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How many birds are killed by cats in Australia?

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ABSTRACT. From analysis of results from 93 studies on the frequency of occurrence of birds in cat dietary samples, and a recently published assessment of the population size of feral cats in largely natural landscapes, we estimate and map the number of birds killed annually in Australia by feral cats. We show that average rates of predation on birds by cats on islands are ca. 10 times higher than for comparable mainland areas. Predation rates on birds are also relatively high in hot, arid regions. Across Australia's natural landscapes, feral cats typically consume 272 million birds yr^{-1} (95% confidence interval [CI]: 169–508 million). However, there is substantial inter-annual variation, depending on changes in the cat population that are driven by rainfall conditions: ranging between 161 million birds yr^{-1} (95% CI: 114–284 million) following dry periods and 757 million birds yr^{-1} (95% CI: 334–1580 million) following wet periods. On average, feral cats kill 35.6 birds km^{-2} yr^{-1} (95% CI: 22.2–66.6). About 99% of these mortalities are native bird species. With a much sparser evidence base, we also estimate that a further 44 million birds are killed annually by feral cats in highly modified landscapes, and 61 million birds are killed annually by pet cats, summing to 377 million birds killed yr^{-1} (i.e., just over 1 million birds per day) by all cats. Feral cats include a significantly higher proportion of birds in their diet than do other main mammalian predators. The national tally of birds killed by cats in Australia is broadly comparable to recent assessments for Canada, but less than that reported for the United States (because the cat population is much higher there). However, it remains challenging to interpret this mortality tally in terms of population viability or conservation concern for Australian birds.

Running head: How many birds are killed by cats?

Additional keywords: conservation, diet, introduced predator, island, mortality, predation

1. Introduction

"Of all bird–mammal interactions, that of the domestic cat catching and killing a bird is probably the most familiar" (Mead 1982) [p. 183]. Notwithstanding the familiarity of this act, the extent to which cats *Felis catus* present a conservation threat to birds in continental areas is poorly resolved, although it is increasingly apparent that predation by pet and feral cats is a major cause of mortality for bird species in many areas (Loss et al. 2012, 2013, 2015; Marra and Santella 2016). In Australia, since their first introduction in 1788, feral cats have spread to now occupy the entire continent and most larger islands (Legge et al. 2017), and have been implicated in the decline and extinction of many native mammal species (Woinarski et al. 2015). The control of feral cats in Australia has recently become a priority for conservation policy and management (Commonwealth of Australia 2015; Department of the Environment 2015). Although there have been some general reviews of impacts of cats on Australian wildlife (Abbott et al. 2014; Denny and Dickman 2010; Dickman 1996, 2009, 2014; Doherty et al. 2017; Paton 1993) and a series of important studies of the ecology (including diet) of feral cats (Coman and Brunner 1972; Doherty et al. 2015; Jones and Coman 1981; Kutt 2011; Paltridge 2002; Pavey et al. 2008; Read and Bowen 2001; Yip et al. 2014), there has been no assessment of the extent of losses of birds due to cat predation at a continental scale in Australia.

One of the first dietary studies of cats in Australia concluded that their impacts on birds were likely to be minor:

> "The common belief that feral cats are serious predators of birds is apparently without basis. Although birds were common in all sampling areas, they were a relatively minor item in the diet [of feral cats]. Presumably, other factors such as difficulty of capture are responsible for the low intake of birds" (Coman and Brunner 1972) [pp. 852-853].

There have been many comparable dietary studies since, such that this interpretation can be re-assessed now with substantially more evidence. In this paper, we collate studies reporting the frequency of occurrence of birds in the diet of feral cats, and combine those data with information from a recent review that estimated the population size of feral cats in Australia (Legge et al. 2017), to derive an estimate of the annual number of birds killed in Australia by feral cats. This approach broadly follows those used to derive national tallies of birds killed by cats in the United States (Dauphiné and Cooper 2009; Loss et al. 2013; Pimentel et al. 2005) and Canada (Blancher 2013), although our analysis is based on many more local-scale studies than any previous assessments. Our focus is on the number of individual birds killed, rather than tallies for individual bird species, because many of the studies collated here reported the total frequency of birds in the diet of cats, but did not identify birds to species.

There are several interpretational caveats in our assessment. In Australia, the density of feral cats varies markedly over time, with notable increases in cat density in arid and semi-arid areas after periods of high rainfall and subsequent irruption of key mammalian prey (Dickman et al. 2014; Legge et al. 2017; Read and Bowen 2001), such that predation pressure (and hence impacts) by feral cats on birds may be

highly variable. Predation pressure by feral cats on birds may respond not only to such dynamic variation in the densities of cats and their main prey sources associated with temporal variation in environmental conditions, but may also vary markedly over time and space in response to differing intensities of management of cats (and the often co-occurring introduced red fox *Vulpes vulpes*) and/or to management of some main prey sources (such as rabbits *Oryctolagus cuniculus*) (see also Appendix D) (Bowen and Read 1998; Courchamp et al. 2000; Holden and Mutze 2002; Marlow and Croft 2016; Read and Bowen 2001). Feral cats are also highly flexible foragers: they readily switch prey types according to the relative abundance of different prey. For example, reptiles feature more prominently (and hence birds less prominently) in the diet of feral cats in Australia during warmer months (Yip et al. 2015). Feral cats may also selectively hunt particular prey species even if rare in the landscape: for example, Spencer et al. (2014) reported that feral cats consumed Forrest's mouse *Leggadina forresti* at a disproportionately high rate relative to their abundance in a study in central Australia. There may also be substantial differences in the hunting behaviour and prey selectivity amongst individual co-occurring cats, with some individual cats preferentially targeting birds (Dickman and Newsome 2015; Molsher et al. 1999), and some differences in diet associated with the size of the cat (Kutt 2012; Moseby et al. 2015).

There have been few previous estimates of the numbers of birds killed by feral cats for any part of Australia. One notable example related to the diet of feral cats on the 131 km^2 sub-Antarctic Macquarie Island (Jones 1977). Based on an estimated population then of 375 feral cats, dietary analysis and cat metabolic requirements, Jones (1977) estimated that this feral cat population killed 47,000 Antarctic prions *Pachyptila desolata* and 11,000 white-headed petrels *Pterodroma lessonii* per year on Macquarie Island; hence, on average, each cat consumed at least 154 individual birds per year, and the cat population collectively consumed at least 443 birds km^{-2} yr^{-1}.

For mainland Australia, the most notable assessment of bird mortality rates attributable to feral cats in natural landscapes at any site is that of Read and Bowen (2001) at Roxby Downs in arid South Australia. Their dietary study found an average of 0.21 individual birds in each cat stomach, and they concluded that each cat consumes at least 0.21 birds per day (assuming that the average passage rate of food in the digestive system of cats is less than 1 day). Based on observed densities of 2 cats km^{-2}, they estimated that the feral cat population at this site consumed well in excess of 150 birds km^{-2} yr^{-1}.

Although our primary interest in this paper is predation by feral cats in natural environments, we note that pet cats can also have detrimental impacts on birds in urban and peri-urban areas, and that their impacts may be locally substantial given that cats in such settings often occur in very high densities (Legge et al. 2017; Paton 1993). So, additional to our assessment of the toll of birds taken by feral cats in largely natural environments, we also estimate the numbers of birds killed by feral cats in highly modified environments (such as around rubbish dumps) and by pet cats. These three segments of the cat population have some notably 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 birds is likely to be far higher than for the other two categories; (ii) feral cats in highly modified landscapes typically occur at very high densities, but derive much of their

diet from food sources provided intentionally or unintentionally by humans and hence have lower *per capita* kill rates of birds than feral cats without such human-provided food sources; and (iii) the number of pet cats in Australia is reasonably well estimated from ownership statistics, but the diet of pet cats is largely provided by their owners, so the pet cat *per capita* kill rate on birds is likely to be much lower than for feral cats. Note that, as defined by Legge et al. (2017), the total area of natural environments and of highly modified landscapes sums to the total land area of Australia (7.69 million km^2, including all islands); hence the total population size of feral cats in Australia is the sum of the estimated cat populations for these two landscape components.

Our focus here is on cats as a direct cause of mortality in Australian birds, but we note also that cats may also have indirect impacts on bird populations through competition (with some studies showing large dietary overlaps of feral cats with some Australian raptor species: Pavey et al. 2008), and indirectly through disease transmission. Notably, the cat is the sole primary host in Australia for toxoplasmosis, demonstrated to be a significant cause of mortality for many bird species (including threatened bird species) in Australia and elsewhere in the world (Dubey 2002; Hartley and Dubey 1991; Work et al. 2000).

Our objectives in this study are to: (i) assess the extent of variation in the frequency of birds in cat diet, and the factors associated with such variation; (ii) derive estimates of the average numbers of birds killed in Australia by cats per year and per unit area; and (iii) seek to interpret the conservation significance of such predation rates. In a companion paper (Woinarski et al. submitted), we consider the ecological traits associated with variation among bird species in the likelihood of predation by cats, and collate records of cat predation on Australia's threatened bird species.

2. Methods

2.1. Feral cats in natural environments

Legge et al. (2017) collated and then modelled 91 site-based estimates of feral cat density to derive an estimate of 2.07 million feral cats in largely natural landscapes of Australia (varying between 1.4 million in drought and average years to 5.6 million after prolonged and extensive wet periods).

For the occurrence of birds in cat diets in Australia, we collated 93 studies (with a minimum of 10 cat dietary samples per study) that provided a quantitative assessment of the frequency of birds in cat stomachs or scats. These studies (Appendix A) were widely spread (Fig. 1) and included a broad representation of Australian natural environments, although we note that some regions (e.g. north-western Australia, and parts of South Australia) had relatively few observations. We include only primary sources in this compilation, and hence omit some widely-used but secondary sources such as McLeod (2004).

Notably, 32 of these studies were also included in a previous consideration of continental variation in the diet of feral cats in Australia (Doherty et al. 2015). In four cases, the same study (or study site) was included as two samples in our collated data base, where the study clearly reported data from nearby sites with contrasting management regimes, or at times of notably contrasting seasonal conditions or resource abundance. Many of the studies collated here spanned several seasons, or the time of year covered by the sampling was not specified, so we do not consider seasonal variation in cat diet in this analysis. The studies occurred over the period 1969-2016, but we do not include year in analyses because a directional trend in diet over decadal scales is unlikely, and Legge et al. (2017) found no evidence of trends in cat densities over this period. Our studies include cat dietary samples from times of drought and high rainfall years.

Collectively, these studies include 9715 cat stomachs or scats. Most of these studies report only frequency of occurrence (i.e. the proportion of scats or stomachs that contained 'birds') rather than a record of the number of individual birds in those samples. However, in a subset of studies (Appendix A), tallies were given for the number of individual birds in those samples that contained birds: averaged over these studies, the mean number of individual birds in cat scats or stomachs that contained birds was 1.34 (±0.07 SE). This value showed no significant variation with frequency of occurrence (Appendix B).

Here, we assume that one stomach or scat sample represents 24 hr worth of prey eaten by an individual cat. This is likely to be a conservative under-estimate of the number of prey killed per day because: (i) prey are largely digested after 12 hr; (ii) cats typically produce more than two scats per day; (iii) cats may kill some birds but not necessarily consume them ('surplus kill'); and (iv) eggs and chicks with largely undeveloped feathers may be rapidly digested and leave little trace (Davies and Prentice 1980; George 1978; Hubbs 1951; Jackson 1951; Loss et al. 2013; Read and Bowen 2001). Furthermore, cats may injure birds in attempted but failed capture (and hence not be detected in cat scats or stomachs), but such wounds may subsequently result in bird deaths. Conversely, cats may also scavenge, so some birds included in cat dietary studies are not necessarily killed by the cat that consumed them (Hayde 1992; Molsher et al. 2017). Also, the fragments of a single bird may be excreted by the cat that consumed the bird in more than one scat, so – where such scats from a single cat are collected and included in analysis – this may result in an over-estimate of the numbers of birds killed.

To analyse variation in the frequency of birds in cat diet samples, we noted 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:

$$island\ size\ index = \log_{10}\left(\text{minimum}\left\{1, \frac{area}{10000}\right\}\right),$$

where *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 0. Islands <10 000 km^2 have negative values, which

become increasingly negative with decreasing island area. From the location of the study, we also determined several climatic and environmental variables to assess their effects on the frequency of birds in cat diet samples. These included mean annual rainfall (Australian Bureau of Meteorology 2016a), mean annual temperature (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 used generalised linear models (GLMs) to examine geographic variation in the frequency of birds in the diet of feral cats. The response variable was the proportion of samples (scats or stomachs) containing birds, and hence was analysed using the binomial error family. By using the binomial error family, the GLMs took into account the lower precision of the observations based on a small number of samples. We examined a set of 40 candidate models representing all combinations of the five explanatory variables described above (island size index, rainfall, temperature, tree cover, ruggedness), including an interaction between rainfall and temperature (to account for a possible negative effect of temperature on water availability). Models were evaluated using a second-order form of Akaike's Information Criterion ($QAIC_c$), which is appropriate for small sample sizes and overdispersed data (Burnham and Anderson 2003). There was evidence of strong overdispersion, so we used the 'quasibinomial' error structure to estimate coefficient standard errors and confidence intervals.

The final model was based on multi-model averaging of the entire candidate set, with each model weighted according to w_i, the Akaike weight, equivalent to the probability of a particular model being the best in the candidate set (Burnham and Anderson 2003). The final model was used to predict the frequency of birds in the diet of cats across Australia's natural environments (i.e. excluding areas of highly modified landscapes).

Multiplying the modelled frequency of birds in cat samples across Australia by the mean number of individual birds in cat diet samples containing birds (1.34) provided a spatial representation of the estimated number of birds killed per feral cat per day. We multiplied this by the modelled density of cats in natural environments 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 birds killed by cats per km^2 per year. We summed this rate across the natural environments of Australia to derive the total number of birds killed by feral cats.

We followed the approach of Loss et al. (2013) and Legge et al. (2017) and characterised the uncertainty of the estimated total number of birds killed by feral cats using bootstrapping. Bootstrapping is an appropriate approach because we needed to propagate errors through a number of analytical steps (e.g. the estimate of the total feral cat population, the number of birds eaten per cat per year). Hence, we simultaneously bootstrapped (20,000 times – which was the maximum feasible given computational constraints) the three underlying datasets: (i) cat density; (ii) frequency of birds in cat samples; and (iii) the mean number of individual birds in cat diet samples containing birds. For each random selection of these underlying data, we recalculated the total number of birds killed. We report the 2.5% and 97.5% quantiles for the 20,000 values of the total number of birds killed.

2.2. Feral cats in highly modified landscapes

Legge et al. (2017) estimated that 0.72 million feral 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 feral cats is unintentionally provided by humans. There were only five Australian studies (with >10 samples) that reported frequency of birds in the diet of feral cats occurring in highly modified environments (Appendix A). This small number provides little scope for assessing variability, so we simply use the average frequency of birds in samples across these five studies and multiply this mean by the density (and hence population size) of feral cats in these environments as estimated by Legge et al. (2017). We also compare the frequency of birds in these diet samples with those from feral cats in natural environments 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 birds killed by pet cats in Australia has been estimated in several Australian studies that have involved cat-owners tallying the number of prey items brought in by pet cats (Barratt 1997, 1998; Paton 1990, 1991, 1993; Trueman 1991). There is substantial variation in such tallies according to the amount of time the pet cat is allowed to roam outside (Trueman 1991).

The actual number of kills by pet cats is likely to be 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 prey actually taken (Blancher 2013): reported values are 12.5% (Maclean 2007), 23% (Loyd et al. 2013), 30% (Kays and DeWan 2004) and 50% (George 1974). In analysis here, we average across Australian studies the number of individual birds reported by pet owners to be killed by their pet cats per year, and scale this up to account for the number of birds killed but not returned to the cat's home, using the mean (29%) from the four studies that provide estimates of this proportion.

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

Australian birds 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, notably the introduced European red fox and dingo (including wild dog) *Canis dingo/familiaris* (Appendix C). For studies that included at least 10 samples of feral cats and at least 10 samples of one other mammalian predator species, we compared the frequency of birds in samples using Wilcoxon matched-pairs tests.

2.5. The number of birds in Australia

A useful contextual reference point for the number of birds killed by cats per year in Australia would be the total Australian bird population size, however to date there has been no such estimate. A robust estimate of Australian bird population size is beyond the ambit of this paper, but we collated 90 site-based bird density estimates from a wide range of terrestrial environments (from tropical rainforests to arid grasslands), including sites from most Australian states and territories (Cogger et al. 2003; Collins et al. 1985; Keast 1985; Loyn 1985; Recher and Holmes 1985; Shields et al. 1985; Smith 1985; Woinarski et al. 1999; Woinarski et al. 1988). We recognise that this set of sites and studies is limited, and many more samples would be useful to provide a more robust estimate. Given that we consider influence of mean annual rainfall on the numbers of birds killed by cats, we also calculate the Spearman rank correlation of average annual rainfall and bird density across this database of 90 sites.

3. Results

3.1. Feral cats in natural environments

Across 93 studies in natural environments in Australia (Appendix A; Fig. 1), the overall frequency of birds in cat scat and stomach samples was 31.6% (95% confidence interval [CI]: 26.9–36.7%), with frequency ranging widely across individuals studies from 4.2 to 92.8%.

Generalised linear modelling suggested that two variables were clear predictors of the frequency of birds in feral cat diet samples: (1) whether the site was on an island or the mainland, and the size of the island; and (2) mean annual rainfall. These variables were included in the eight most highly ranked models, all with a high level of support ($QAIC_c \leq 6.5$; Table 1). Models containing the island size and rainfall variables had R^2 of ≥0.50.

By far the best predictor of the frequency of birds in feral cat diet samples was the size of the landmass from which the sample came, i.e. mainland vs. island, and size of the island. Bird frequency in cat samples from islands was more than double that of cats from mainland areas (56.1% vs. 25.5%, $p < 0.0001$) (Fig. 2a). The three studies from the Tasmanian mainland had frequencies of birds in cat samples (18.5%) that are closer to the average for the Australian mainland (25.6%) than to that for smaller islands. The frequency of birds in cat samples from island studies was significantly negatively related to island area ($r^2 = 0.90$, $p < 0.001$) (Fig. 2b).

Mean annual rainfall had a substantially weaker, though very clear, effect on the frequency of birds in cat dietary samples. Birds were much more likely to be present in the diets of cats at low-rainfall sites (Fig. 3). The modelled relationships between the frequency of birds in cat diets and the full set of explanatory variables were used to project the frequency across Australia (Fig. 4a). The spatially-weighted mean frequency of birds in cat dietary samples across the Australian mainland and islands was

25.8% (95% CI: 21.2-31.9%). Notably, the mainland's highest predictions of frequency of birds in cat diets tended to occur in areas with relatively sparse underlying data, e.g. parts of arid South Australia – suggesting that there may be a greater level of uncertainty associated with the predictions for these areas.

There was a significant negative relationship between the frequency of birds in cat dietary samples and the frequency of rabbits in those same samples (p <0.001; Appendix D). However, the frequency of rabbits in cat diet samples was not included in the spatial predictions, because of limited information about the spatial distribution of rabbit occurrence, and because this is also likely to show substantial temporal dynamism.

The product of (i) the modelled frequency of birds in cat diet samples across Australia; (ii) the mean number of individual birds in each sample containing birds (1.34); (iii) the modelled density of cats in natural environments across Australia (Legge et al. 2017); and (iv) 365.25 (days in a year), provides a spatial representation of the estimated number of birds killed by cats km^{-2} yr^{-1} (Fig. 4b). This mapping shows a clear contrast in the numbers of birds killed between mesic coastal Australia (with mean modelled rate of 18 birds killed km^{-2} yr^{-1}) and arid areas of the Australian interior (with mean modelled rate of 58 birds killed km^{-2} yr^{-1}). Less clearly shown in this map (given the scale) are the very high rates of cat-caused mortality of birds on islands (mean modelled rate of 107 birds killed km^{-2} yr^{-1}).

Summing this rate across Australia provides an estimate of 272 million birds (95% CI: 169–508 million) killed by feral cats across the natural environments of Australia each year (varying from 161 million [95% CI: 114–284 million] in dry or average years to 757 million [95% CI: 334–1580 million] in 'wet' years, assuming the proportion of birds in cat diet is constant across drought and wet years) (Fig. 5). On average, a feral cat kills 129 birds per year (95% CI: 102–166) (Fig. 5). The average number of birds killed by feral cats in natural environments is 35.6 birds km^{-2} yr^{-1} (95% CI: 22.2–66.6), varying from 21.1 birds km^{-2} yr^{-1} (95% CI: 14.9–37.3) in dry and average years to 99.3 birds km^{-2} yr^{-1} (95% CI: 43.8–207.1) in wet years. From the data reported in Table 1, the mean percentage of these birds that were native was 99.0% (N=43, s.e.=0.6).

3.2. Feral cats in highly modified landscapes

The mean frequency of birds in diet samples from the four studies of feral cats in highly modified environments was 14.4% (median 15.0%, s.e. 2.8, range 8.3-19.3). This frequency is appreciably lower than for cats in largely natural environments, although the small sample size of studies relating to highly modified landscapes constrains statistical testing (Mann-Whitney U test, z=1.71, p=0.087).

Unfortunately, none of the studies of cat diet in modified environments noted the proportion of birds killed that were native or the number of individual birds in cat samples that had birds. The most conservative assumption is that only one individual bird was in a cat stomach or scat that contained birds; an alternative assumption is to apply the mean number of 1.34 individual birds reported in cat samples containing birds from the large collation of studies of feral cats in natural environments. Hence,

using these values as lower and upper bounds, individual cats in highly modified landscapes kill, on average, between 52.6 and 70.5 birds yr^{-1}: henceforth we use the midpoint of these tallies (61.5 birds cat^{-1} yr^{-1}).

Multiplying the total population size of feral cats in highly modified landscapes (0.72 million: Legge et al. (2017)) by this *per capita* annual take produces an estimate of 44.3 million birds killed per year by feral cats in modified environments.

3.3. Pet cats

Pet owners reported an average of 8.0 birds observed to be taken home as prey per cat per year in a sample of 700 cats from mainly around Adelaide (Paton 1990, 1991, 1993), 2.3 in Canberra from a sample of 138 cats (Barratt 1997), and 3.3 in Hobart from a sample of 166 cats (Trueman 1991) – i.e. an average of 4.53 birds per year across these studies. Scaling this mean by the average proportion of all kills that are returned home (29%), the average number of birds killed by individual pet cats is 15.6 birds cat^{-1} yr^{-1}. Hence, with a total Australian population of 3.88 million pet cats, the estimated annual tally of birds killed by pet cats is 60.6 million.

Unsurprisingly (given the typically higher abundance of introduced birds in urban areas), introduced bird species comprise a higher proportion of the birds killed by pet cats in Australia than for feral cats in largely natural environments – e.g. native birds comprised 58% of all birds killed by pet cats in Canberra (Barratt 1997), 73% in Hobart (Trueman 1991) and 88% in Adelaide (Paton 1991).

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

Comparative data on the frequency of birds in samples of feral cats and other co-occurring mammalian predators are summarised in Appendix C. Across 22 studies where the diet of co-occurring cats and foxes was reported, the frequency of birds was appreciably higher in the diet of cats (mean=29.1%) than of foxes (mean=17.3%) (Wilcoxon-matched pairs test z=3.13. p=0.0017). Across 15 studies in which the diet of co-occurring cats and dogs (including dingoes) was reported, the frequency of birds was more than twice as high in the diet of cats (mean=34.1%) than of dogs/dingoes (mean=14.0%) (z=3.41, p=0.001). Only two studies with sample sizes of >10 samples per species have considered the diet of cats and a co-occurring native marsupial predator, in both cases, the spotted-tailed quoll *Dasyurus maculatus* (Burnett 2001; Glen et al. 2011). In these studies, the frequency of birds was appreciably higher in the diet of cats (mean=22.6%) than in the diet of the marsupial carnivore (mean=9.3%).

3.5. The number of birds in Australia

Across the 90 site estimates collated here, the mean bird density reported was 14.2 birds ha^{-1} (95% CI: 12.1–16.3), suggesting a total Australian terrestrial bird population of ca. 10.9 billion (95% CI: 9.3–12.5

billion). Across sites, bird density was weakly positively correlated with mean annual rainfall (r_s=0.26, $p<0.05$).

4. Discussion

Predation by cats has been a major cause of the extinction of many bird species on many islands (Blackburn et al. 2004; Bonnaud et al. 2011; Doherty et al. 2016; Duncan and Blackburn 2007; Medina et al. 2011; Nogales et al. 2013), but the species-level impacts of cat predation on birds in continental areas remain poorly resolved. Here we show that the average frequency of birds in the diet of cats on Australian islands is at least twice that of mainland areas. This finding is consistent with (but more marked than) previous recognition of the higher frequency of birds in cat diet samples from Australian islands than the mainland (Doherty et al. 2015); and similar results have been reported for islands elsewhere (Fitzgerald and Karl 1979; Fitzgerald and Veitch 1985). The high proportion of birds in the diet of cats on islands relative to those on the mainland may be because many islands support large numbers of breeding seabirds and/or because many islands may lack alternative prey sources, particularly mammals. Furthermore, island endemic bird species that have not co-evolved with mammalian predators may experience increased predation rates due to prey naivety (Banks and Dickman 2007; Blackburn et al. 2004; Medina et al. 2011; Salo et al. 2007). We can now extend this result further, by considering also the relative densities of cats on islands and mainland areas. Given that the density of cats on Australian islands is typically ca. five times that of cats in mainland areas (Legge et al. 2017), the overall take of birds by cats (per unit area) is about ten-fold higher on Australian islands than on comparable mainland areas, with this rate especially high on smaller islands. Given this contrast, it is unsurprising that the viability of bird species on islands may be far more jeopardised by cats than on mainland areas. Nonetheless, islands (not including Tasmania) comprise only a small proportion of the total Australian land mass (0.42%) and, although birds on islands suffer high rates of predation, our modelled results indicate that island birds contribute only 4.0% of the total number of birds killed by cats in Australia: the overwhelming majority of cat predation on Australian birds is on the mainland.

Previous studies have suggested that variation in the frequency of occurrence of birds in cat samples in continental Australia is not strongly associated with any climate feature (Denny and Dickman 2010) or to latitude, longitude or productivity (Doherty et al. 2015). Analysis of the larger database compiled here demonstrates instead that the diet of feral cats includes a higher proportion of birds in drier regions. Given that cat density also tends to be higher in such regions, at least in higher rainfall years (Legge et al. 2017), the total number of birds killed by cats per unit area in arid and semi-arid environments of inland Australia is up to three orders of magnitude higher than in Australia's mesic fringe. This may be because cats hunt more effectively and more birds occur on or near the ground in the low open woodlands, shrublands and grasslands that characterise Australia's arid and semi-arid areas than is the case in the denser tall forests that characterise Australia's higher rainfall areas. Although this is a plausible explanation, we note that variation in the frequency of birds in cat samples was unrelated to the simple vegetation cover variable we used in our analysis. Our limited assessment of spatial variation in bird density indicates that higher incidence of birds in cat diets in arid areas is not because there are more

birds in arid and semi-arid areas than in higher rainfall areas – indeed, the reverse is so. Hence, cats take more birds, and a higher proportion of the local bird population, in arid and semi-arid areas than in more mesic areas.

Although native and introduced mammals comprise most of the diet of feral cats in Australia, as elsewhere in the world (Bonnaud et al. 2011; Bradshaw 1992; Turner and Meister 1988), and reptiles may be a major food item in arid and semi-arid areas (Doherty et al. 2015), the data collated here demonstrate that birds comprise an important item of feral cat diet, and that cats consume large numbers of birds. Our spatially-weighted mean frequency (25.8%) of birds in feral cat samples reported here is remarkably similar to that reported by Doherty et al. (2015) (26.9%) from a collation of fewer studies (though with substantial overlap between the underlying datasets). Notably, the early study by Coman and Brunner (1972), which concluded that predation by feral cats was unlikely to have a significant impact on birds, had one of the lowest frequencies of birds reported in cat diet (4.7%) across the substantial collation of studies presented here. Hence its conclusion – that cat predation is unlikely to have any significant impact on the status of birds in Australia – is not supported by our more comprehensive analysis. The mean frequency reported here for birds in feral cat diet samples from Australia is also appreciably higher than that of 20.7% reported globally from 15 studies (Fitzgerald and Turner 2000).

The estimate reported here of 129 birds consumed annually per feral cat in natural environments is substantially higher than that reported from smaller samples in two Australian mainland areas (27 birds cat^{-1} yr^{-1} in Victoria by Coman and Brunner (1972), and 75 birds cat^{-1} yr^{-1} for semi-arid South Australia by Read and Bowen (2001)), but somewhat less than the 154 birds cat^{-1} yr^{-1} reported for Macquarie Island (Jones 1977).

We estimate an average of 35.6 birds km^{-2} yr^{-1} are killed by feral cats in largely natural environments. This estimated average rate of birds killed by cats in natural environments per unit area is appreciably lower than the sole preceding mainland estimate of 150 birds km^{-2} yr^{-1} given for Roxby Downs in semi-arid South Australia (Read and Bowen 2001), with this difference largely attributable to the unusually high cat densities given in that study, and that our estimate represents an average take across all Australian environments, including those in which the take of birds by cats is relatively low. Notably the Roxby Downs estimate is lower than our modelled maximum rate of birds killed by cats (332 birds km^{-2} yr^{-1}), also in arid Australia.

Our estimates for the numbers of birds killed by pet cats and feral cats in modified environments are based on few samples. Our estimate that pet cats kill 15.6 birds cat^{-1} yr^{-1} is within the range reported by studies elsewhere in the world: for example, 5 birds cat^{-1} yr^{-1} in Dunedin (New Zealand) (van Heezik et al. 2010), 5.9 birds cat^{-1} yr^{-1} in Bristol (England) (Baker et al. 2005), 12 birds cat^{-1} yr^{-1} in rural environments and 30 birds cat^{-1} yr^{-1} in urban environments in Poland (Krauze-Gryz et al. in press), and 36-72 birds cat^{-1} yr^{-1} for free-roaming pet cats in Michigan (USA) (Lepczyk et al. 2004).

The results presented here suggest that feral cats are far more substantial predators of birds than Australia's two other eutherian predators, the red fox and wild dog (including dingo). Our results compare the *per capita* relative frequency of birds in the diet of these three mammalian predators, but cats often (but not always: e.g. Pavey et al. (2008)) also occur at higher densities (Read and Bowen 2001) and occur across more Australian land area than do foxes and dogs, hence the overall take of birds by cats is likely to be substantially higher than for foxes and dogs. Furthermore, cats – but not dogs and generally not foxes – may hunt in part arboreally (Saunders 1991), and so may take a wider range of birds and their eggs and young than do dogs and foxes. The limited available information suggests that cats may also be more substantial predators of birds than a native marsupial carnivore (Appendix C, for spotted-tailed quoll), with comparable results also in a study with much smaller sample size for two native marsupial predators occurring with feral cats: Tasmanian devil *Sarcophilus harrisii* and eastern quoll *D. viverrinus* (Taylor 1986).

Across the three components of Australia's cat population, the total estimated number of birds killed is 377 million per year, with 72% of this tally contributed by feral cats in natural environments, 12% by feral cats in highly modified environments, and 16% by pet cats. Comparable national-scale assessments of the number of birds killed per year include 100-350 million birds killed by cats in Canada (Blancher 2013), about 27 million birds killed by pet cats in Great Britain (Woods et al. 2003), 240 million birds killed by feral cats in the United States (Pimentel et al. 2005), with a more substantial evidence base subsequently resulting in that estimate increased to 1-4 billion birds killed by all cats in the contiguous United States (Dauphiné and Cooper 2009; Loss et al. 2013). Our Australian estimate is of comparable magnitude to these estimates, but differs in some notable respects from the area for which the most detailed comparison is possible, the United States (Table 2). The United States has a far higher density and total population of cats (feral cats and pets) than for Australia. We presume this is largely because of the far higher human population density (even in most rural areas), and hence more cats, in the United States than is typical for Australia. However, our estimates indicate that on a *per capita* basis, cats in Australia kill far more birds than in the United States, or than in Canada (24 to 64 birds cat^{-1} yr^{-1}: Blancher (2013)). Although this estimated *per capita* predation rate on birds is higher for cats in Australia than in the United States, the markedly higher population of cats in the United States means that the total estimated number of birds killed by cats there is almost an order of magnitude higher than our estimate for Australia. We note also that our estimate of *per capita* predation of birds by cats includes a factor for the number of individual birds in cat dietary samples that contain birds: this factor is generally not considered in most other analyses, such that the rate of cat predation on birds may be under-estimated in many other studies.

Predation of birds by cats is one of the largest human-related mortality factors for birds (Blancher 2013; Loss et al. 2012, 2013, 2015). Some studies elsewhere in the world have linked, with varying degrees of uncertainty, high predation rates by cats to ongoing reduction in the abundance of at least some bird species, even in mainland settings (Baker et al. 2005, 2008; Balogh et al. 2011; Churcher and Lawton 1987; Crooks and Soulé 1999; Lepczyk et al. 2004; Thomas et al. 2012; van Heezik et al. 2010; Woods et al. 2003).

Our estimates of an average of 272 million birds (of which ca. 99% are native) killed annually in natural landscapes in Australia by feral cats, increasing to 377 million yr^{-1} (i.e. >1.0 million birds day^{-1}) with inclusion of the numbers of birds killed by pet cats and feral cats in modified landscapes, are very large tallies. However, the ecological and conservation significance of these kill tallies is difficult to contextualise, because (i) there are no reliable estimates of the total population of birds in Australia; (ii) predation may fall disproportionately on some bird species; (iii) some bird 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 birds killed across Australia. Furthermore, in contrast to the situation in some other continents (Loss et al. 2015), it is difficult to interpret the relative impacts of cat predation on Australian birds, because there has been little broad scale assessment in Australia of the mortality rates and impacts upon birds of other threatening factors. Our estimates of numbers of birds killed by cats and the total Australian bird population indicate that the cats kill about 3.5% of Australia's terrestrial bird population (with this percentage figure conservatively excluding all bird kills on islands, for which seabirds may make a large contribution). We recognise that this estimate of proportion killed is indicative only, and that a more robust estimate of total Australian bird population would be desirable.

At a population level, the susceptibility of bird species to cat predation may be affected by a range of demographic and other factors. Many Australian bird species are long-lived but have relatively low reproductive outputs (Woinarski 1985, 1989; Yom-Tov 1987; Yom-Tov et al. 1992), and bird species with such demographic characteristics may be particularly susceptible to decline with high predation rates. Cat densities and impacts vary markedly across Australia. For birds (and other native species), the impacts of cat predation may be most severe during the period of transition from high rainfall conditions to drought when populations of some bird species may be concentrated in drought refuge areas that happen still to have high densities of cats (Pavey et al. 2014; Pavey and Nano 2013). The extent and impact of cat predation on birds 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. 2014, 2016). Cat predation may also subvert the assumed conservation security provided to native species by the conservation reserve system, given that feral cats occur in similar density within and outside Australia's reserve system (Legge et al. 2017).

The large amount of predation by cats on Australian birds reported here, even in mainland areas, is sufficient evidence to raise some conservation concern. This rate may or may not of itself be sufficient to drive severe population declines of any bird species, but it is an ongoing chronic depletion that may lead to long-term reduction in bird populations and reduced resilience and increased susceptibility of some bird species to additional threats. To better resolve the conservation impact of such predation rates, the evidence base needs to be substantially improved. One high priority is to more precisely assess the responses (including changes in abundance, breeding success and habitat use) of a range of bird species to reduction in cat abundance due to the increasing cat control efforts now being made in many areas. One of the few Australian studies of this type conducted to date reported marked local increases in population size for eastern bristlebirds *Dasyornis brachypterus* following effective control of introduced predators (in this case, mostly red foxes) (Lindenmayer et al. 2009). The ongoing

establishment of increasingly large predator-proof exclosures, and programs to eradicate cats on islands, present additional opportunities for more detailed studies of the impacts of cats (and cat control) on the abundance and population viability of many bird species. However, existing exclosures may be mostly too small for many bird species, and the environments in many exclosures may now be influenced by very high densities of threatened mammals, confounding ready assessment of impacts due to introduced predators alone (Kemp and Roshier 2016). There are relatively few bird species in Australia for which demographic parameters are well known, for which population viability analyses have been undertaken, or for which factors limiting population size are well resolved. However, understanding the population-level consequences of particular rates of predation by feral cats (or any other factor), including consideration of possible age- or sex-related differences in predation rates, requires such context (Newton 1998). A priority for further research is to derive or estimate relevant demographic variables for bird species that are potentially susceptible to cat predation, and thence to model the likely population-level impacts of current predation levels or impacts under a range of potential cat management programs. The consideration of population-level impacts of cat predation on a range of bird species in Dunedin (New Zealand) provides a reasonable model for this approach (van Heezik et al. 2010).

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. Resulting increases in the number, and size, of islands from which cats have been eradicated, increasing numbers of predator-proof exclosures and increasing numbers and total extent of areas subject to intensive cat-baiting programs are likely to provide some substantial collateral conservation benefits to Australian bird species. But such benefits may be even more pronounced if the conservation of bird species is used more proactively as a factor in the development of these conservation programs. This could occur for example, if the location of susceptible seabird colonies is a major factor in the identification of islands prioritised for cat eradication, or if the mainland location of predator-susceptible threatened bird species is used to help determine the site and intensity of cat-baiting programs.

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References

Abbott, I., Peacock, D., Short, J., 2014. The new guard: the arrival and impacts of cats and foxes, In Carnivores of Australia: past, present and future. eds A.S. Glen, C.R. Dickman, pp. 69-104. CSIRO Publishing, Collingwood.
Animal Medicines Australia, 2016. Pet ownership in Australia. Summary 2016. http://animalmedicinesaustralia.org.au/wp-content/uploads/2016/11/AMA_Pet-Ownership-in-Australia-2016-Report_sml.pdf. Accessed 21/07/2017.
Australian Bureau of Meteorology, 2016a. Average Annual, Seasonal and Monthly Rainfall. http://www.bom.gov.au/jsp/ncc/climate_averages/rainfall/index.jsp. Accessed 06/07/2016.
Australian Bureau of Meteorology, 2016b. Average Annual and Monthly Maximum, Minimum, and Mean Temperature. http://www.bom.gov.au/jsp/ncc/climate_averages/temperature/index.jsp. Accessed 06/07/2016.
Baker, P.J., Bentley, A.J., Ansell, R.J., Harris, S., 2005. Impact of predation by domestic cats *Felis catus* in an urban area. Mammal Review 35, 302-312.
Baker, P.J., Molony, S.E., Stone, E., Cuthill, I.C., Harris, S., 2008. Cats about town: is predation by free-ranging pet cats *Felis catus* likely to affect urban bird populations? Ibis 150, 86-99.
Balogh, A.L., Ryder, T.B., Marra, P.P., 2011. Population demography of Gray Catbirds in the suburban matrix: sources, sinks and domestic cats. Journal of Ornithology 152, 717-726.
Banks, P.B., Dickman, C.R., 2007. Alien predation and the effects of multiple levels of prey naiveté. Trends in Ecology & Evolution 22, 229–230.
Barratt, D.G., 1997. Predation by house cats, *Felis catus* (L.), in Canberra, Australia. I. Prey composition and preference. Wildlife Research 24, 263-277.
Barratt, D.G., 1998. Predation by house cats, *Felis catus* (L.), in Canberra, Australia. II. Factors affecting the amount of prey caught and estimates of the impact on wildlife. Wildlife Research 25, 475-487.
Blackburn, T.M., Cassey, P., Duncan, R.P., Evans, K.L., Gaston, K.J., 2004. Avian extinction and mammalian introductions on oceanic islands. Science 305, 1955-1958.
Blancher, P., 2013. Estimated number of birds killed by house cats (*Felis catus*) in Canada. Avian Conservation and Ecology 8, 3.
Bonnaud, E., Medina, F.M., Vidal, E., Nogales, M., Tershy, B., Zavaleta, E., Donlan, C.J., Keitt, B., Le Corre, M., Horwath, S.V., 2011. The diet of feral cats on islands: a review and a call for more studies. Biological Invasions 13, 581-603.
Bowen Z., Read J., 1998. Population and demographic patterns of rabbits (*Oryctolagus cuniculus*) at Roxby Downs in arid South Australia and the influence of rabbit haemorrhagic disease. Wildlife Research 25, 655–662.
Bradshaw, J.W.S., 1992. The behaviour of the domestic cat. CAB International, Wallingford UK.
Burnett, S.E., 2001. Ecology and conservation status of the northern spot-tailed quoll, *Dasyurus maculatus* with reference to the future of Australia's marsupial carnivores. PhD. thesis. James Cook University, Townsville.
Burnham, K.P., Anderson, D.R., 2003. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer, New York.
Churcher, P.B., Lawton, J.H., 1987. Predation by domestic cats in an English village. Journal of Zoology 212, 439-455.
Cogger, H., Ford, H., Johnson, C., Holman, J., Butler, D., 2003. Impacts of land clearing on Australian wildlife in Queensland. World Wide Fund for Nature Australia, Brisbane.
Collins, B.G., Wykes, B.J., Nichols, O.G., 1985. Re-colonization of restored bauxite mineland by birds in southwestern Australian forests, In Birds of eucalypt forests and woodland: ecology, conservation, management. eds H. Ford, A. Keast, H. Recher, D. Saunders, pp. 341-354. Surrey Beatty and Sons, Sydney.

693 Coman, B.J., Brunner, H., 1972. Food habits of the feral house cat in Victoria. The Journal of Wildlife
694 Management 36, 848-853.
695 Commonwealth of Australia, 2015. Threatened species strategy, Department of Environment and Energy
696 Canberra. http://www.environment.gov.au/biodiversity/threatened/publications/threatened-species-
697 strategy. Accessed 20/6/2017.
698 Courchamp, F., Langlais, M., Sugihara, G., 2000. Rabbits killing birds: modelling the hyperpredation
699 process. Journal of Animal Ecology 69, 154-164.
700 Crooks, K.R., Soulé, M.E., 1999. Mesopredator release and avifaunal extinctions in a fragmented system.
701 Nature 400, 563-566.
702 Dauphiné, N., Cooper, R.J., 2009. Impacts of free-ranging domestic cats (*Felis catus*) on birds in the
703 United States: a review of recent research with conservation and management recommendations, In
704 Tundra to tropics: connecting birds, habitats and people. Proceedings of the 4th International Partners
705 in Flight Conference, 13-16 February 2008, McAllen, Texas. eds T.D. Rich, C. Arizmendi, D.W. Demarest,
706 C. Thompson, pp. 205-219. Partners in Flight, McAllen, Texas.
707 Davies, W., Prentice, R., 1980. The feral cat in Australia. Wildlife in Australia 17, 20-26.
708 Denny, E.A., Dickman, C.R., 2010. Review of cat ecology and management strategies in Australia.
709 Invasive Animals Cooperative Research Centre, Canberra.
710 Department of the Environment, 2015. Threat abatement plan for predation by feral cats, Canberra.
711 Dickman, C.R., 1996. Overview of the Impacts of Feral Cats on Australian Native Fauna. Australian
712 Nature Conservation Agency, Canberra.
713 Dickman, C.R., 2009. House cats as predators in the Australian environment: impacts and management.
714 Human-Wildlife Conflicts 3, 41-48.
715 Dickman, C.R., 2014. Measuring and managing the impacts of cats, In Carnivores of Australia: past,
716 present and future. eds A.S. Glen, C.R. Dickman, pp. 173-195. CSIRO Publishing, Collingwood.
717 Dickman, C.R., Newsome, T.M., 2015. Individual hunting behaviour and prey specialisation in the house
718 cat *Felis catus*: implications for conservation and management. Applied Animal Behaviour Science 173,
719 76-87.
720 Dickman, C.R., Wardle, G.M., Foulkes, J.N., de Preu, N., 2014. Desert complex environments, In
721 Biodiversity and environmental change. eds D. Lindenmayer, E. Burns, N. Thurgate, A. Lowe, pp. 379-
722 438. CSIRO Publishing, Collingwood.
723 Doherty, T.S., Davis, R.A., Etten, E.J.B., Algar, D., Collier, N., Dickman, C.R., Edwards, G., Masters, P.,
724 Palmer, R., Robinson, S., 2015. A continental-scale analysis of feral cat diet in Australia. Journal of
725 Biogeography 42, 964-975.
726 Doherty, T.S., Dickman, C.R., Johnson, C.N., Legge, S.M., Ritchie, E.G., Woinarski, J.C.Z., 2017. Impacts
727 and management of feral cats *Felis catus* in Australia. Mammal Review 47, 83-97.
728 Doherty, T.S., Glen, A.S., Nimmo, D.G., Ritchie, E.G., Dickman, C.R., 2016. Invasive predators and global
729 biodiversity loss. Proceedings of the National Academy of Sciences 113, 11261–11265.
730 Dubey, J.P., 2002. A review of toxoplasmosis in wild birds. Veterinary Parasitology 106, 121-153.
731 Duncan, R.P., Blackburn, T.M., 2007. Causes of extinction in island birds. Animal Conservation 10, 149-
732 150.
733 Fitzgerald, A.M., Karl, B.J., 1979. Foods of feral house cats (*Felis catus* L.) in forest of the Orongorongo
734 Valley, Wellington. New Zealand Journal of Zoology 6, 107-126.
735 Fitzgerald, B.M., Turner, D.C., 2000. Hunting behaviour of domestic cats and their impact on prey
736 populations, In The domestic cat: the biology of its behaviour. eds D.C. Turner, P. Bateson, pp. 149–175.
737 Cambridge University Press, Cambridge.
738 Fitzgerald, B.M., Veitch, C.R., 1985. The cats of Herekopare Island, New Zealand; their history, ecology
739 and effects on birdlife. New Zealand Journal of Zoology 12, 319-330.

George, W.G., 1974. Domestic cats as predators and factors in winter shortages of raptor prey. Wilson Bulletin 86, 384-396.
George, W.G., 1978. Domestic cats as density independent hunters and 'surplus' killers. Carnivore Genetics Newsletter 3, 282-287.
Glen, A.S., Pennay, M., Dickman, C.R., Wintle, B.A., Firestone, K.B., 2011. Diets of sympatric native and introduced carnivores in the Barrington Tops, eastern Australia. Austral Ecology 36, 290-296.
Graham, C.A., Maron, M., McAlpine, C.A., 2013. Influence of landscape structure on invasive predators: feral cats and red foxes in the brigalow landscapes, Queensland, Australia. Wildlife Research 39, 661-676.
Hansen, M.C., DeFries, R.S., Townshend, J.R.G., Carroll, M., Dimiceli, C., Sohlberg, R.A., 2003. Global percent tree cover at a spatial resolution of 500 m: first results of the MODIS vegetation continuous fields algorithm. Earth Interactions 7, art10.
Hartley, W.J., Dubey, J.P., 1991. Fatal toxoplasmosis in some native Australian birds. Journal of Veterinary Diagnostic Investigation 3, 167-169.
Hayde, K.A., 1992. Ecology of the feral cat *Felis catus* on Great Dog Island. B.Sc. (Hons.) thesis. University of Tasmania, Hobart.
Holden, C., Mutze, G., 2002. Impact of rabbit haemorrhagic disease on introduced predators in the Flinders Ranges, South Australia. Wildlife Research 29, 615-626.
Hubbs, E.L., 1951. Food habits of feral house cats in the Sacramento Valley. California Fish & Game 37, 177-189.
Jackson, W.B., 1951. Food habits of Baltimore, Maryland, cats in relation to rat populations. Journal of Mammalogy 32, 458-461.
Jarvis, A., Reuter, H.I., Nelson, A., Guevara, E., 2008. Hole-filled SRTM for the globe Version 4, available from the CGIAR-CSI SRTM 90m Database.
Jones, E., 1977. Ecology of the feral cat, *Felis catus* (L.),(Carnivora: Felidae) on Macquarie Island. Australian Wildlife Research 4, 249-262.
Jones, E., Coman, B.J., 1981. Ecology of the feral cat, *Felis catus* (L.), in south-eastern Australia I. Diet. Australian Wildlife Research 8, 537-547.
Kays, R.W., DeWan, A.A., 2004. Ecological impact of inside/outside house cats around a suburban nature preserve. Animal Conservation 7, 273–283.
Keast, A., 1985. Bird community structure in southern forests and northern woodlands: a comparison, In Birds of Eucalypt forests and woodland: ecology, conservation, management. eds H. Ford, A. Keast, H. Recher, D. Saunders, pp. 97-116. Surrey Beatty and Sons, Sydney.
Kemp, L., Roshier, D., 2016. A trial of release protocols for re-introduction of the bush stone-curlew to southern Australia, In Global re-introduction perspectives: 2016. ed. P.S. Soorae, pp. 117-122. IUCN/SSC Re-introduction Specialist Group & Environment Agency, Abu Dhabi UAE.
Krauze-Gryz, D., Żmihorski, M., Gryz, J., in press. Annual variation in prey composition of domestic cats in rural and urban environment. Urban Ecosystems.
Kutt, A.S., 2011. The diet of the feral cat (*Felis catus*) in north-eastern Australia. Acta Theriologica 56, 157-169.
Kutt, A.S., 2012. Feral cat (*Felis catus*) prey size and selectivity in north-eastern Australia: implications for mammal conservation. Journal of Zoology 287, 292-300.
Legge, S., Murphy, B.P., McGregor, H., Woinarski, J.C.Z., Augusteyn, J., Ballard, G., Baseler, M., Buckmaster, T., Dickman, C.R., Doherty, T., Edwards, G., Eyre, T., Fancourt, B., Ferguson, D., Forsyth, D.M., Geary, W.L., Gentle, M., Gillespie, G., Greenwood, L., Hohnen, R., Hume, S., Johnson, C.N., Maxwell, N., McDonald, P., Morris, K., Moseby, K., Newsome, T., Nimmo, D., Paltridge, R., Ramsey, D., Read, J., Rendall, A., Rich, M., Ritchie, E., Rowland, J., Short, J., Stokeld, D., Sutherland, D.R., Wayne, A.F.,

787 Woodford, L., Zewe, F., 2017. Enumerating a continental-scale threat: how many feral cats are in
788 Australia? Biological Conservation 206, 293-303.
789 Lepczyk, C.A., Mertig, A.G., Liu, J., 2004. Landowners and cat predation across rural-to-urban landscapes.
790 Biological Conservation 115, 191-201.
791 Lindenmayer, D.B., MacGregor, C., Wood, J.T., Cunningham, R.B., Crane, M., Michael, D., Montague-
792 Drake, R., Brown, D., Fortescue, M., Dexter, N., 2009. What factors influence rapid post-fire site re-
793 occupancy? A case study of the endangered Eastern Bristlebird in eastern Australia. International
794 Journal of Wildland Fire 18, 84-95.
795 Loss, S.R., Will, T., Marra, P.P., 2012. Direct human-caused mortality of birds: improving quantification of
796 magnitude and assessment of population impact. Frontiers in Ecology and the Environment 10, 357-364.
797 Loss, S.R., Will, T., Marra, P.P., 2013. The impact of free-ranging domestic cats on wildlife of the United
798 States. Nature Communications 4, 1396.
799 Loss, S.R., Will, T., Marra, P.P., 2015. Direct mortality of birds from anthropogenic causes. Annual Review
800 of Ecology, Evolution, and Systematics 46, 99-120.
801 Loyd, K. A. T., Hernandez, S. M., Carroll, J. P., Abernathy, K. J., Marshall, G. J., 2013. Quantifying free-
802 roaming domestic cat predation using animal-borne video cameras. Biological Conservation 160, 183-
803 189.
804 Loyn, R.H., 1985. Ecology, distribution and density of birds in Victorian forests, In Birds of Eucalypt
805 forests and woodland: ecology, conservation, management. eds H. Ford, A. Keast, H. Recher, D.
806 Saunders, pp. 33-46. Surrey Beatty and Sons, Sydney.
807 Maclean, M., 2007. Impact of domestic cat predation on bird and small mammal populations. Ph.D.
808 thesis. University of Exeter.
809 Marlow N.J., Croft D.B., 2016. The effect of rabbit-warren ripping on the consumption of native fauna by
810 foxes in the arid zone of New South Wales. Conservation Science Western Australia 10, 1–13.
811 Marra, P.P., Santella, C., 2016. Cat Wars: the devastating consequences of a cuddly killer. Princeton
812 University Press, Princeton.
813 McGregor, H.W., Legge, S., Jones, M.E., Johnson, C.N., 2014. Landscape management of fire and grazing
814 regimes alters the fine-scale habitat utilisation by feral cats. PLoS ONE 9, e109097.
815 McGregor, H.W., Legge, S.M., Jones, M.E., Johnson, C.N., 2016. Extraterritorial hunting expeditions to
816 intense fire scars by feral cats. Scientific Reports 6, 22559.
817 McLeod, R., 2004. Counting the cost: impact of invasive animals in Australia 2004. Cooperative Research
818 Centre for Pest Animal Control, Canberra.
819 Mead, C.J., 1982. Ringed birds killed by cats. Mammal Review 12, 183-186.
820 Medina, F.M., Bonnaud, E., Vidal, E., Tershy, B.R., Zavaleta, E.S., Josh Donlan, C., Keitt, B.S., Corre, M.,
821 Horwath, S.V., Nogales, M., 2011. A global review of the impacts of invasive cats on island endangered
822 vertebrates. Global Change Biology 17, 3503-3510.
823 Molsher, R., Newsome, A., Dickman, C., 1999. Feeding ecology and population dynamics of the feral cat
824 (*Felis catus*) in relation to the availability of prey in central-eastern New South Wales. Wildlife Research
825 26, 593-607.
826 Molsher, R.L., Newsome, A.E., Newsome, T.M., Dickman, C.R., 2017. Mesopredator management:
827 effects of red fox control on the abundance, diet and use of space by feral cats. PLoS ONE 12, e168460.
828 Moseby, K.E., Peacock, D.E., Read, J.L., 2015. Catastrophic cat predation: a call for predator profiling in
829 wildlife protection programs. Biological Conservation 191, 331-340.
830 Newton, I., 1998. Population limitation in birds. Academic Press, London.
831 Nogales, M., Vidal, E., Medina, F.M., Bonnaud, E., Tershy, B.R., Campbell, K.J., Zavaleta, E.S., 2013. Feral
832 cats and biodiversity conservation: the urgent prioritization of island management. Bioscience 63, 804-
833 810.

834 Paltridge, R., 2002. The diets of cats, foxes and dingoes in relation to prey availability in the Tanami
835 Desert, Northern Territory. Wildlife Research 29, 389-403.
836 Paton, D., 1990. Domestic cats and wildlife: results from initial questionnaire. Bird Observer 696, 34-35.
837 Paton, D.C., 1991. Loss of wildlife to domestic cats, In The impact of cats on native wildlife. ed. C. Potter,
838 pp. 64-69. Australian National Parks & Wildlife Service, Canberra.
839 Paton, D.C., 1993. Impacts of domestic and feral cats on wildlife, In Cat Management Workshop
840 Proceedings – 1993. eds G. Siepen, C. Owens, pp. 9-15. Queensland Department of Environment and
841 Heritage, Brisbane.
842 Pavey, C.R., Cole, J.R., McDonald, P.J., Nano, C.E.M., 2014. Population dynamics and spatial ecology of a
843 declining desert rodent *Pseudomys australis*: the importance of refuges for persistence. Journal of
844 Mammalogy 95, 615-625.
845 Pavey, C.R., Eldridge, S.R., Heywood, M., 2008. Population dynamics and prey selection of native and
846 introduced predators during a rodent outbreak in arid Australia. Journal of Mammalogy 89, 674-683.
847 Pavey, C.R., Nano, C.E.M., 2013. Changes in richness and abundance of rodents and native predators in
848 response to extreme rainfall in arid Australia. Austral Ecology 38, 777-785.
849 Pimentel, D., Zuniga, R., Morrison, D., 2005. Update on the environmental and economic costs
850 associated with alien-invasive species in the United States. Ecological Economics 52, 273-288.
851 Read, J., Bowen, Z., 2001. Population dynamics, diet and aspects of the biology of feral cats and foxes in
852 arid South Australia. Wildlife Research 28, 195-203.
853 Recher, H.F., Holmes, R.T., 1985. Foraging ecology and seasonal patterns of abundance ina forest
854 avifauna, In Birds of eucalypt forests and woodland: ecology, conservation, management. eds H. Ford, A.
855 Keast, H. Recher, D. Saunders, pp. 79-96. Surrey Beatty and Sons, Sydney.
856 Salo, P., Korpimäki, E., Banks, P.B., Nordström, M., Dickman, C.R., 2007. Alien predators are more
857 dangerous than native predators to prey populations. Proceedings of the Royal Society of London B:
858 Biological Sciences 274, 1237-1243.
859 Saunders, D.A., 1991. The effect of land clearing on the ecology of Carnaby's Cockatoo and the inland
860 Red-tailed Black-Cockatoo in the wheatbelt of Western Australia. Acta XX Congressus Internationalis
861 Ornithologici 1, 658-665.
862 Shields, J.M., Kavanagh, R.P., Roghan-Jones, W.G., 1985. Forest avifauna of the Upper Hastings River, In
863 Birds of eucalypt forests and woodland: ecology, conservation, management. eds H. Ford, A. Keast, H.
864 Recher, D. Saunders, pp. 55-64. Surrey Beatty and Sons, Sydney.
865 Smith, P., 1985. Woodchip logging and birds near Bega, New South Wales, In Birds of Eucalypt forests
866 and woodland: ecology, conservation, management. eds H. Ford, A. Keast, H. Recher, D. Saunders, pp.
867 259-271. Surrey Beatty and Sons, Sydney.
868 Spencer, E.E., Crowther, M.S., Dickman, C.R., 2014. Diet and prey selectivity of three species of
869 sympatric mammalian predators in central Australia. Journal of Mammalogy 95, 1278-1288.
870 Taylor, R.J., 1986. Notes on the diet of the carnivorous mammals of the upper Henty River region,
871 western Tasmania. Papers and Proceedings of the Royal Society of Tasmania 120, 7-10.
872 Thomas, R.L., Fellowes, M.D.E., Baker, P.J., 2012. Spatio-temporal variation in predation by urban
873 domestic cats (*Felis catus*) and the acceptability of possible management actions in the UK. PLoS ONE 7,
874 e49369.
875 Trueman, P., 1991. The impact of domestic and semi-domestic cats on the wildlife of southern
876 Tasmania. B.Sc. (Hons.) thesis. University of Tasmania.
877 Turner, D.C., Meister, O., 1988. Hunting behaviour of the domestic cat, In The domestic cat: the biology
878 of its behaviour. eds D.C. Turner, P. Bateson, pp. 111-121. Cambridge University Press, Cambridge.
879 van Heezik, Y., Smyth, A., Adams, A., Gordon, J., 2010. Do domestic cats impose an unsustainable
880 harvest on urban bird populations? Biological Conservation 143, 121-130.

Woinarski, J.C.Z., 1985. Breeding biology and life history of small leaf-gleaning birds in Australian forests: response to a stable environment? Proceedings of the Ecological Society of Australia 14, 159-168.
Woinarski, J.C.Z., 1989. Some life history comparisons of small leaf-gleaning bird species in south-eastern Australia. Corella 13, 73-80.
Woinarski, J.C.Z., Burbidge, A.A., Harrison, P.L., 2015. The ongoing unravelling of a continental fauna: decline and extinction of Australian mammals since European settlement. Proceedings of the National Academy of Sciences 15, 4531-4540.
Woinarski, J.C.Z., Fisher, A., Milne, D., 1999. Distribution patterns of vertebrates in relation to an extensive rainfall gradient and variation in soil texture in the tropical savannas of the Northern Territory, Australia. Journal of Tropical Ecology 15, 381-398.
Woinarski, J.C.Z., Tidemann, S.C., Kerin, S., 1988. Birds in a tropical mosaic: the distribution of bird species in relation to vegetation patterns. Australian Wildlife Research 15, 171-196.
Woods, M., McDonald, R.A., Harris, S., 2003. Predation of wildlife by domestic cats *Felis catus* in Great Britain. Mammal Review 33, 174-188.
Work, T.M., Massey, J.G., Rideout, B.A., Gardiner, C.H., Ledig, D.B., Kwok, O.C.H., Dubey, J.P., 2000. Fatal toxoplasmosis in free-ranging endangered ‘Alala from Hawaii. Journal of Wildlife Diseases 36, 205-212.
Yip, S.J.S., Dickman, C.R., Denny, E.A., Cronin, G.M., 2014. Diet of the feral cat, *Felis catus*, in central Australian grassland habitats: do cat attributes influence what they eat? Acta Theriologica 59, 263-270.
Yip, S.J.S., Rich, M., Dickman, C.R., 2015. Diet of the feral cat, *Felis catus*, in central Australian grassland habitats during population cycles of its principal prey. Mammal Research 60, 39-50.
Yom-Tov, Y., 1987. The reproductive rates of Australian passerines. Wildlife Research 14, 319-330.
Yom-Tov, Y., McCleery, R., Purchase, D., 1992. The survival rate of Australian passerines. Ibis 134, 374-379.

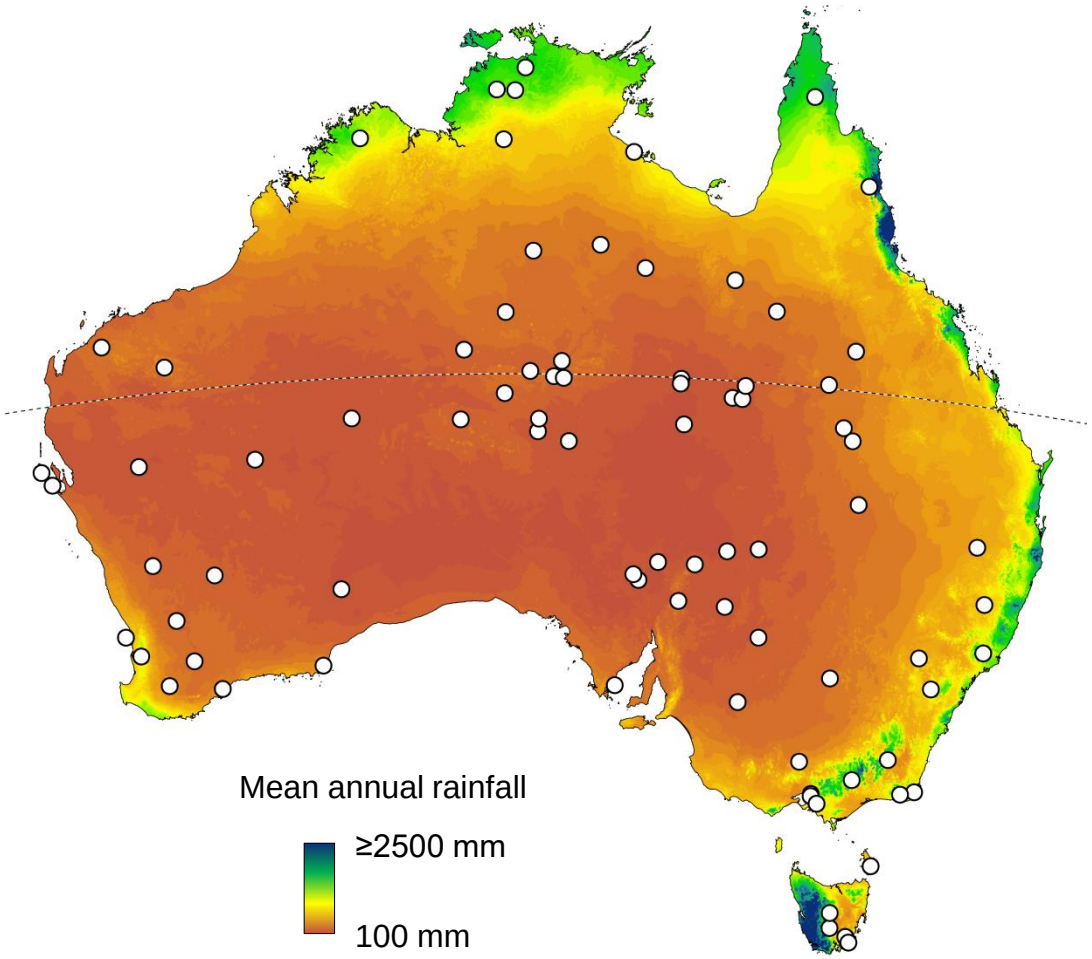


Figure 1. Locations of cat dietary studies collated in this study. There are 84 sites (in some cases with several studies at each site) in natural vegetation (72 on the Australian mainland, three in Tasmania and 9 on smaller islands, including Macquarie and Christmas Islands, not shown on map). There are another five sites at rubbish tips. The map background shows mean annual rainfall (Australian Bureau of Meteorology 2016b). The dashed line indicates the Tropic of Capricorn.

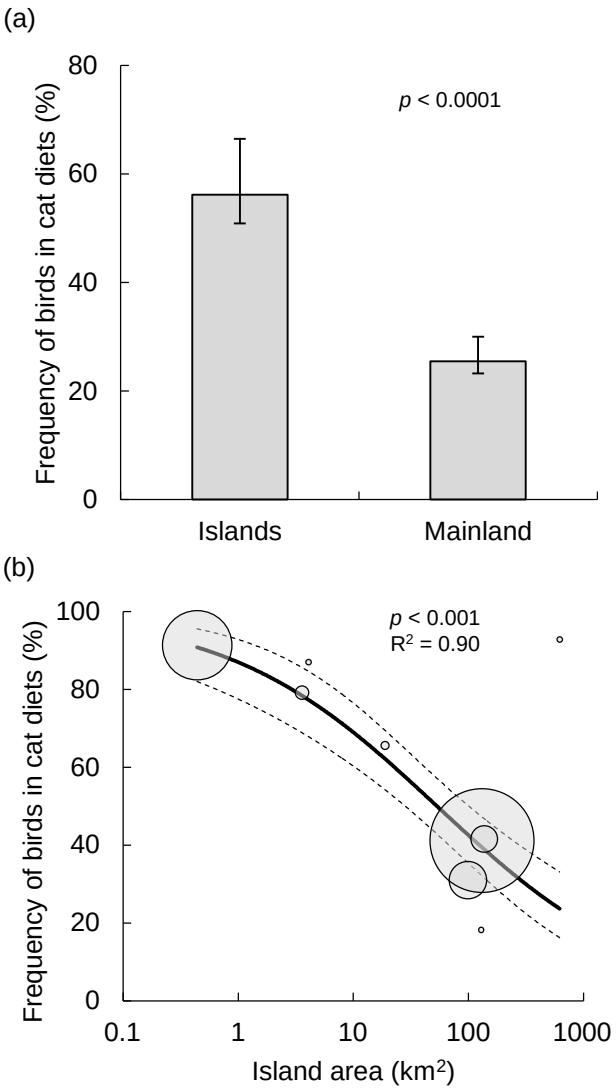
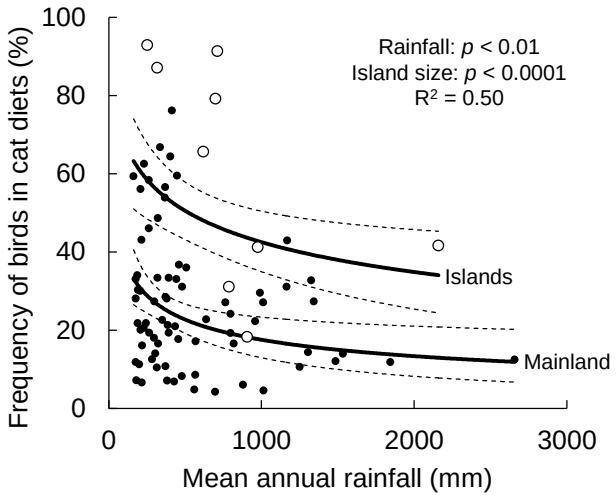


Figure 2. Variation in the frequency of birds in cat diet samples on: (a) the mainland, comprising Tasmania (*n* = 3) and greater Australian mainland (*n* = 72), and smaller islands (*n* = 11); and (b) in relation to island size (for islands smaller than Tasmania, 64 519 km^2). In (b) the circles indicate the observed values, with the size of the circle proportional to the number of samples used to generate the estimate, ranging from 11 (smallest circle) to 756 (largest circle). In both (a) and (b) the predictions are from generalized linear models (quasibinomial errors). The error bars in (a) indicate standard errors, while the dashed lines in (b) indicate the 95% confidence intervals of the position of the regression line. For (b), the model coefficients are provided in Appendix E.



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925 Figure 3. Variation in the frequency of birds in cat diet samples in relation to mean annual rainfall.
926 Observations from the mainland, comprising Tasmania and greater Australian mainland, are indicated by
927 filled circles, while those from islands smaller than Tasmania, 64 519 km^2, are indicated by unfilled
928 circles. Regression lines represent the predictions of generalized linear models (quasibinomial errors),
929 with separate regression lines shown for the mainland and smaller islands. The dashed lines indicate the
930 95% confidence intervals of the position of the regression lines. The model coefficients are provided in
931 Appendix E.

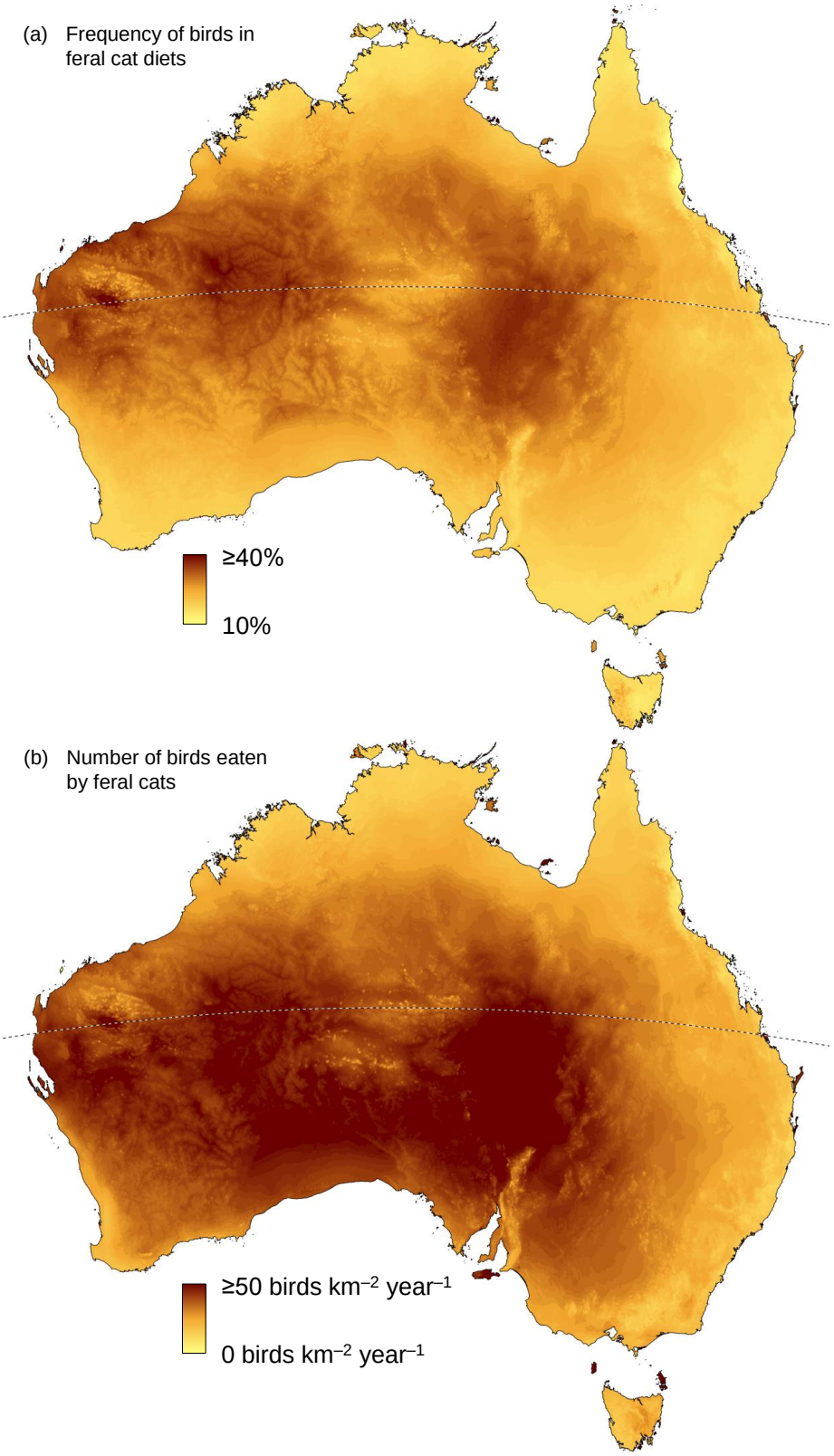

Figure 4. Model projections of (a) the frequency of birds in cat diets, and (b) the number of birds eaten by cats each year, in natural environments throughout Australia. For (a), predictor variables in the

936 regression model are: island size index; mean annual rainfall; mean annual temperature; tree cover; and
937 ruggedness. The dashed lines indicate the Tropic of Capricorn.
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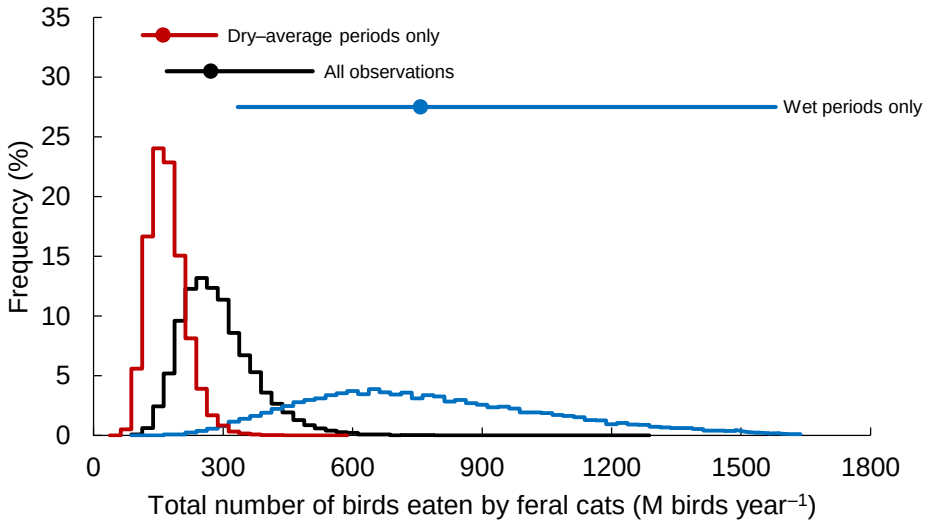
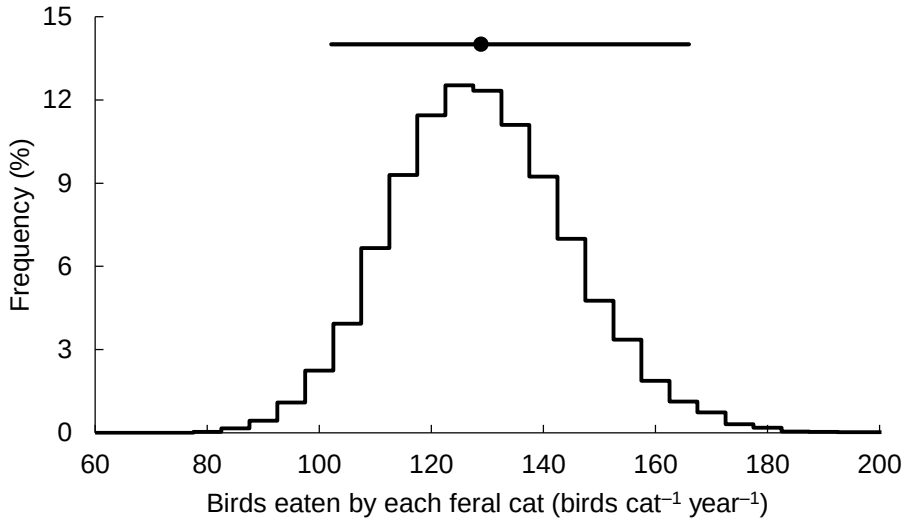
(a) Total number of birds eaten



(b) Number of birds eaten by each feral cat



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942 Figure 5. Uncertainty in (a) the total number of birds eaten, and (b) the number of birds eaten by each
943 feral cat, based on bootstrapping of the dataset 20,000 times. At the top of each panel is the mean
944 (filled circle) and 95% confidence bounds (lines). In (a), this is shown separately for analyses with cat
945 density observations from wet periods, dry–average periods, and including all observations (wet and
946 dry–average).

Table 1. Best ranked models explaining variation in frequency of birds in cat diets in natural environments throughout Australia, and the results of the model selection procedure. The models are shown ranked in ascending order of the model selection criterion, $\Delta QAIC_c$, which is the difference between the model's $QAIC_c$ value and the minimum $QAIC_c$ value in the candidate set. w_i is the Akaike weight, or the probability of the model being the best in the candidate set. The most highly ranked model ($\Delta QAIC_c < 2$) is shaded grey; models with very limited support ($\Delta QAIC_c > 5$), are not included in the table. 'Rainfall' is mean annual rainfall; 'temperature' is mean annual temperature; 'tree cover' is mean tree cover in a 5-km radius; 'ruggedness' is standard deviation of elevation in a 5-km radius. Model coefficients are provided in Appendix E.

Model	$\Delta QAIC_c$	w_i	R^2
~ island size index + $\log_{10}$ (rainfall) * temperature	0.0	0.37	0.54
~ island size index + $\log_{10}$ (rainfall) * temperature + tree cover	2.4	0.11	0.54
~ island size index + $\log_{10}$ (rainfall) * temperature + ruggedness	2.4	0.11	0.54
~ island size index + $\log_{10}$ (rainfall)	2.9	0.09	0.50
~ island size index + $\log_{10}$ (rainfall) + temperature	3.0	0.08	0.51
~ island size index + $\log_{10}$ (rainfall) + ruggedness	4.3	0.04	0.50
~ island size index + $\log_{10}$ (rainfall) * temperature + tree cover + ruggedness	4.8	0.03	0.54

Table 2. Comparison of cat population estimates and predation rates on birds between Australia (this study) and contiguous United States (Loss et al. 2013). Note that in our assessment, we segregate Australian feral cats into two components, those in natural landscapes (*) and those in modified landscapes (**). Note that some values given in the Table are not accompanied by confidence limits because these are nonsensical (e.g. for land area) or not reported in the primary source.

Parameter	**Contiguous USA**	**Australia**
Land area	8.08 million km^2	7.69 million km^2
Owned cats		
Cat population size	84 million	3.9 million
No. of birds killed cat^{-1} yr^{-1}	8.1	20.0
No. of birds killed by cats yr^{-1}	684 million	77.6 million
*Feral cats**		
Cat population size	30–80 million	2.1 million (95% CI: 1.4–3.5 million)
Cat density	3.7–9.9 cats km^{-2}	0.27 cats km^{-2} (95% CI: 0.18–0.45)
No. of birds killed cat^{-1} yr^{-1}	[21–55]	129 (95% CI: 102–166)
No. of birds killed by cats yr^{-1}	1.65 billion	272 million (95% CI: 169–508 million)
*Feral cats in highly modified landscapes***		
Cat population size	n/a	0.7 million
No. of birds killed cat^{-1} yr^{-1}	n/a	61.5
No. of birds killed by cats yr^{-1}	n/a	44.3 million
Total birds killed by all cats yr^{-1}	2.4 billion (95% CI: 1.4–3.7 billion)	394 million
Estimated total land bird population	10-20 billion	10.9 billion (95% CI: 9.3–12.5 billion)
Estimated proportion of bird population killed by cats yr^{-1}	12–24%	3.6%