Biological Conservation 214 (2017) 76–87

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

# How many birds are killed by cats in Australia?

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ARTICLE INFO

*Keywords:*
Conservation
Diet
Introduced predator
Island
Mortality
Predation

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.

## 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.

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http://dx.doi.org/10.1016/j.biocon.2017.08.006
Received 14 February 2017; Received in revised form 28 July 2017; Accepted 4 August 2017
Available online 09 August 2017

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 among 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 < 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.

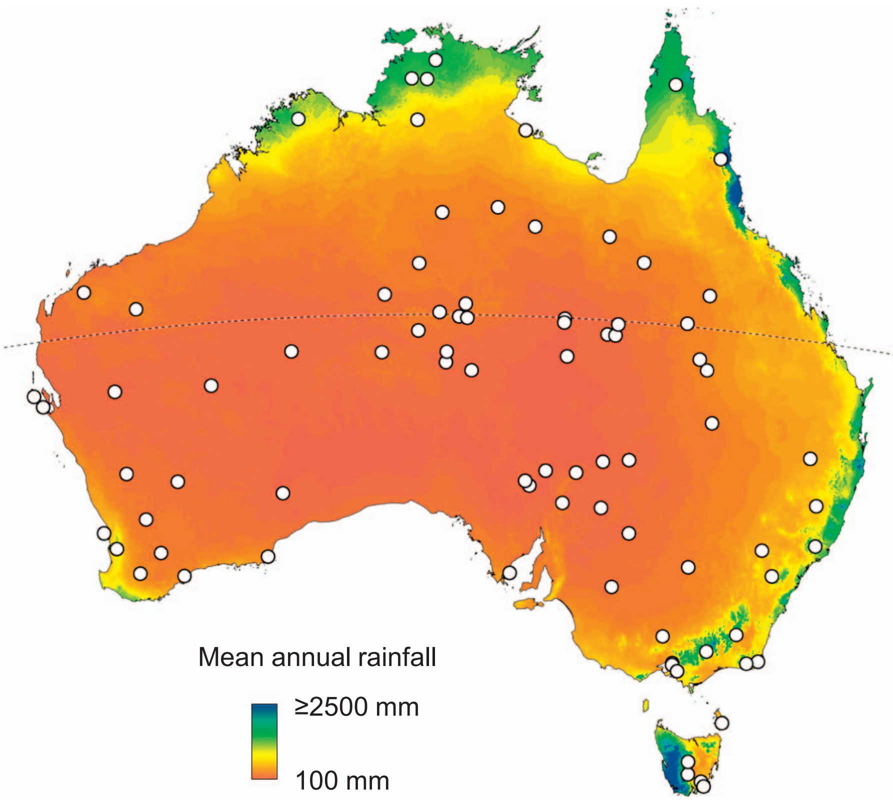


**Fig. 1.** Locations of cat dietary studies collated in this study. There are 84 sites (in some cases with several studies at each site) in natural vegetation (72 on the Australian mainland, three in Tasmania and 9 on smaller islands, including Macquarie and Christmas Islands, not shown on map). There 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.

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 h 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 h; (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:

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

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 generalized 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%.

Generalized 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 $\geq 0.50$.

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

**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 |

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 five 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

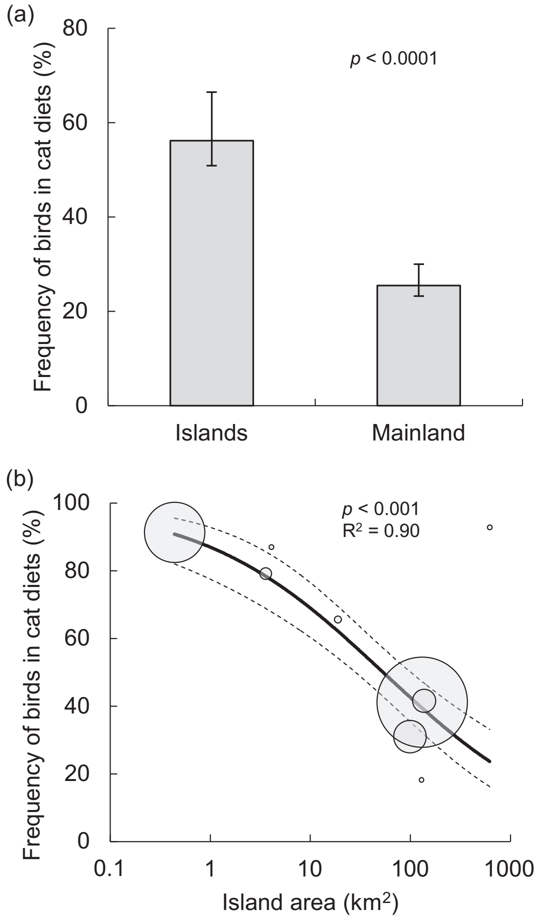


**Fig. 2.** Variation in the frequency of birds in cat diet samples on: (a) the mainland, comprising Tasmania (n = 3) and greater Australian mainland (n = 72), and smaller islands (n = 11); and (b) in relation to island size (for islands smaller than Tasmania, 64,519 km$^2$). In (b) the circles indicate 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.

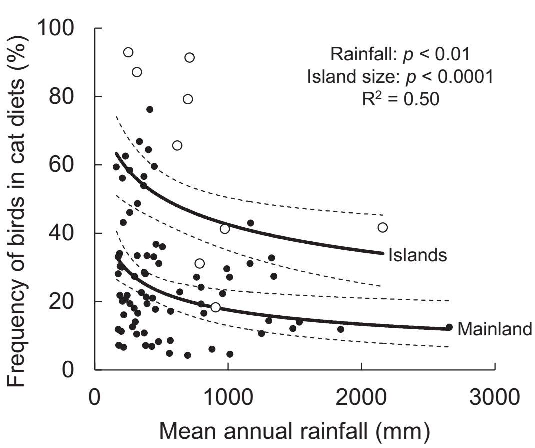


**Fig. 3.** Variation in the frequency of birds in cat diet samples in relation to mean annual rainfall. Observations from the mainland, comprising Tasmania and greater Australian mainland, are indicated by filled circles, while those from islands smaller than Tasmania, 64,519 km$^2$, are indicated by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

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

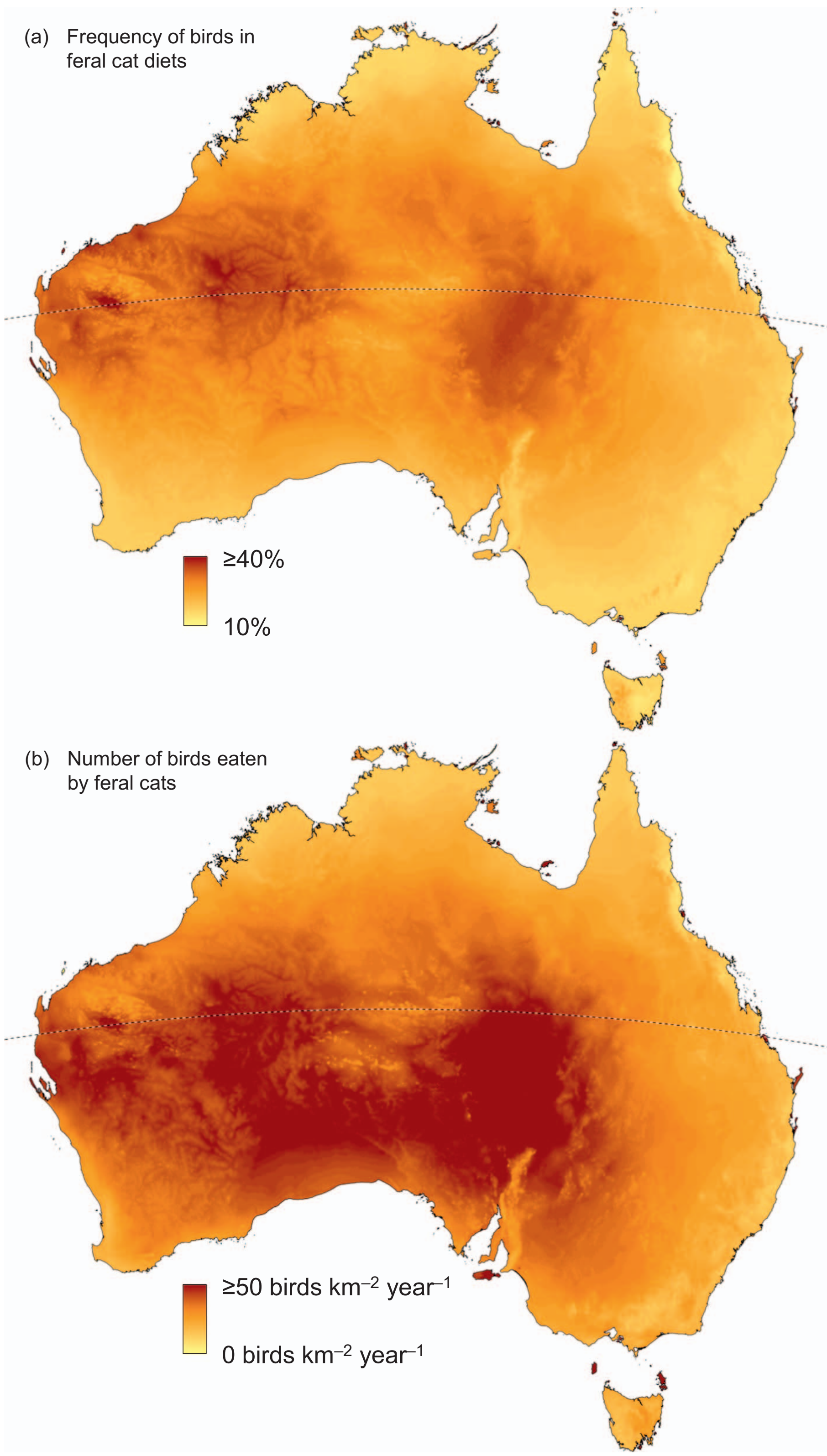


**Fig. 4.** Model projections of (a) the frequency of birds in cat diets, and (b) the number of birds eaten by cats each year, in natural environments throughout Australia. For (a), predictor variables in the regression model are: island size index; mean annual rainfall; mean annual temperature; tree cover; and ruggedness. The dashed lines indicate the Tropic of Capricorn.

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

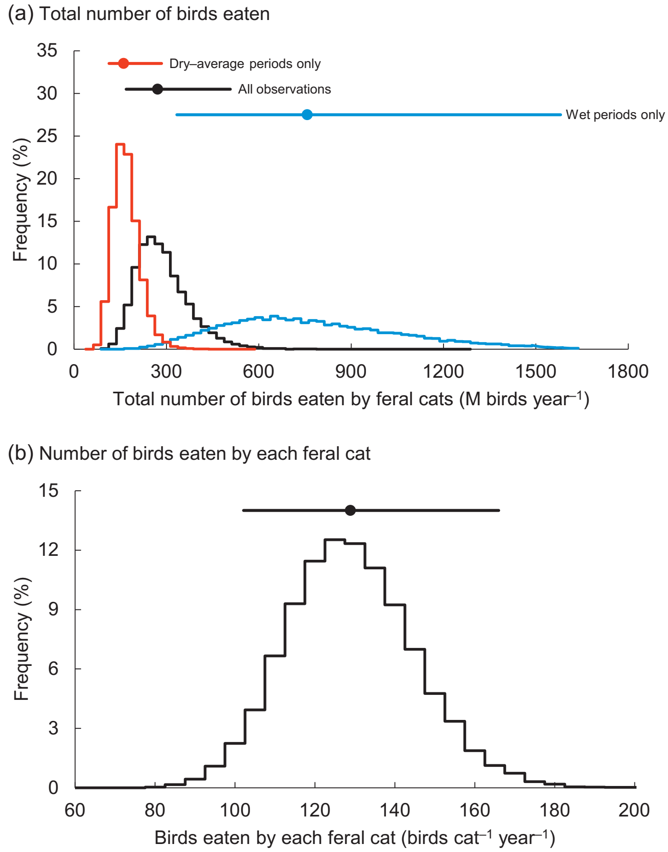


**Fig. 5.** Uncertainty in (a) the total number of birds eaten, and (b) the number of birds eaten by each feral cat, based on bootstrapping of the dataset 20,000 times. At the top of each panel is the mean (filled circle) and 95% confidence bounds (lines). In (a), this is shown separately for analyses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

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

**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% |

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 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.

## Acknowledgements

The collation, analysis and preparation of this paper was supported by the Australian Government's National Environmental Science Program (Threatened Species Recovery Hub). We thank the Australian Research Council for grant funding (project DP 140104621) to CRD. This paper rests on data arising from the labours of many people who have searched for and through cat faeces and the internal organs of dead cats: that effort is much appreciated. We thank two anonymous referees for comments that improved this paper.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2017.08.006.

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