIANI, J. M., T. K. FULLER, R. M. SAUVAJOT, AND E. C. YORKE. 2000. Competition and
21 intraguild predation among three sympatric carnivores. *Oecologia* 125:258-270.

22 FRANK, A. S., ET AL. 2014. Experimental evidence that feral cats cause local extirpation of
23 small mammals in Australia's tropical savannas. *Journal of Applied Ecology* 51:1486-1493.

1 HERTEINSSON, P., AND D. W. MACDONALD. 1992. Interspecific competition and the
2 geographical distribution of red and arctic foxes *Vulpes vulpes* and *Alopex lagopus*. *Oikos*
3 1992:505-515.

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

6 KORPIMÄKI, E. 1987. Dietary shifts, niche relationships and reproductive output of coexisting
7 Kestrels and Long-eared Owls. *Oecologia* 74:277-285.

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

10 LEGGE, S. 2017. Enumerating a continental-scale threat: How many feral cats are in
11 Australia? *Biological Conservation* 206:293-303.

12 LETNIC, M. AND C. R. DICKMAN. 2005. The responses of small mammals to patches
13 regenerating after fire and rainfall in the Simpson Desert, Australia. *Austral Ecology* 30:24–
14 39.

15 LINNELL, J. D. C., AND O. STRAND. 2000. Interference interactions, co - existence and
16 conservation of mammalian carnivores. *Diversity and Distributions* 6:169-176.

17 MACDONALD, D. W., AND C. SILLERO-ZUBIRI. 2004. Wild canids—an introduction and
18 dramatis personae. Pp. 3–36 in *Biology and conservation of wild canids* (D. W. Macdonald
19 and S. Sillero-Zubiri, eds.). Oxford University Press, Oxford.

20 MAHON, P. S., P. B. BANKS, AND C. R. DICKMAN. 1998. Population indices for wild
21 carnivores: a critical study in sand-dune habitat, south-western Queensland. *Wildlife*
22 *Research* 25:11-22.

1 MCDONALD, P. J., A. D. GRIFFITHS, C. E. M. NANO, C. R. DICKMAN, S. J. WARD, AND G. W.
2 LUCK. 2015. Landscape-scale factors determine occupancy of the critically endangered
3 central rock-rat in arid Australia: the utility of camera trapping. *Biological Conservation*
4 191:93-100.

5 MCDONALD, P. J., C. E. M. NANO, S. J. WARD, A. STEWART, C. R. PAVEY, G. W. LUCK, AND
6 C. R. DICKMAN. 2017. Habitat as a mediator of mesopredator - driven mammal extinction.
7 *Conservation Biology* 31:1183-1191.

8 MCDONALD, P.J., A. STEWART, AND C. R. DICKMAN. 2018. Applying the niche
9 reduction hypothesis to modelling distributions: A case study of a critically endangered
10 rodent. *Biological Conservation* 217C:207-212.

11 MCDONALD, P. J., A. STEWART, A. T. SCHUBERT, C. E. M. NANO, C. R. DICKMAN, AND G. W.
12 LUCK. 2016. Fire and grass cover influence occupancy patterns of rare rodents and feral cats
13 in a mountain refuge: implications for management. *Wildlife Research* 43:121-129.

14 MCGREGOR, H., S. LEGGE, M. E. JONES, AND C. N. JOHNSON. 2015. Feral cats are better killers
15 in open habitats, revealed by animal-borne video. *PLoS One* 10:e0133915.

16 MOEHRENSCLAGER, A., R. LIST, AND D. W. MACDONALD. 2007. Escaping intraguild
17 predation: Mexican kit foxes survive while coyotes and golden eagles kill Canadian swift
18 foxes. *Journal of Mammalogy* 88:1029-1039.

19 MOSEBY, K. E., B. HILL, AND J. L. READ. 2009. Arid Recovery—A comparison of reptile
20 and small mammal populations inside and outside a large rabbit, cat and fox - proof
21 enclosure in arid South Australia. *Austral Ecology* 34:156-169.

1 MOSEBY, K. E., H. NEILLY, J. L. READ, AND H. A. CRISP. 2012. Interactions between a top
2 order predator and exotic mesopredators in the Australian rangelands. *International Journal of*
3 *Ecology* 2012:250352.

4 NANO, C. E. M., AND P. J. CLARKE. 2008. Variegated desert vegetation: Covariation of
5 edaphic and fire variables provides a framework for understanding mulga - spinifex
6 coexistence. *Austral Ecology* 33:848-862.

7 NEWSOME, T. M., ET AL. 2015. Resolving the value of the dingo in ecological restoration.
8 *Restoration Ecology* 23:201-208.

9 PALTRIDGE, R. 2002. The diets of cats, foxes and dingoes in relation to prey availability in
10 the Tanami Desert, Northern Territory. *Wildlife Research* 29:389-403.

11 PAVEY, C. R., S. R. ELDRIDGE, AND M. HEYWOOD. 2008. Native and introduced predator
12 population dynamics and prey selection during a rodent outbreak in arid Australia. *Journal of*
13 *Mammalogy* 89:674-683.

14 PEARRE, S., AND R. MAASS. 1998. Trends in the prey size-based trophic niches of feral
15 and house cats *Felis catus* L. *Mammal Review* 28:125-39.

16 SIDOROVICH, V. E., H. KRUUK, AND D. W. MACDONALD. 1999. Body size, and interactions
17 between European and American mink (*Mustela lutreola* and *M. vison*) in Eastern Europe.
18 *Journal of Zoology* 248:521-527.

19 SPENCER, E. E., M. S. CROWTHER, AND C. R. DICKMAN. 2014. Diet and prey selectivity of three
20 species of sympatric mammalian predators in central Australia. *Journal of Mammalogy*
21 95:1278-1288.

22 SWANSON, A., ET AL. 2014. Cheetahs and wild dogs show contrasting patterns of suppression
23 by lions. *Journal of Animal Ecology* 83:1418-1427.

1 THACKWAY, R., AND I. D. CRESWELL. 1995. An interim bioregionalisation for Australia.
2 Australian Nature Conservation Agency, Canberra.

3 TRIGGS, B. E. 1996. Tracks, scats and other traces: a field guide to Australian mammals.
4 Oxford University Press, Melbourne.

5 WIENS, J. A. 1989. The ecology of bird communities: processes and variations. Cambridge
6 University Press, Cambridge.

7 WOINARSKI, J. C. Z., A. A. BURBIDGE, AND P. L. HARRISON. 2015. Ongoing unraveling of a
8 continental fauna: decline and extinction of Australian mammals since European settlement.
9 Proceedings of the National Academy of Sciences of the United States of America 112:4531-
10 4540.

11 WATTS, C. H. S., AND H. J. ASLIN. 1981. The rodents of Australia. Angus and Robertson,
12 Sydney, Australia.

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FIGURE LEGENDS

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).

FIG. 2. (a) 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-size mammal; *S mammal* = small mammal; *Annual_rain* = rainfall (mm) in 12 months prior to scat collection.

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

FIG. 4. % volume (dark gray) and frequency occurrence (light gray) of medium and large mammals species identified from dingo (*Canis lupus dingo*) scats in the MacDonnell Ranges, Northern Territory, central Australia.

TABLE 1. 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. Dietary components contributing $\geq 90\%$ of within-group similarity for each species are shown in bold.

Food category	Av ab cat	Av ab dingo	Av diss	% cont	Cum %
Small mammal	54.66	2.8	26.93	28.57	28.57
Medium mammal	0	49.74	24.87	26.39	54.95
Large 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

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.

Species	Overlap type	Location	Predicted overlap	Observed	Expected	<i>P</i> -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

Frequency = % frequency occurrence of prey items in diet, Volume = % volumetric representation of prey items in diet.

