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Introduced cats (Felis catus) eating a continental fauna

The number of mammals killed in Australia

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Introduced cats (*Felis catus*) eating a continental fauna: the number of mammals killed in Australia


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Abstract

Predation by cats (*Felis catus*) is implicated in the decline and extinction of many Australian mammal species. We estimate the number of mammals killed by cats across Australia through meta-analysis of data on the frequency of mammals in cat diet samples from 107 studies. For feral cats in largely natural landscapes, the spatially-weighted mean frequency of mammals in diet samples was 70% (44% for native species, 34% for introduced species). Frequency was significantly higher on the mainland, and in areas of low temperature and topographic ruggedness. Geographic patterns varied markedly between native and introduced mammals, with native mammals most frequent in northern Australia. We estimate that: (i) 815 million individuals yr$^{-1}$ are killed by feral cats in natural landscapes, 56% of which are native species; (ii) 149 million individuals yr$^{-1}$ are killed by unowned cats in highly modified landscapes; and (iii) 180 million individuals yr$^{-1}$ are killed by pet cats. For the latter two components, mainly introduced species are killed. Collectively, across the three components of the cat population, 1,144 million individuals yr$^{-1}$ are killed by cats, of which, at least 40% (459 million individuals yr$^{-1}$) are native species. It remains challenging to interpret this tally in terms of its impact on population viability for Australian mammals, because demographic information is not available for most species. However, our estimate of annual mammal mortality due to cat predation is substantially higher than that due to another key threatening process, land clearing.

Running head: Predation by cats on Australian mammals

Keywords: conservation; diet; feral cat; introduced predator; mortality; predation

1. Introduction

Globally, mammals constitute the dominant component of the diet of free-roaming cats (*Felis catus*) in most environments and locations (Fitzgerald 1988; Fitzgerald and Turner 2000), including mainland Australia (Doherty et al. 2015). Since their first introduction to Australia following British colonisation in 1788 (Abbott 2008), cats have spread to occupy the entire continent and most larger islands (Abbott et al. 2014; Legge et al. 2017). During this time, the Australian mammal fauna has suffered an unprecedented rate of extinction and decline: 10% of 273 endemic terrestrial species are now extinct, and a further 21% are threatened with extinction (Johnson 2006; Woinarski et al. 2015). Cats have been strongly implicated in many of these mammal declines (Johnson 2006; Woinarski et al. 2015), and are now known to prey upon most Australian mammal species (Woolley et al. submitted). However, there has been no previous quantitative review of the extent of cat predation on Australian mammals and its variation across the continent. Here we extend a previous study by Doherty et al. (2015) that considered continental-scale variation in the frequency of occurrence of mammals (and other groups) in cat diet samples. We follow an approach used to assess the extent of predation by cats on Australian birds (Woinarski et al. 2017) and reptiles (Woinarski et al. 2018a), by combining information on the spatially-modelled density of feral cats, the frequency of
occurrence of mammals reported in a large compilation of local studies of cat diet, and the number of individual mammals reported in individual cat samples from a subset of those studies.

There are several interpretational caveats in our assessment. In Australia, the density of feral cats varies markedly over time, with increases evident in arid and semi-arid areas after periods of high rainfall and the subsequent irruption of key mammalian prey (Dickman et al. 2014; Legge et al. 2017; Read and Bowen 2001), such that rates of predation by feral cats on mammals may show high temporal variability. The conservation and broader ecological impacts of predation by cats on mammals may also vary widely between areas and times in response to variation in the abundance of introduced mammalian prey species, especially the European rabbit (Oryctolagus cuniculus) and house mouse (Mus musculus) (Read and Bowen 2001). Feral cats are also highly flexible foragers, switching prey types according to relative abundance. For example, reptiles feature more prominently in the diet of feral cats in Australia during warmer months when reptiles are most active (Woinarski et al. 2018b; Yip et al. 2015). Conversely, in some situations feral cats selectively hunt particular prey even if it is rare. For example, Spencer et al. (2014) reported that feral cats consumed Forrest’s mouse (Leggadina forresti) at a disproportionately high rate relative to its abundance in a study in central Australia. There may also be substantial differences in the hunting behaviour and prey selectivity among individual co-occurring cats (Dickman and Newsome 2015; Molsher et al. 1999) and some differences in diet associated with size of individual cats (Kutt 2012; Moseby et al. 2015; Yip et al. 2014).

Although our primary interest here is in the numbers of Australian mammals killed by feral cats in largely natural environments, we note that pet cats can also have detrimental impacts on mammals in urban and peri-urban areas, even when well-fed by humans (Adamec 1976; Legge et al. 2017; Paton 1993). Therefore, additional to our assessment of the toll of mammals taken by feral cats in largely natural environments, we also estimated the numbers of mammals killed by unowned cats in highly modified environments (such as around rubbish dumps and in urban areas) and by pet cats. These three segments of the Australian cat population have different characteristics that merit their separate consideration: (i) feral cats in largely natural landscapes generally occur at lower densities but, given that they must hunt their own food, their per capita intake of mammals is likely to be far higher than for the other two categories; (ii) unowned cats in highly modified landscapes typically occur at high densities, but derive much of their diet from food sources provided intentionally or unintentionally by humans (e.g. Hutchings 2003) and hence may have lower per capita kill rates of mammals than cats without access to human-provided food sources; and (iii) the diet of pet cats is largely provided by their owners, so the pet cat per capita kill rate on mammals is likely to be much lower than that for feral cats.

Our study seeks to estimate the numbers of mammals preyed upon by cats in Australia. We recognise that this figure does not necessarily provide a reliable indication of impact, for example upon the population viability or conservation status of Australian mammal species. However, some studies have incorporated rates of feral cat predation into population viability analyses for particular Australian mammal species, finding that observed or inferred rates of predation by cats can be a major driver of population decline (Clark et al. 1995; Dufty 1994; Lacy and Clark 1990; Whitehead et
al. 2018). Furthermore, many studies have demonstrated that predation by feral cats is the main cause of ongoing mammal declines (Marlow et al. 2015; Moseby et al. 2011; Short 2016). High rates of mortality due to predation have marked impacts in Australian mammals, because many native rodent and marsupial species have low reproductive rates (Yom-Tov 1985), and thus, predation is less likely to be compensatory (i.e. to skim off only the doomed surplus) than is characteristically the case for many mammal species with high reproductive rates on other continents (and introduced mammals in Australia).

Our objectives in this study are to: (i) assess the extent of variation in the frequency of occurrence of mammals in cat diet, and the factors associated with such variation; (ii) derive estimates of the number of mammals (and major groupings of mammals) killed in Australia by cats per year, and its spatial variation; and (iii) interpret the conservation significance of such predation rates.

2. Methods

2.1 Numbers of mammals killed by feral cats in largely natural environments

Our analytical pathway follows that used in parallel estimates of the numbers of birds and reptiles killed by cats in Australia (Woinarski et al. 2017; Woinarski et al. 2018a). To estimate the number of mammals killed by cats per km² per day, we took the product of: (i) modelled cat density, projected across Australia (from Legge et al. 2017); (ii) modelled frequency of occurrence of mammals in cat diet samples, projected across Australia; and (iii) the predicted number of individual mammals in those cat samples that contained mammals.

For the frequency of occurrence of mammals in cat diet samples (i.e. the proportion of samples that contained mammals), we collated information from 107 studies, conducted over the period 1969–2018. All of the studies considered included a quantitative assessment of the frequency of mammals in cat stomachs or scats (12,293 scats or stomachs in total). These studies (Appendix A) were widely spread (Fig. 1) and included a broad representation of Australia’s natural environments, with sampling taking place both in times of drought and in high rainfall years.

The classifications of mammals in cat dietary studies varied, with a range of categories used. For example, some report frequency for: (i) each mammal species; (ii) major taxonomic groups; (iii) all mammals combined; (iv) different size classes of mammals; and (v) native vs. introduced mammals. Where publications only included data summaries, we sought primary data (i.e. records of mammal occurrence in individual scats or stomach samples) from the data custodians. In some cases, where the raw data were unavailable, we used combinatorial probability to group frequency values reported for individual species or groups into higher taxonomic units, given that frequency values are not additive. For example, if a dietary study reported frequency for possum species A (frequency<sub>possum A</sub>) as 0.3, possum species B (frequency<sub>possum B</sub>) as 0.2, and possum species C (frequency<sub>possum C</sub>) as 0.1, we estimated the overall frequency for possums (frequency<sub>possum</sub>) as:
We acknowledge that using combinatorial probability to estimate frequency of broad taxonomic groups is imperfect. The primary limitation is that this approach assumes that taxa are distributed randomly across stomach or scat samples. In reality, they could also be either: (i) overdispersed (i.e. each stomach or scat tends to only contain one taxon), and hence the combinatorial probability will be an underestimate; or (ii) underdispersed or clustered (i.e. multiple taxa tend to occur in the same stomachs or scats, with an overabundance of stomachs and scats with no mammals), and hence the combinatorial probability will be an overestimate. We consider that the use of combinatorial probabilities is unlikely to bias our results in any particular direction, given that scenarios (i) and (ii), above, would introduce bias in opposite directions.

Most of the collated studies report only frequency rather than the number of individual mammals in those samples. However, in 32 studies that analysed stomachs only (Appendix A), tallies were given for the number of individual mammals in those samples that contained mammals. The number of individual mammals in a cat stomach sample containing mammals is likely to be influenced by the size of the mammalian prey. For example, if available over a 24-h period, a cat may be more likely to take many small rodents (weight <50 g) than many bilbies (weight ca. 1400 g); however, such prey species-specific tallies were not generally available in the source datasets. We identified a relationship between the number of individual mammals (in those samples that contained mammals), and the frequency of occurrence of mammals in all the stomach samples (Fig. 2). We modelled this relationship using a linear least-squares regression model of the form:

$$\log_{10}(N - 0.99) \sim \log_{10}(\text{frequency})$$

where $N$ is the mean number of individual mammals in those stomach samples that contained mammals (i.e. values of 0 were excluded), and $\text{frequency}$ is the frequency of occurrence of mammals in those samples.

We assume that one stomach sample represents the prey eaten by an individual cat in a 24-h period (Krauze-Gryz et al. 2012; Liberg 1982). This is likely to be a conservative underestimate of the number of prey killed per day because cats may kill some individual mammals but not necessarily consume them, or at least not consume identifiable pieces of them (McGregor et al. 2015). Conversely, cats may also scavenge, so some mammals included in cat dietary studies are not necessarily killed by the cat that consumed them (Hayde 1992; Molsher et al. 2017).

We used a set of six environmental attributes of each study site to assess and model the extent of variation in the frequency of mammals in cat diet. One attribute was whether the study was from an island or the mainlands of Australia and Tasmania (64 519 km$^2$) and, if on an island, the size of the island. We derived a composite variable expressing whether the site was an island, and the size of the island:
island size index = \log_{10} \left( \min \left\{ 1, \frac{\text{area}}{10000} \right\} \right),

where \text{area} is island area in km$^2$. Hence, any land mass or island with an area ≥10 000 km$^2$ (i.e. the Tasmanian and Australian mainlands) has an index of zero. Islands <10 000 km$^2$ have negative values, which become increasingly negative with decreasing island area. From the location of each study, we also determined mean annual temperature (Australian Bureau of Meteorology 2016a), mean annual rainfall (Australian Bureau of Meteorology 2016b), mean tree cover within a 5-km radius (Hansen et al. 2003) and topographic ruggedness (standard deviation of elevation within a 5-km radius) (Jarvis et al. 2008). We also obtained a modelled score of contemporary rabbit abundance across Australia (S.C. Brown and D.A. Fordham, unpublished), with three abundance classes (high, low, absent), and extracted the abundance score for each study location.

We used generalized linear models (GLMs), in the statistical package R (ver. 3.4.2; R Core Team 2017), to examine variation in the frequency of mammals (and of taxonomic and other subsets of mammals) in feral cat stomach and scat samples. The response variable was the proportion of samples (scats or stomachs) containing mammals, and hence was analysed using the binomial error family. By using this error family, the GLMs accounted for the lower precision of the studies that had smaller numbers of cat diet samples.

As candidate models, we examined all combinations of: (i) the six explanatory variables described above (island size index, temperature, rainfall, tree cover, ruggedness, rabbit abundance); (ii) plus an interaction between temperature and rainfall (to account for a possible negative effect of temperature on water availability), and (iii) a term representing the proportion of observations in each study that were from scats. The proportion scats term was necessary as exploratory analysis showed that frequency of mammals was higher in scats than stomachs, suggesting that mammal remains are detectable for longer in scats than stomachs. Other than the island size index, variables were left untransformed, as there was no theoretical rationale for transforming them and no evidence that transformation improved model fit. The island size index incorporated a log-transformation (see equation earlier) as exploratory analysis showed that this improved model fit.

We compared the 160 models using QAIC$_c$, a second-order form of Akaike’s Information Criterion (Burnham and Anderson 2003). QAIC$_c$, rather than simply AIC$_c$, was necessary because the data were over-dispersed. The model with the lowest value of QAIC$_c$ was used for inference about the relationships between frequency of mammals in cat diets and the explanatory variables. Multi-model averaging of the entire set of models, weighted by Akaike weight ($w_i$) (Burnham and Anderson 2003) was used to predict the frequency of mammals in cat stomachs across Australia’s largely natural landscapes (i.e. excluding areas of highly modified landscapes). These spatial predictions were made for stomach samples only, as these are more likely to reflect the diet of the cat in the previous 24 h.

The predicted frequency of mammals in cat stomachs was used to estimate the number of individual mammals in those diet samples that contained mammals, using the linear least-squares regression
model described earlier \((\log_{10} [\text{individuals} – 0.99] \sim \log_{10} [\text{frequency}])\) (Fig. 2). Multiplying the predicted frequency of mammals in cat stomachs across Australia by the predicted number of individual mammals in those stomach samples with mammals provided a spatial representation of the estimated number of mammals killed per feral cat per day. We multiplied this by the modelled density of cats in largely natural landscapes across Australia (Legge et al. 2017), and then by 365.25 (days in a year), to provide a spatial representation of the estimated number of mammals killed by cats per km\(^2\) per year. We summed this rate across the largely natural landscapes of Australia to derive the total number of mammals killed by feral cats each year.

We followed the approach of Loss et al. (2013) and Woinarski et al. (2017; 2018a), and characterised the uncertainty of the estimated total number of mammals killed by feral cats using bootstrapping. We simultaneously bootstrapped (10 000 times) the three underlying datasets: (i) cat density; (ii) frequency of mammals in cat stomach samples; and (iii) the number of individual mammals in cat stomach samples containing mammals. For each random selection of these underlying data, we recalculated the total number of mammals killed. We report the 2.5% and 97.5% quantiles for the 10 000 values of the total number of mammals killed.

The same analytical pathway was repeated for major subsets of mammals: all native mammals, all introduced mammals, rabbits and the much more spatially restricted European brown hare \((Lepus europaeus)\), introduced rodents (mostly house mouse and black rat \([Rattus rattus]\)), native rodents, dasyurids (Family Dasyuridae), possums and gliders (Suborder Phalangerida), macropods and potoroids (Suborder Macropodiformes) and bandicoots and bilbies (Order Peramelemorphia).

### 2.2 Unowned cats in highly modified landscapes

Legge et al. (2017) estimated that 0.72 million unowned cats occur in the ca. 57 000 km\(^2\) of Australia that comprise highly modified landscapes (such as rubbish dumps, intensive piggeries, urban areas) where food supplementation for unowned cats is unintentionally provided by humans. In urban areas, cats such as these are sometimes called ‘stray cats’, but we have avoided that term because it potentially implies that these are individuals that were once pets. There were only eight Australian studies that reported frequency of mammals in the diet of unowned cats occurring in highly modified environments, namely rural rubbish dumps (Appendix A). This small number provides little scope for assessing variability, so we simply use the average frequency of mammals in samples across these eight studies and multiply this mean by an estimate of the number of individual mammals in those cat samples that contained mammals and by the population size of unowned cats in modified environments, as estimated by Legge et al. (2017). We also compare the frequency of mammals in these diet samples with those from feral cats in largely natural landscapes using Mann-Whitney U-tests, but interpret the results with caution because the small sample size constrains such a comparison.

### 2.3 Pet cats
From national surveys of pet ownership, the population of pet cats in Australia is estimated at 3.88 million (Animal Medicines Australia 2016). The average number of mammals killed by pet cats in Australia has been estimated in several Australian studies that have involved cat-owners regularly tallying the number of prey items brought to their home by their pet cats. Here, we restrict consideration to only those studies that were based on a near-random set of pet cats (Barratt 1997, 1998; Paton 1990; Paton 1991; Paton 1993; Trueman 1991); we omitted several studies that excluded from their data analysis cats that apparently took no prey.

The actual number of kills (of vertebrate prey) by pet cats is appreciably higher than these owner-reported tallies, given that studies on other continents (no such studies have been undertaken in Australia) indicate that pet cats typically return home with only a proportion of the prey they have killed (Blancher 2013): reported estimates are 8.8% (Krauze-Gryz et al. 2012), 12.5% (Maclean 2007), 23% (Loyd et al. 2013), and 30% (Kays and DeWan 2004). Here, we average across Australian studies the number of individual mammals reported by pet owners to be killed by their pet cats per year, and scale this up to account for the number of mammals killed but not returned to the cat’s home, using the mean (18.6% of mammals killed are brought home) from the four studies of pet cats that provide robust estimates of this proportion.

2.4 Comparison of frequency of mammals in the diet of feral cats with that of other co-occurring mammalian predators

Australian mammals face many introduced and native predators in addition to cats. A subset of the feral cat diet studies collated here also included comparable and contemporaneous sampling of the diet of other co-occurring mammalian predators, the introduced European red fox (Vulpes vulpes) and wild dogs including dingoes (Canis familiaris and C. dingo, respectively) (Appendix B). For studies that included at least 10 samples of feral cats and at least 10 samples of one or both of these two other mammalian predator species at the same location, we compared the frequency of mammals in samples between these predator species, using Wilcoxon matched-pairs tests.

In addition to comparing the frequency of mammals in the diet of co-occurring mammalian predators, we also use this set of studies to compare the size range of mammals taken by these three predators. For each predator species in each study, we calculated the median size of mammalian prey (using adult body weight) recorded in the diet samples, and then compared this value between cats and foxes, and between cats and dogs/dingoes, across all studies where this information was available for these pairings of predators, again using Wilcoxon matched-pairs tests.

3. Results

3.1 Feral cats in largely natural landscapes

Across 107 studies in largely natural landscapes in Australia, the mean frequency of mammals in cat diet samples was 68% for stomachs and 70% for scats. The mean frequency of native mammals was
35% for stomachs and 37% for scats, and for introduced mammals it was 37% for stomachs and 36% for scats.

Generalised linear modelling suggested that three environmental variables were correlated with the frequency of mammals in feral cat diet samples: (i) island size ($p<0.001$); (ii) mean annual temperature ($p<0.01$); and (iii) ruggedness ($p<0.05$). The best model had $R^2$ of 0.39. Mammal frequency in cat diet samples increased with increasing island size (Fig. 3a). Frequency was higher in areas with low temperature (Fig. 3b) and ruggedness (Fig. 3c). There was also a clear pattern of scats having higher frequency of mammals than stomach samples ($p<0.05$); on average this difference was about 12%.

When native and introduced mammals were modelled separately, the environmental correlates of frequency in cat diet samples differed markedly. For native mammals, there was a dramatic increase in frequency with increasing temperature, and to a lesser extent rainfall and tree cover (Fig. 4b–d), such that in warm, mesic climate zones most cat diet samples are expected to contain native mammals. Conversely, for introduced mammals, there was a dramatic decrease in frequency with increasing temperature, and to a lesser extent rainfall and tree cover (Fig. 5b–d), such that in cool, arid climate zones most cat diet samples are expected to contain introduced mammals. The best models of frequency for native and introduced mammals had $R^2$ of 0.64 and 0.56, respectively.

The modelled relationships were used to predict the frequency of mammals in cat stomach samples across Australia (Fig. 6a–c). The spatially-weighted mean frequency of mammals in cat stomach samples across the Australian mainland and islands was 70% (44% for native mammals, 34% for introduced mammals), i.e. at any instant 70% of feral cats would be expected to have the remains of one or more individual mammals in their stomachs.

The contrasting spatial patterns for native and introduced mammals are clearly seen in the mapped frequencies (Fig. 6b, c). Native mammals are predicted to be most frequent in cat diet samples in the warm, mesic northern half of the continent, while introduced mammals are most frequent in the drier parts of the southern half of the continent. Modelling the relative frequency of native mammals (compared to introduced mammals) in cat diet samples reinforces this pattern (Fig. 7b–c, Fig. 8).

The estimated number of mammals killed by feral cats across largely natural landscapes in Australia in a typical year is 815 million (95% confidence interval [CI]: 530–1 414 million) (Appendix C: Fig. C1). Of these individuals, 459 million (95% CI: 252–756) are native (i.e. 56%). On average, a feral cat kills 393 mammals per year (95% CI: 316–470), 221 of which are native (95% CI: 136–263) (Fig. C2). The number of mammals killed by cats averages 107 km$^2$ yr$^{-1}$; for native mammals this figure is 60 km$^2$ yr$^{-1}$.

The mammal group that contributes most to the diet of feral cats in natural landscapes is native rodents (268 million yr$^{-1}$; 33% of the total number of mammals killed, and 58% of native mammals killed) (Fig. 9). This offtake is strongly concentrated in northern Australia (Appendix D: Fig. C8a). This
is followed by rabbits and hares (both introduced) (202 million yr\(^{-1}\); 25% of the total number of mammals killed) (Fig. 9). Unsurprisingly, spatial variation in the numbers of rabbits killed by cats is largely concordant with the known distribution of rabbits, mainly in the drier parts of southern Australia (Van Dyck and Strahan 2008) (Fig. C8a), despite our rabbit abundance variable being uncorrelated with frequency of rabbits in cat diet samples. Mammals other than rodents make up 42% of the native mammal offtake by feral cats in natural landscapes (191 million yr\(^{-1}\)), including dasyurids (18%), possums and gliders (5%), macropods and potoroids (4%) and bandicoots and bilbies (1%) (Fig. 9).

3.2 Unowned cats in highly modified landscapes

The mean frequency of mammals in diet samples from the eight studies of unowned cats in highly modified environments was 43.2% ±9.9 (SE) (range: 10.0–91.6). This is significantly lower (Mann-Whitney U-test: \(z = 2.53, p = 0.011\)) than for feral cats in largely natural landscapes (68.0%, \(n = 105\)). Six of these studies in highly modified environments included frequency of native and introduced mammal species: across these studies, cats at such sites consumed a far higher proportion of introduced mammals (mean frequency: 45.5%) than of native mammals (mean frequency: 5.8%) (Wilcoxon matched-pair test: \(z = 1.99, p = 0.046\)).

Unfortunately, only one of the studies of cat diet in modified environments noted the number of individual mammals in cat samples that had mammals (mean of 1.2 individual mammals from 152 samples that contained mammals). The most conservative assumption is that only one individual mammal was in a cat stomach or scat that contained mammals; an alternative assumption is to apply the mean number of 1.62 individual mammals reported in cat samples containing mammals from the large collation of studies of feral cats in largely natural landscapes. Hence, using these values as lower and upper bounds, individual cats in highly modified landscapes kill, on average, between 158 and 255 individuals yr\(^{-1}\): henceforth we use the midpoint of these tallies (207 individuals cat\(^{-1}\) yr\(^{-1}\)).

Multiplying the total population size of unowned cats in highly modified landscapes (0.72 million: Legge et al. 2017) by this per capita annual take produces an estimate of 149 million individuals yr\(^{-1}\) killed by unowned cats in modified environments.

3.3 Pet cats

Pet owners observed their cats bringing home a mean of 15.7 mammals cat\(^{-1}\) yr\(^{-1}\) from a sample of 700 cats from mainly around Adelaide (Table 4 in Paton 1990), 6.9 mammals cat\(^{-1}\) yr\(^{-1}\) from a sample of 138 cats in Canberra (Barratt 1998) and 2.9 mammals cat\(^{-1}\) yr\(^{-1}\) from a sample of 166 cats in Hobart (Trueman 1991). The mean across these three studies is 8.6 individuals cat\(^{-1}\) yr\(^{-1}\). Scaling this mean by the mean proportion of all kills that are returned home (mean of four non-Australian studies: 18.6%), the estimated number of mammals killed by individual pet cats is 46.4 individuals cat\(^{-1}\) yr\(^{-1}\). Hence, with a total Australian population of 3.88 million pet cats, the estimated annual tally of mammals killed by pet cats is 180 million yr\(^{-1}\).
Unsurprisingly, given the typically high abundance of introduced mammals in urban areas, introduced mammal species comprised a higher proportion of the mammals killed by pet cats than by feral cats in largely natural landscapes — introduced mammals comprised >98% of the identifiable mammals killed by pet cats in Canberra (Barratt 1998). In Trueman’s (1991) study in Hobart, 30.5–93.3% of mammals killed by pet cats were native; the uncertainty reflects that the authors did not provide a breakdown of native vs. introduced rodents. Paton (1990) did not provide a breakdown of native vs. introduced mammals in his Adelaide study.

3.4 Comparison of frequency of mammals in the diet of feral cats with that of other co-occurring mammalian predators

Comparative data on the frequency of mammals in samples of feral cats and other co-occurring mammalian predators are summarised in Appendix B. Across 20 studies where the diet of co-occurring cats and foxes was reported, the mean frequency of mammals in cat diets (72.6% ±4.7 [SE]) was not significantly different than in fox diets (70.8% ±5.9 [SE]; Wilcoxon-matched pairs test: \( z = 0.30, p = 0.77 \)). Across 15 studies in which the diet of co-occurring cats and dogs/dingoes was reported, the frequency of mammals in cat diets (77.2% ±5.1 [SE]) was not significantly different than in dog diets (84.9% ±4.0 [SE]; Wilcoxon-matched pairs test: \( z = 0.91, p = 0.36 \)).

Although there was no significant difference in the frequency of mammals in cat diets relative to that in fox or dog/dingo diets across this set of studies, there were significant differences among predators in mammalian prey size. Across the set of studies that considered the diets of co-occurring cats and foxes, cats took smaller mammal species than did foxes (mean of medians for cats 544 g ±193 [SE] cf. for foxes 3 686 g ±2 800 [SE]; Wilcoxon-matched pairs test: \( z = 2.4, p = 0.016, N = 14 \)). Across the set of studies that considered the diets of co-occurring cats and dogs/dingoes, cats took smaller mammalian prey than did dogs/dingoes (mean of medians for cats 323 g ±206 [SE] cf. for dogs/dingoes 16 529 g ±5 383 [SE]; Wilcoxon-matched pairs test: \( z = 2.4, p = 0.018, N = 8 \)).

4. Discussion

The most striking feature of the results presented here is the marked spatial contrast in the proportions of introduced and native mammals in the diet of feral cats in Australia: introduced species (particularly rabbits and house mice) dominate the mammal component of cat diets across lower rainfall areas and most of southern Australia, but native mammals dominate in northern Australia (and also in higher rainfall and forested areas of southeastern and southwestern Australia) (Fig. 6, 8). This disjunction largely matches the pattern of historic and ongoing loss of native mammals across Australia, with many native mammals, especially those in the preferred dietary size range for cats, already lost from, or persisting only in small numbers in, the continent’s low rainfall areas (Burbidge and McKenize 1989; Burbidge et al. 2008; McKenzie et al. 2007). Native mammals have persisted better in northern Australia and in some higher rainfall areas of southern temperate Australia; however, many are now exhibiting marked and ongoing declines (Woinarski et al. 2010;
Woinarski et al. 2001; Ziembicki et al. 2013; Ziembicki et al. 2015), especially those in the preferred dietary size range for cats, which our analysis suggests is 300–550 g. The pattern we observed is also consistent with that previously described at a local scale by Read and Bowen (2001) and at a national scale by Doherty et al. (2015), who reported an inverse relationship between the frequency of rabbits and of native mammals in the diet of feral cats across Australia. However, our present study provides far more spatial acuity to this pattern, and provides explicit estimates of the numbers of mammals killed.

Our results highlight two markedly different ecological universes in Australia: a half-continent in which one introduced predator species feeds mainly on one introduced prey species (the European rabbit), and a half-continent in which introduced prey species are largely absent and feral cats instead consume mainly native mammals (Fig. 6, 8). The importance of rabbits in the diet of feral cats in the natural landscapes of southern Australia has been long recognised (Catling 1988; Coman and Brunner 1972; Jones and Coman 1981; Read and Bowen 2001). Likewise, many previous studies have recognised the importance of house mice in the diet of feral cats in some arid and semi-arid areas (Jones and Coman 1981; Martin et al. 1996), and of introduced rodents generally in the diet of cats in more densely settled and modified areas of temperate Australia (Barratt 1997; Dickman 2009; Matthews et al. 1999). However, our study provides a comprehensive national context and spatial circumscription for this feature. To some extent, this spatial patterning reflects the cat’s relatively non-selective diet: the groups that are most common in the landscape, and in the preferred weight range, tend to dominate cat diets (e.g. rabbits in southern Australia, native mammals in northern Australia). However, the spatial patterning in our results does not mean that the impacts of cats on native mammals are mostly confined to northern Australia, or that cats may be having a net conservation benefit by preying upon introduced mammals – especially rabbits – in southern Australia. This is because high densities of introduced mammals may support high densities of cats, such that even when native mammals comprise only a small proportion of cat diets, the impact of cat predation on the population viability of native mammals may be substantial. Indeed, where rabbit densities are reduced by management intervention, the density of cats tends to decrease over time and the density of native mammal species (especially those preferred by cats) can increase as a result (Pedler et al. 2016). Conversely, sudden and severe reductions in rabbit densities can lead to a short-term, though intense, increase in predation of native mammals by cats, due to prey-switching (Lurgi et al. 2018). Furthermore, at most times and places in Australia, predation by cats does not generally constrain the population size of rabbits and introduced rodents (Newsome et al. 1989; Norbury and Jones 2015; Pech et al. 1992).

Our modelling demonstrates that mammals occur more frequently in the diet of cats on mainland areas than on islands. This is consistent with the prevalence of abundant nesting seabirds (rather than mammals) in the diets of cats on many islands (Jones 1977; Woinarski et al. 2017), the natural lack of land mammals on many islands, especially smaller ones (Abbott and Burbidge 1995), and/or the rapid historic loss of native mammals (mostly due to predation by cats) on many other Australian islands (Algar et al. 2011; Burbidge and Manly 2002), such that mammals are no longer available to be a major component of the diet of cats on these islands. Some previous studies have noted that topographic relief may also be a major influence on cat abundance and impact in Australia, with
native mammal species tending to persist better in more rugged rocky areas (Burbidge and McKenzie 1989; McDonald et al. 2017) either due to lower abundance of cats (Hohnen et al. 2016), or greater ability of mammals to avoid predation in rocky areas. Our finding that mammals occur less frequently in the diet of cats in rugged areas (Fig. 4e) is more consistent with the latter explanation.

We estimate that a feral cat in a largely natural landscape kills, on average, 431 individuals cat\(^{-1}\) yr\(^{-1}\) (57% of which are native), summing across the feral cat population occurring in natural environments to 894 million mammals yr\(^{-1}\). From a much smaller dataset, we estimate that unowned cats in highly modified environments have a lower per capita take, of 207 mammals cat\(^{-1}\) yr\(^{-1}\) (most of which are introduced), summing across that component of the feral cat population to 149 million mammals yr\(^{-1}\). The per capita take by pet cats is lower still, at 46 mammals cat\(^{-1}\) yr\(^{-1}\) (most of which are introduced), summing across the pet cat population to 180 million mammals yr\(^{-1}\). Hence, collectively, cats in Australia take about 1.223 million mammals yr\(^{-1}\) (>42%, or >509 million, of which are native). There are few studies in Australia against which our results can be compared directly. However, one detailed local study at Roxby Downs in semi-arid South Australia provided an estimate of feral cats killing 50 native mammals km\(^{-2}\) yr\(^{-1}\) (Read and Bowen 2001). This tally is similar to our predicted value for this area (32 native mammals km\(^{-2}\) yr\(^{-1}\)), as well as our national average (67 native mammals km\(^{-2}\) yr\(^{-1}\)). We note that the actual impact of this level of predation is difficult to evaluate given that we have very limited demographic information (e.g. population sizes, maximum rates of population increase, carrying capacity in the absence of cat predation) for most Australian mammal species.

Our results indicate that at sites of co-occurrence, the proportion of mammals in the diet of individual cats is similar to that of individual foxes and dogs/dingoes, although there are significant differences between these predator species in the size of mammalian prey. There are no comparable estimates of the national tallies of mammals taken by foxes and dogs/dingoes, but these are likely to be considerably less than the tally reported here for cats, given that cats have a wider distribution across Australia and often occur at similar or even higher densities (Read and Bowen 2001; Read et al. 2019).

As context for our estimate of the number of mammals killed by cats each year across Australia, we can compare it to mortality due another main threatening process, land clearing. Cogger et al. (2003) provided an estimate for the number of individual mammals killed by land clearing across Australia. Based on their estimates of the density of native mammals (excluding bats), with this value ranging widely between bioregions from 200 to 5,200 individuals km\(^{-2}\), and a then rate of vegetation clearance of ca. 4.500 km\(^{2}\) yr\(^{-1}\) in Queensland (the Australian state with the highest rate of loss of native vegetation), they concluded that land clearing resulted in the death of at least 2.1 million native mammals yr\(^{-1}\). The national rate of land clearing has declined, unevenly, since then, and in 2013–2014 was ca. 2.000 km\(^{2}\) yr\(^{-1}\) (Evans 2016). However, land clearing in Queensland increased again in 2015–2016, with 0.9 million native mammals estimated to be killed there in each of those years (Cogger et al. 2017). These annual rates of loss of mammals due to habitat clearance are far less than our estimates of the numbers of native mammals lost annually to cat predation (cf. 509 million native mammals killed each year by feral cats in largely natural landscapes). However, we
recognise that such comparisons have interpretational constraints: clearing typically results in permanent loss of habitat, potentially leading to the extinction of local populations, whereas a larger annual tally of mammals killed due to cat predation may have a far less acute impacts on the long-term population viability of individual mammal species or communities, provided that populations can persist at reduced densities.

The mean number of 9 individuals cat⁻¹ yr⁻¹ known to be brought home by pet cats in the three Australian studies (uncorrected for the proportion killed but not returned) is within the range reported in studies elsewhere, e.g. 0.7 in an urban area in Auckland, New Zealand (Gillies and Clout 2003), ca. 5 in urban Dunedin, New Zealand (van Heezik et al. 2010), ca. 14 in a suburb bordering native vegetation in Auckland (Gillies and Clout 2003), ca. 15 in Britain (Woods et al. 2003), ca. 17 in an area adjacent to a nature reserve in Albany, USA (Kays and DeWan 2004), cf. 21 in rural and urban environments in Poland (Krauze-Gryz et al. 2012), ca. 22 in a village in Switzerland (Tschanz et al. 2011), and 24 rodents for free-roaming pet cats in California, USA (Crooks and Soule 1999). So, although our database for the diet of pet cats in Australia is sparse, the reported values for their take of mammals appear to be consistent with many studies elsewhere.

The nine million pet cats in Britain (which comprise about 90% of the total cat population: Harris et al. 1995) were estimated to kill ca. 57 million mammals in the 5-month ‘summer’ period (Woods et al. 2003). In the USA, cats are estimated to kill 6.9 to 20.7 billion mammals per year (Loss et al. 2013). This tally, which includes both native and introduced species, is an order of magnitude greater than our estimates for Australia, despite being a similar land area, primarily because there are far more cats in America. Indeed, the estimated per capita take of mammals by cats in the USA is less than that we report here for Australia (Table 1). Woinarski et al. (2017) also reported a comparably higher per capita rate of predation by cats on birds in Australia relative to that reported by Loss et al. (2013) for the USA, and considered that this could be explained by our inclusion of a factor for the number of individual animals in cat diet samples: this factor is generally not considered in most other analyses, such that the number of animals killed by cats may be underestimated in many other studies.

Although our tally of mammals killed by cats in Australia is an order of magnitude less than the comparable figure for the USA, it is still a large number. However, the ecological and conservation significance of our tally is difficult to assess, because (i) there is reliable demographic information for few native mammal species in Australia; (ii) predation may be more intense upon some mammal species or species-groups (Read et al. 2019; Woolley et al. submitted); (iii) some mammal species may be able to sustain high mortality rates and maintain viable populations but others may not; and (iv), as demonstrated here, there is substantial spatial variation in the numbers and proportion of native mammals killed across Australia. Nonetheless, there is substantial evidence that predation by cats contributed to or caused the widespread loss and extinction of many Australian mammal species (Radford et al. 2018; Woinarski et al. 2015), and continues to cause to the ongoing decline of many others (Clark et al. 1995; Dufty 1994; Lacy and Clark 1990; Marlow et al. 2015; Moseby et al. 2011; Short 2016; Whitehead et al. 2018). The evidence of ongoing impact of predation by cats on the Australian native mammal fauna suggests that the annual tally of 508 million native mammals
killed by cats per year is ecologically significant: such continuing rates of predation are exceeding the level at which at least some native mammal species can sustain viable populations.

The extent and impact of cat predation on mammals may also be magnified by interactions with other factors, such as habitat fragmentation, fire regimes and habitat degradation due to over-grazing (Graham et al. 2013; McGregor et al. 2017; McGregor et al. 2014; McGregor et al. 2016). Cat predation may also subvert the assumed conservation security provided to native mammals by the conservation reserve system, given that feral cats occur in similar density within and outside Australia’s reserve system (Legge et al. 2017). Partly in response to the major role of feral cats in the ongoing decline of the Australian mammal fauna, the recently released Threatened Species Strategy for Australia (Commonwealth of Australia 2015) placed considerable emphasis on the control of feral cats. Substantial conservation benefits to Australia’s native mammal species can be provided by: (i) eradicating cats from more, and larger, islands; (ii) increasing the number of predator-proof exclosures; and (iii) increasing the number and extent of areas subject to intensive cat control (Legge et al. 2018).

Appendix A. Collation of Australian studies reporting the frequency of mammals in feral cat diet samples

Appendix B. Collation of Australian studies reporting the frequency of mammals in the diets of cats and co-occurring mammalian predators

Appendix C. Results of bootstrapping simulations

Appendix D. Summaries of models of frequency of mammal subgroups in feral cat diet samples


Marlow, N.J., Thomas, N.D., Williams, A.A.E., Macmahon, B., Lawson, J., Hitchen, Y., Angus, J., Berry, O., 2015. Cats (Felis catus) are more abundant and are the dominant predator of woylies (Bettongia penicillata) after sustained fox (Vulpes vulpes) control. Australian Journal of Zoology 63, 18-27.


Woinarski, J.C.Z., South, S.L., Drummond, P., Johnston, G.R., Nankivell, A., 2018b. The diet of the feral cat (Felis catus), red fox (Vulpes vulpes) and dog (Canis familiaris) over a three-year period at Witchelina Reserve, in arid South Australia. Australian Mammalogy 40, 204-213.


Table 1. Comparison between Australia (the current study) and the contiguous USA (Loss et al. 2013) in cat population size and predation rates on mammals. Note that in our assessment, we segregate Australia’s unowned cats into two components: those in largely natural landscapes (i.e. feral cats) and those in highly modified landscapes. This distinction was not made by Loss et al. (2013), so we have included their estimates alongside our estimates for feral cats in largely natural landscapes, below, even though theirs include unowned cats in highly modified landscapes. The estimates of mammals killed per pet cat and per unowned cat in the USA (Loss et al. 2013) are based on seven studies from the USA and Europe for both of these classes of cat.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Contiguous USA (Loss et al. 2013)</th>
<th>Australia (this study)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Land area</td>
<td>8.08 million km²</td>
<td>7.69 million km²</td>
</tr>
</tbody>
</table>

**Pet cats**

- Cat population size: 84 million vs. 3.9 million
- Mammals killed cat⁻¹ yr⁻¹: 11.1-29.5 vs. 46.4
- Mammals killed by cats yr⁻¹ (95% CI: 571–2515 million) vs. 1249 million
- Proportion native: NA vs. Low

**Feral cats in largely natural landscapes**

- Cat population size: 30–80 million vs. 2.1 million
- Cat density: 3.7–9.9 cats km⁻² vs. 0.27 cats km⁻²
- Mammals killed cat⁻¹ yr⁻¹: 139–329 vs. 393 (95% CI: 316–470)
- Mammals killed yr⁻¹ (95% CI: 5,616–19,254 million) vs. 10,903 million
- Proportion native: NA vs. 56%

**Unowned cats in highly modified landscapes**

- Cat population size: NA vs. 0.7 million
- Mammals killed cat⁻¹ yr⁻¹: NA vs. 207
- Mammals killed yr⁻¹: NA vs. 149 million
- Proportion native: NA vs. Low

**Total mammals killed by cats yr⁻¹**

- 12,269 million (95% CI: 6,902–20,712 million) vs. 1,144 million
- Proportion native: NA vs. >40%
Fig. 1. The occurrence of cat dietary studies used in this study, 107 of which occurred in largely natural landscapes, indicated by white circles (94 on the Australian mainland, 3 in Tasmania and 11 on smaller islands, including Macquarie and Christmas Islands, not shown on map), and 8 of which occurred at rural rubbish dumps or other highly modified environments, indicated by black asterisks. The coloured shading indicates mean annual rainfall (Australian Bureau of Meteorology 2016b). The dashed line indicates the Tropic of Capricorn.
Fig. 2. The modelled relationship between the number of individual mammals in cat diet samples containing mammals and the frequency of occurrence of mammals in cat diet samples, according to a linear least-squares regression model of the form: $\log_{10}(\text{individuals} - 0.9) \sim \log_{10}(\text{frequency})$, with $p<0.001$ and $R^2$ of 0.39. The bold line indicates the predictions of the regression mode, and the thin lines indicate 95% confidence intervals.
Fig. 3. Variation in the frequency of occurrence of mammals (including both native and introduced species) in cat diet samples (stomachs and/or scats) in relation to significant predictor variables: (a) island size ($p<0.001$); (b) mean annual temperature ($p<0.01$); and (c) ruggedness ($p<0.05$). There was no significant interaction between mean annual temperature and rainfall. Regression lines represent the predictions of a generalised linear model with 95% confidence intervals. $R^2$ of the model was 0.39.
Fig. 4. Variation in the frequency of occurrence of native mammals in cat diet samples (stomachs and/or scats) in relation to significant predictor variables: (a) island size ($p<0.001$); (b) mean annual temperature ($p<0.001$); (c) mean annual rainfall ($p<0.001$); (d) tree cover ($p<0.05$); and (e) ruggedness ($p<0.05$). There was also a significant interaction between mean annual temperature and rainfall ($p<0.001$). Regression lines represent the predictions of a generalised linear model with 95% confidence intervals. $R^2$ of the model was 0.64.
Fig. 5. Variation in the frequency of occurrence of introduced mammals in cat diet samples (stomachs and/or scats) in relation to significant predictor variables: (a) island size ($p<0.01$); (b) mean annual temperature ($p<0.001$); (c) mean annual rainfall ($p<0.001$); and (d) tree cover ($p<0.01$). There was also a significant interaction between mean annual temperature and rainfall ($p<0.001$). Regression lines represent the predictions of a generalised linear model with 95% confidence intervals. $R^2$ of the model was 0.56.
Fig. 6. Model projections of the frequency of occurrence of mammals in cat stomachs in largely natural landscapes throughout Australia. The dashed lines indicate the Tropic of Capricorn.
Fig. 7. Variation in the relative frequency of native mammals in cat diet samples (stomachs and/or scats), expressed as native frequency / (native frequency + introduced frequency), in relation to significant predictor variables: (a) island size ($p<0.001$); (b) mean annual temperature ($p<0.001$); (c) mean annual rainfall ($p<0.001$); and (d) ruggedness ($p<0.05$). There was also a significant interaction between mean annual temperature and rainfall ($p<0.001$). Regression lines represent the predictions of a generalised linear model with 95% confidence intervals. $R^2$ of the model was 0.77.
Fig. 8. Model projections of the relative frequency of native vs. introduced mammals in cat diet samples, expressed as native frequency / (native frequency + introduced frequency), in largely natural landscapes throughout Australia. The solid black line indicates relative frequency of 50% (i.e. native mammals and introduced mammals occur at equal frequencies. The dashed line indicates the Tropic of Capricorn.
Fig. 9. The estimated total number of mammals killed by feral cats each year in largely natural landscapes across Australia.