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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

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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

104 highly variable. Predation pressure by feral cats on birds may respond not only to such dynamic
105 variation in the densities of cats and their main prey sources associated with temporal variation in
106 environmental conditions, but may also vary markedly over time and space in response to differing
107 intensities of management of cats (and the often co-occurring introduced red fox *Vulpes vulpes*) and/or
108 to management of some main prey sources (such as rabbits *Oryctolagus cuniculus*) (see also Appendix D)
109 (Bowen and Read 1998; Courchamp et al. 2000; Holden and Mutze 2002; Marlow and Croft 2016; Read
110 and Bowen 2001). Feral cats are also highly flexible foragers: they readily switch prey types according to
111 the relative abundance of different prey. For example, reptiles feature more prominently (and hence
112 birds less prominently) in the diet of feral cats in Australia during warmer months (Yip et al. 2015). Feral
113 cats may also selectively hunt particular prey species even if rare in the landscape: for example, Spencer
114 et al. (2014) reported that feral cats consumed Forrest's mouse *Leggadina forresti* at a
115 disproportionately high rate relative to their abundance in a study in central Australia. There may also
116 be substantial differences in the hunting behaviour and prey selectivity amongst individual co-occurring
117 cats, with some individual cats preferentially targeting birds (Dickman and Newsome 2015; Molsher et
118 al. 1999), and some differences in diet associated with the size of the cat (Kutt 2012; Moseby et al.
119 2015).

120
121 There have been few previous estimates of the numbers of birds killed by feral cats for any part of
122 Australia. One notable example related to the diet of feral cats on the 131 km² sub-Antarctic Macquarie
123 Island (Jones 1977). Based on an estimated population then of 375 feral cats, dietary analysis and cat
124 metabolic requirements, Jones (1977) estimated that this feral cat population killed 47,000 Antarctic
125 prions *Pachyptila desolata* and 11,000 white-headed petrels *Pterodroma lessonii* per year on Macquarie
126 Island; hence, on average, each cat consumed at least 154 individual birds per year, and the cat
127 population collectively consumed at least 443 birds km⁻² yr⁻¹.

128
129 For mainland Australia, the most notable assessment of bird mortality rates attributable to feral cats in
130 natural landscapes at any site is that of Read and Bowen (2001) at Roxby Downs in arid South Australia.
131 Their dietary study found an average of 0.21 individual birds in each cat stomach, and they concluded
132 that each cat consumes at least 0.21 birds per day (assuming that the average passage rate of food in
133 the digestive system of cats is less than 1 day). Based on observed densities of 2 cats km⁻², they
134 estimated that the feral cat population at this site consumed well in excess of 150 birds km⁻² yr⁻¹.

135
136 Although our primary interest in this paper is predation by feral cats in natural environments, we note
137 that pet cats can also have detrimental impacts on birds in urban and peri-urban areas, and that their
138 impacts may be locally substantial given that cats in such settings often occur in very high densities
139 (Legge et al. 2017; Paton 1993). So, additional to our assessment of the toll of birds taken by feral cats in
140 largely natural environments, we also estimate the numbers of birds killed by feral cats in highly
141 modified environments (such as around rubbish dumps) and by pet cats. These three segments of the
142 cat population have some notably different characteristics that merit their separate consideration: (i)
143 feral cats in largely natural landscapes generally occur at lower densities but, given that they must hunt
144 their own food, their *per capita* intake of birds is likely to be far higher than for the other two categories;
145 (ii) feral cats in highly modified landscapes typically occur at very high densities, but derive much of their

146 diet from food sources provided intentionally or unintentionally by humans and hence have lower *per*
147 *capita* kill rates of birds than feral cats without such human-provided food sources; and (iii) the number
148 of pet cats in Australia is reasonably well estimated from ownership statistics, but the diet of pet cats is
149 largely provided by their owners, so the pet cat *per capita* kill rate on birds is likely to be much lower
150 than for feral cats. Note that, as defined by Legge et al. (2017), the total area of natural environments
151 and of highly modified landscapes sums to the total land area of Australia (7.69 million km², including all
152 islands); hence the total population size of feral cats in Australia is the sum of the estimated cat
153 populations for these two landscape components.

154
155 Our focus here is on cats as a direct cause of mortality in Australian birds, but we note also that cats may
156 also have indirect impacts on bird populations through competition (with some studies showing large
157 dietary overlaps of feral cats with some Australian raptor species: Pavey et al. 2008), and indirectly
158 through disease transmission. Notably, the cat is the sole primary host in Australia for toxoplasmosis,
159 demonstrated to be a significant cause of mortality for many bird species (including threatened bird
160 species) in Australia and elsewhere in the world (Dubey 2002; Hartley and Dubey 1991; Work et al.
161 2000).

162
163 Our objectives in this study are to: (i) assess the extent of variation in the frequency of birds in cat diet,
164 and the factors associated with such variation; (ii) derive estimates of the average numbers of birds
165 killed in Australia by cats per year and per unit area; and (iii) seek to interpret the conservation
166 significance of such predation rates. In a companion paper (Woinarski et al. submitted), we consider the
167 ecological traits associated with variation among bird species in the likelihood of predation by cats, and
168 collate records of cat predation on Australia's threatened bird species.

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170

171 **2. Methods**

172

173 *2.1. Feral cats in natural environments*

174

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

178

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

186

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

197
198 Collectively, these studies include 9715 cat stomachs or scats. Most of these studies report only
199 frequency of occurrence (i.e. the proportion of scats or stomachs that contained 'birds') rather than a
200 record of the number of individual birds in those samples. However, in a subset of studies (Appendix A),
201 tallies were given for the number of individual birds in those samples that contained birds: averaged
202 over these studies, the mean number of individual birds in cat scats or stomachs that contained birds
203 was 1.34 (± 0.07 SE). This value showed no significant variation with frequency of occurrence (Appendix
204 B).

205
206 Here, we assume that one stomach or scat sample represents 24 hr worth of prey eaten by an individual
207 cat. This is likely to be a conservative under-estimate of the number of prey killed per day because: (i)
208 prey are largely digested after 12 hr; (ii) cats typically produce more than two scats per day; (iii) cats
209 may kill some birds but not necessarily consume them ('surplus kill'); and (iv) eggs and chicks with
210 largely undeveloped feathers may be rapidly digested and leave little trace (Davies and Prentice 1980;
211 George 1978; Hubbs 1951; Jackson 1951; Loss et al. 2013; Read and Bowen 2001). Furthermore, cats
212 may injure birds in attempted but failed capture (and hence not be detected in cat scats or stomachs),
213 but such wounds may subsequently result in bird deaths. Conversely, cats may also scavenge, so some
214 birds included in cat dietary studies are not necessarily killed by the cat that consumed them (Hayde
215 1992; Molsher et al. 2017). Also, the fragments of a single bird may be excreted by the cat that
216 consumed the bird in more than one scat, so – where such scats from a single cat are collected and
217 included in analysis – this may result in an over-estimate of the numbers of birds killed.

218
219 To analyse variation in the frequency of birds in cat diet samples, we noted whether the study was from
220 an island or the mainlands of Australia and Tasmania (64 519 km²), and – if on an island – the size of the
221 island. We derived a composite variable expressing whether the site was an island, and the size of the
222 island:

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224
$$\textit{island size index} = \log_{10} \left(\text{minimum} \left\{ 1, \frac{\textit{area}}{10000} \right\} \right),$$

225
226 where *area* is island area in km². Hence, any land mass or island with an area $\geq 10\,000$ km² (i.e. the
227 Tasmanian and Australian mainlands) has an index of 0. Islands $< 10\,000$ km² have negative values, which

228 become increasingly negative with decreasing island area. From the location of the study, we also
229 determined several climatic and environmental variables to assess their effects on the frequency of
230 birds in cat diet samples. These included mean annual rainfall (Australian Bureau of Meteorology
231 2016a), mean annual temperature (Australian Bureau of Meteorology 2016b), mean tree cover within a
232 5-km radius (Hansen et al. 2003) and topographic ruggedness (standard deviation of elevation within a
233 5-km radius) (Jarvis et al. 2008).

234

235 We used generalised linear models (GLMs) to examine geographic variation in the frequency of birds in
236 the diet of feral cats. The response variable was the proportion of samples (scats or stomachs)
237 containing birds, and hence was analysed using the binomial error family. By using the binomial error
238 family, the GLMs took into account the lower precision of the observations based on a small number of
239 samples. We examined a set of 40 candidate models representing all combinations of the five
240 explanatory variables described above (island size index, rainfall, temperature, tree cover, ruggedness),
241 including an interaction between rainfall and temperature (to account for a possible negative effect of
242 temperature on water availability). Models were evaluated using a second-order form of Akaike's
243 Information Criterion (QAIC_c), which is appropriate for small sample sizes and overdispersed data
244 (Burnham and Anderson 2003). There was evidence of strong overdispersion, so we used the
245 'quasibinomial' error structure to estimate coefficient standard errors and confidence intervals.

246

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

252

253 Multiplying the modelled frequency of birds in cat samples across Australia by the mean number of
254 individual birds in cat diet samples containing birds (1.34) provided a spatial representation of the
255 estimated number of birds killed per feral cat per day. We multiplied this by the modelled density of cats
256 in natural environments across Australia (Legge et al. 2017), and then by 365.25 (days in a year), to
257 provide a spatial representation of the estimated number of birds killed by cats per km² per year. We
258 summed this rate across the natural environments of Australia to derive the total number of birds killed
259 by feral cats.

260

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

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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 km² 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.

312

313 2.5. *The number of birds in Australia*

314

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

325

326

327 3. Results

328

329 3.1. *Feral cats in natural environments*

330

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

334

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

340

341 By far the best predictor of the frequency of birds in feral cat diet samples was the size of the landmass
342 from which the sample came, i.e. mainland vs. island, and size of the island. Bird frequency in cat
343 samples from islands was more than double that of cats from mainland areas (56.1% vs. 25.5%,
344 $p < 0.0001$) (Fig. 2a). The three studies from the Tasmanian mainland had frequencies of birds in cat
345 samples (18.5%) that are closer to the average for the Australian mainland (25.6%) than to that for
346 smaller islands. The frequency of birds in cat samples from island studies was significantly negatively
347 related to island area ($r^2 = 0.90$, $p < 0.001$) (Fig. 2b).

348

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

354 25.8% (95% CI: 21.2-31.9%). Notably, the mainland's highest predictions of frequency of birds in cat
355 diets tended to occur in areas with relatively sparse underlying data, e.g. parts of arid South Australia –
356 suggesting that there may be a greater level of uncertainty associated with the predictions for these
357 areas.

358

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

364

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

373

374 Summing this rate across Australia provides an estimate of 272 million birds (95% CI: 169–508 million)
375 killed by feral cats across the natural environments of Australia each year (varying from 161 million [95%
376 CI: 114–284 million] in dry or average years to 757 million [95% CI: 334–1580 million] in ‘wet’ years,
377 assuming the proportion of birds in cat diet is constant across drought and wet years) (Fig. 5). On
378 average, a feral cat kills 129 birds per year (95% CI: 102–166) (Fig. 5). The average number of birds killed
379 by feral cats in natural environments is 35.6 birds $\text{km}^{-2} \text{yr}^{-1}$ (95% CI: 22.2–66.6), varying from 21.1 birds
380 $\text{km}^{-2} \text{yr}^{-1}$ (95% CI: 14.9–37.3) in dry and average years to 99.3 birds $\text{km}^{-2} \text{yr}^{-1}$ (95% CI: 43.8–207.1) in wet
381 years. From the data reported in Table 1, the mean percentage of these birds that were native was
382 99.0% (N=43, s.e.=0.6).

383

384 *3.2. Feral cats in highly modified landscapes*

385

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

390

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

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

399
400 Multiplying the total population size of feral cats in highly modified landscapes (0.72 million: Legge et al.
401 (2017)) by this *per capita* annual take produces an estimate of 44.3 million birds killed per year by feral
402 cats in modified environments.

403 404 3.3. Pet cats

405
406 Pet owners reported an average of 8.0 birds observed to be taken home as prey per cat per year in a
407 sample of 700 cats from mainly around Adelaide (Paton 1990, 1991, 1993), 2.3 in Canberra from a
408 sample of 138 cats (Barratt 1997), and 3.3 in Hobart from a sample of 166 cats (Trueman 1991) – i.e. an
409 average of 4.53 birds per year across these studies. Scaling this mean by the average proportion of all
410 kills that are returned home (29%), the average number of birds killed by individual pet cats is 15.6 birds
411 cat⁻¹ yr⁻¹. Hence, with a total Australian population of 3.88 million pet cats, the estimated annual tally of
412 birds killed by pet cats is 60.6 million.

413
414 Unsurprisingly (given the typically higher abundance of introduced birds in urban areas), introduced bird
415 species comprise a higher proportion of the birds killed by pet cats in Australia than for feral cats in
416 largely natural environments – e.g. native birds comprised 58% of all birds killed by pet cats in Canberra
417 (Barratt 1997), 73% in Hobart (Trueman 1991) and 88% in Adelaide (Paton 1991).

418 419 3.4. Comparison of frequency of birds in the diet of feral cats with that of other co-occurring mammalian 420 predators

421
422 Comparative data on the frequency of birds in samples of feral cats and other co-occurring mammalian
423 predators are summarised in Appendix C. Across 22 studies where the diet of co-occurring cats and
424 foxes was reported, the frequency of birds was appreciably higher in the diet of cats (mean=29.1%) than
425 of foxes (mean=17.3%) (Wilcoxon-matched pairs test $z=3.13$. $p=0.0017$). Across 15 studies in which the
426 diet of co-occurring cats and dogs (including dingoes) was reported, the frequency of birds was more
427 than twice as high in the diet of cats (mean=34.1%) than of dogs/dingoes (mean=14.0%) ($z=3.41$,
428 $p=0.001$). Only two studies with sample sizes of >10 samples per species have considered the diet of cats
429 and a co-occurring native marsupial predator, in both cases, the spotted-tailed quoll *Dasyurus*
430 *maculatus* (Burnett 2001; Glen et al. 2011). In these studies, the frequency of birds was appreciably
431 higher in the diet of cats (mean=22.6%) than in the diet of the marsupial carnivore (mean=9.3%).

432 433 3.5. The number of birds in Australia

434
435 Across the 90 site estimates collated here, the mean bird density reported was 14.2 birds ha⁻¹ (95% CI:
436 12.1–16.3), suggesting a total Australian terrestrial bird population of ca. 10.9 billion (95% CI: 9.3–12.5

437 billion). Across sites, bird density was weakly positively correlated with mean annual rainfall ($r_s=0.26$,
438 $p<0.05$).

439
440

441 **4. Discussion**

442

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

465

466 Previous studies have suggested that variation in the frequency of occurrence of birds in cat samples in
467 continental Australia is not strongly associated with any climate feature (Denny and Dickman 2010) or to
468 latitude, longitude or productivity (Doherty et al. 2015). Analysis of the larger database compiled here
469 demonstrates instead that the diet of feral cats includes a higher proportion of birds in drier regions.
470 Given that cat density also tends to be higher in such regions, at least in higher rainfall years (Legge et al.
471 2017), the total number of birds killed by cats per unit area in arid and semi-arid environments of inland
472 Australia is up to three orders of magnitude higher than in Australia's mesic fringe. This may be because
473 cats hunt more effectively and more birds occur on or near the ground in the low open woodlands,
474 shrublands and grasslands that characterise Australia's arid and semi-arid areas than is the case in the
475 denser tall forests that characterise Australia's higher rainfall areas. Although this is a plausible
476 explanation, we note that variation in the frequency of birds in cat samples was unrelated to the simple
477 vegetation cover variable we used in our analysis. Our limited assessment of spatial variation in bird
478 density indicates that higher incidence of birds in cat diets in arid areas is not because there are more

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

482
483 Although native and introduced mammals comprise most of the diet of feral cats in Australia, as
484 elsewhere in the world (Bonnaud et al. 2011; Bradshaw 1992; Turner and Meister 1988), and reptiles
485 may be a major food item in arid and semi-arid areas (Doherty et al. 2015), the data collated here
486 demonstrate that birds comprise an important item of feral cat diet, and that cats consume large
487 numbers of birds. Our spatially-weighted mean frequency (25.8%) of birds in feral cat samples reported
488 here is remarkably similar to that reported by Doherty et al. (2015) (26.9%) from a collation of fewer
489 studies (though with substantial overlap between the underlying datasets). Notably, the early study by
490 Coman and Brunner (1972), which concluded that predation by feral cats was unlikely to have a
491 significant impact on birds, had one of the lowest frequencies of birds reported in cat diet (4.7%) across
492 the substantial collation of studies presented here. Hence its conclusion – that cat predation is unlikely
493 to have any significant impact on the status of birds in Australia – is not supported by our more
494 comprehensive analysis. The mean frequency reported here for birds in feral cat diet samples from
495 Australia is also appreciably higher than that of 20.7% reported globally from 15 studies (Fitzgerald and
496 Turner 2000).

497
498 The estimate reported here of 129 birds consumed annually per feral cat in natural environments is
499 substantially higher than that reported from smaller samples in two Australian mainland areas (27 birds
500 $\text{cat}^{-1} \text{yr}^{-1}$ in Victoria by Coman and Brunner (1972), and 75 birds $\text{cat}^{-1} \text{yr}^{-1}$ for semi-arid South Australia by
501 Read and Bowen (2001)), but somewhat less than the 154 birds $\text{cat}^{-1} \text{yr}^{-1}$ reported for Macquarie Island
502 (Jones 1977).

503
504 We estimate an average of 35.6 birds $\text{km}^{-2} \text{yr}^{-1}$ are killed by feral cats in largely natural environments.
505 This estimated average rate of birds killed by cats in natural environments per unit area is appreciably
506 lower than the sole preceding mainland estimate of 150 birds $\text{km}^{-2} \text{yr}^{-1}$ given for Roxby Downs in semi-
507 arid South Australia (Read and Bowen 2001), with this difference largely attributable to the unusually
508 high cat densities given in that study, and that our estimate represents an average take across all
509 Australian environments, including those in which the take of birds by cats is relatively low. Notably the
510 Roxby Downs estimate is lower than our modelled maximum rate of birds killed by cats (332 birds km^{-2}
511 yr^{-1}), also in arid Australia.

512
513 Our estimates for the numbers of birds killed by pet cats and feral cats in modified environments are
514 based on few samples. Our estimate that pet cats kill 15.6 birds $\text{cat}^{-1} \text{yr}^{-1}$ is within the range reported by
515 studies elsewhere in the world: for example, 5 birds $\text{cat}^{-1} \text{yr}^{-1}$ in Dunedin (New Zealand) (van Heezik et al.
516 2010), 5.9 birds $\text{cat}^{-1} \text{yr}^{-1}$ in Bristol (England) (Baker et al. 2005), 12 birds $\text{cat}^{-1} \text{yr}^{-1}$ in rural environments
517 and 30 birds $\text{cat}^{-1} \text{yr}^{-1}$ in urban environments in Poland (Krauze-Gryz et al. in press), and 36-72 birds cat^{-1}
518 yr^{-1} for free-roaming pet cats in Michigan (USA) (Lepczyk et al. 2004).

519

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

532
533 Across the three components of Australia's cat population, the total estimated number of birds killed is
534 377 million per year, with 72% of this tally contributed by feral cats in natural environments, 12% by
535 feral cats in highly modified environments, and 16% by pet cats. Comparable national-scale assessments
536 of the number of birds killed per year include 100-350 million birds killed by cats in Canada (Blancher
537 2013), about 27 million birds killed by pet cats in Great Britain (Woods et al. 2003), 240 million birds
538 killed by feral cats in the United States (Pimentel et al. 2005), with a more substantial evidence base
539 subsequently resulting in that estimate increased to 1-4 billion birds killed by all cats in the contiguous
540 United States (Dauphiné and Cooper 2009; Loss et al. 2013). Our Australian estimate is of comparable
541 magnitude to these estimates, but differs in some notable respects from the area for which the most
542 detailed comparison is possible, the United States (Table 2). The United States has a far higher density
543 and total population of cats (feral cats and pets) than for Australia. We presume this is largely because
544 of the far higher human population density (even in most rural areas), and hence more cats, in the
545 United States than is typical for Australia. However, our estimates indicate that on a *per capita* basis,
546 cats in Australia kill far more birds than in the United States, or than in Canada (24 to 64 birds $\text{cat}^{-1} \text{yr}^{-1}$:
547 Blancher (2013)). Although this estimated *per capita* predation rate on birds is higher for cats in
548 Australia than in the United States, the markedly higher population of cats in the United States means
549 that the total estimated number of birds killed by cats there is almost an order of magnitude higher than
550 our estimate for Australia. We note also that our estimate of *per capita* predation of birds by cats
551 includes a factor for the number of individual birds in cat dietary samples that contain birds: this factor
552 is generally not considered in most other analyses, such that the rate of cat predation on birds may be
553 under-estimated in many other studies.

554
555 Predation of birds by cats is one of the largest human-related mortality factors for birds (Blancher 2013;
556 Loss et al. 2012, 2013, 2015). Some studies elsewhere in the world have linked, with varying degrees of
557 uncertainty, high predation rates by cats to ongoing reduction in the abundance of at least some bird
558 species, even in mainland settings (Baker et al. 2005, 2008; Balogh et al. 2011; Churcher and Lawton
559 1987; Crooks and Soulé 1999; Lepczyk et al. 2004; Thomas et al. 2012; van Heezik et al. 2010; Woods et
560 al. 2003).

561

562 Our estimates of an average of 272 million birds (of which ca. 99% are native) killed annually in natural
563 landscapes in Australia by feral cats, increasing to 377 million yr⁻¹ (i.e. >1.0 million birds day⁻¹) with
564 inclusion of the numbers of birds killed by pet cats and feral cats in modified landscapes, are very large
565 tallies. However, the ecological and conservation significance of these kill tallies is difficult to
566 contextualise, because (i) there are no reliable estimates of the total population of birds in Australia; (ii)
567 predation may fall disproportionately on some bird species; (iii) some bird species may be able to
568 sustain high mortality rates and maintain viable populations but others may not; and (iv) as
569 demonstrated here, there is substantial spatial variation in the numbers and proportion of birds killed
570 across Australia. Furthermore, in contrast to the situation in some other continents (Loss et al. 2015), it
571 is difficult to interpret the relative impacts of cat predation on Australian birds, because there has been
572 little broad scale assessment in Australia of the mortality rates and impacts upon birds of other
573 threatening factors. Our estimates of numbers of birds killed by cats and the total Australian bird
574 population indicate that the cats kill about 3.5% of Australia's terrestrial bird population (with this
575 percentage figure conservatively excluding all bird kills on islands, for which seabirds may make a large
576 contribution). We recognise that this estimate of proportion killed is indicative only, and that a more
577 robust estimate of total Australian bird population would be desirable.

578
579 At a population level, the susceptibility of bird species to cat predation may be affected by a range of
580 demographic and other factors. Many Australian bird species are long-lived but have relatively low
581 reproductive outputs (Woinarski 1985, 1989; Yom-Tov 1987; Yom-Tov et al. 1992), and bird species with
582 such demographic characteristics may be particularly susceptible to decline with high predation rates.
583 Cat densities and impacts vary markedly across Australia. For birds (and other native species), the
584 impacts of cat predation may be most severe during the period of transition from high rainfall conditions
585 to drought when populations of some bird species may be concentrated in drought refuge areas that
586 happen still to have high densities of cats (Pavey et al. 2014; Pavey and Nano 2013). The extent and
587 impact of cat predation on birds may also be magnified by interactions with other factors, such as
588 habitat fragmentation, fire regimes and habitat degradation due to over-grazing (Graham et al. 2013;
589 McGregor et al. 2014, 2016). Cat predation may also subvert the assumed conservation security
590 provided to native species by the conservation reserve system, given that feral cats occur in similar
591 density within and outside Australia's reserve system (Legge et al. 2017).

592
593 The large amount of predation by cats on Australian birds reported here, even in mainland areas, is
594 sufficient evidence to raise some conservation concern. This rate may or may not of itself be sufficient
595 to drive severe population declines of any bird species, but it is an ongoing chronic depletion that may
596 lead to long-term reduction in bird populations and reduced resilience and increased susceptibility of
597 some bird species to additional threats. To better resolve the conservation impact of such predation
598 rates, the evidence base needs to be substantially improved. One high priority is to more precisely
599 assess the responses (including changes in abundance, breeding success and habitat use) of a range of
600 bird species to reduction in cat abundance due to the increasing cat control efforts now being made in
601 many areas. One of the few Australian studies of this type conducted to date reported marked local
602 increases in population size for eastern bristlebirds *Dasyornis brachypterus* following effective control of
603 introduced predators (in this case, mostly red foxes) (Lindenmayer et al. 2009). The ongoing

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

620
621 Partly in response to the major role of feral cats in the ongoing decline of the Australian mammal fauna,
622 the recently released Threatened Species Strategy for Australia (Commonwealth of Australia 2015)
623 placed considerable emphasis on the control of feral cats. Resulting increases in the number, and size, of
624 islands from which cats have been eradicated, increasing numbers of predator-proof exclosures and
625 increasing numbers and total extent of areas subject to intensive cat-baiting programs are likely to
626 provide some substantial collateral conservation benefits to Australian bird species. But such benefits
627 may be even more pronounced if the conservation of bird species is used more proactively as a factor in
628 the development of these conservation programs. This could occur for example, if the location of
629 susceptible seabird colonies is a major factor in the identification of islands prioritised for cat
630 eradication, or if the mainland location of predator-susceptible threatened bird species is used to help
631 determine the site and intensity of cat-baiting programs.

632

633

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635

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642

643

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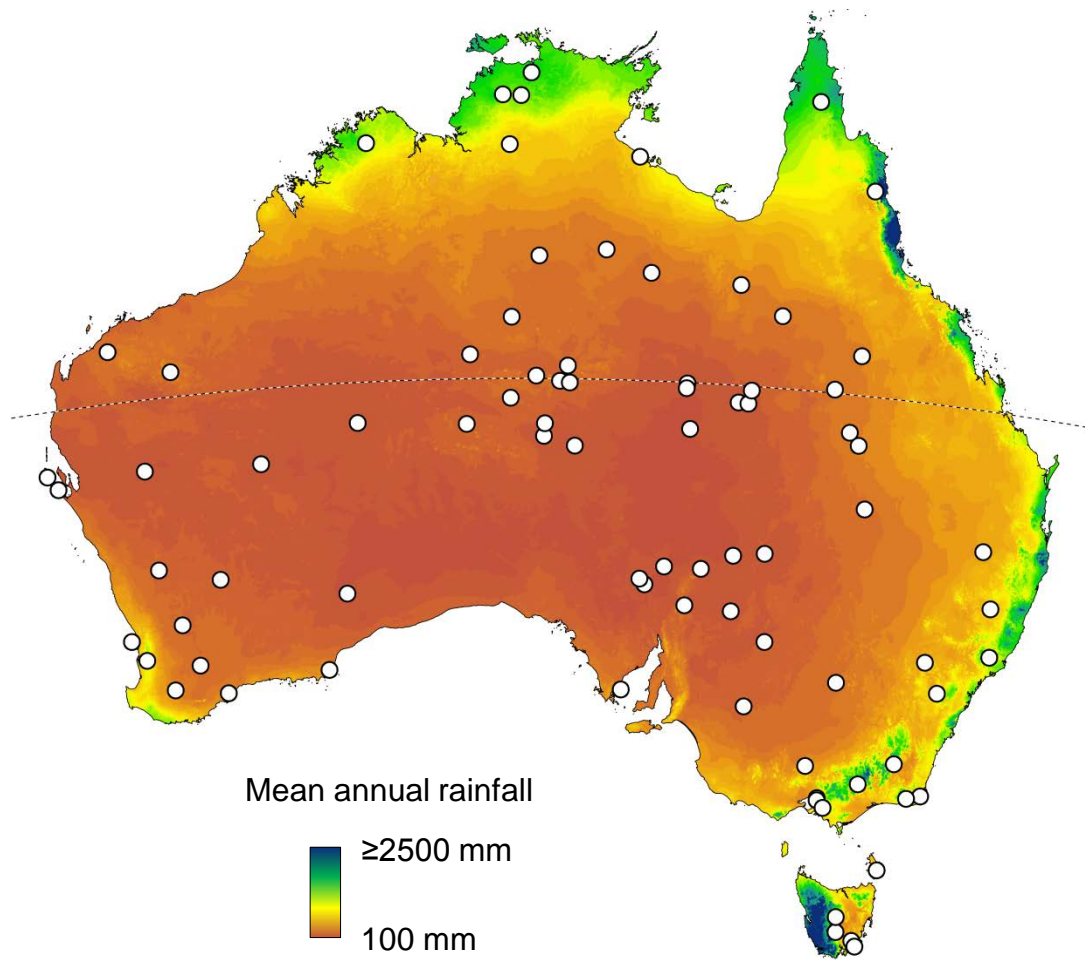
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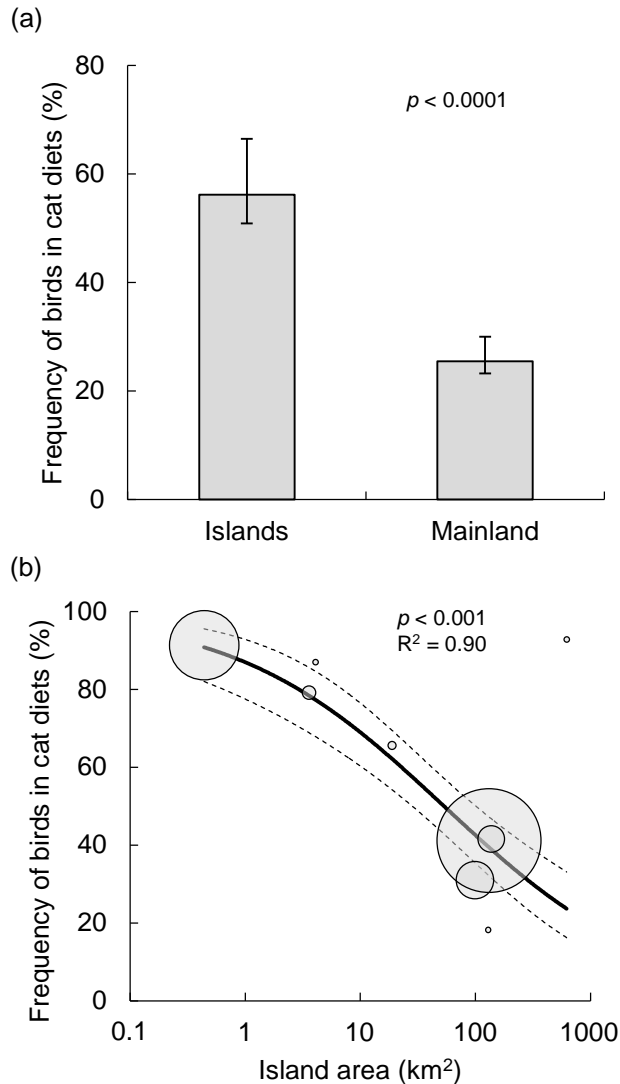
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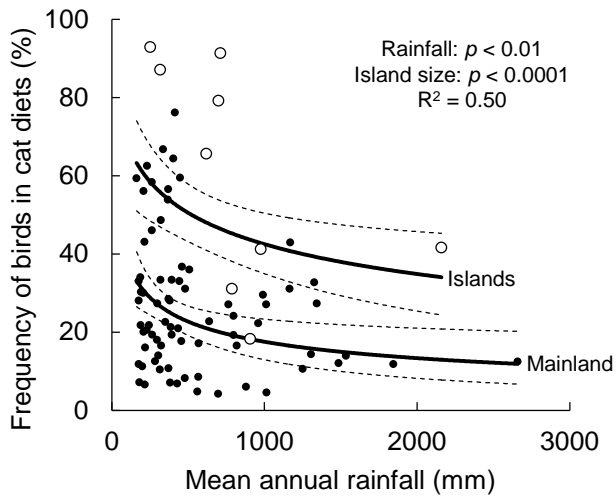
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908 Figure 1. Locations of cat dietary studies collated in this study. There are 84 sites (in some cases with
909 several studies at each site) in natural vegetation (72 on the Australian mainland, three in Tasmania and
910 9 on smaller islands, including Macquarie and Christmas Islands, not shown on map). There are another
911 five sites at rubbish tips. The map background shows mean annual rainfall (Australian Bureau of
912 Meteorology 2016b). The dashed line indicates the Tropic of Capricorn.



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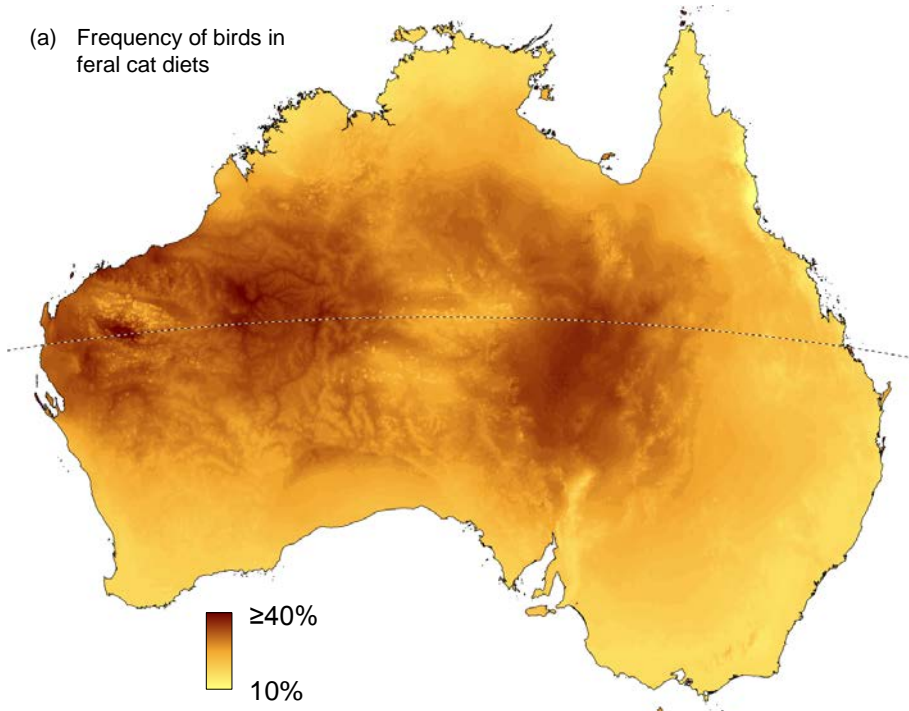
915 Figure 2. Variation in the frequency of birds in cat diet samples on: (a) the mainland, comprising
916 Tasmania ($n = 3$) and greater Australian mainland ($n = 72$), and smaller islands ($n = 11$); and (b) in
917 relation to island size (for islands smaller than Tasmania, 64 519 km²). In (b) the circles indicate the
918 observed values, with the size of the circle proportional to the number of samples used to generate the
919 estimate, ranging from 11 (smallest circle) to 756 (largest circle). In both (a) and (b) the predictions are
920 from generalized linear models (quasibinomial errors). The error bars in (a) indicate standard errors,
921 while the dashed lines in (b) indicate the 95% confidence intervals of the position of the regression line.
922 For (b), the model coefficients are provided in Appendix E.



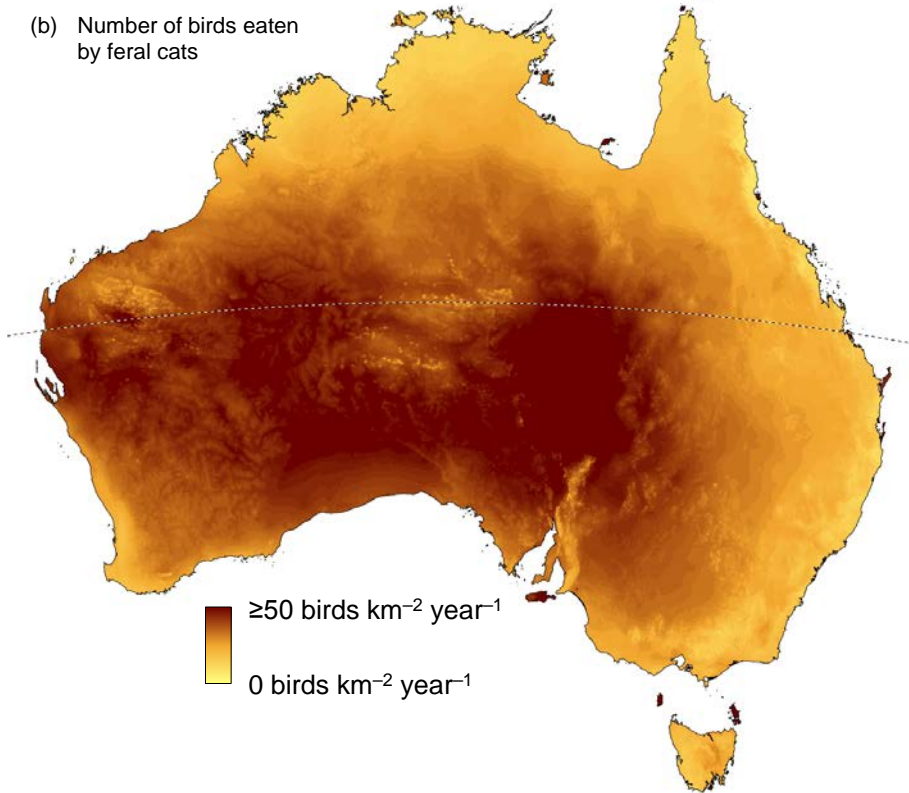
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925 Figure 3. Variation in the frequency of birds in cat diet samples in relation to mean annual rainfall.
 926 Observations from the mainland, comprising Tasmania and greater Australian mainland, are indicated by
 927 filled circles, while those from islands smaller than Tasmania, 64 519 km², 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.

(a) Frequency of birds in feral cat diets



(b) Number of birds eaten by feral cats

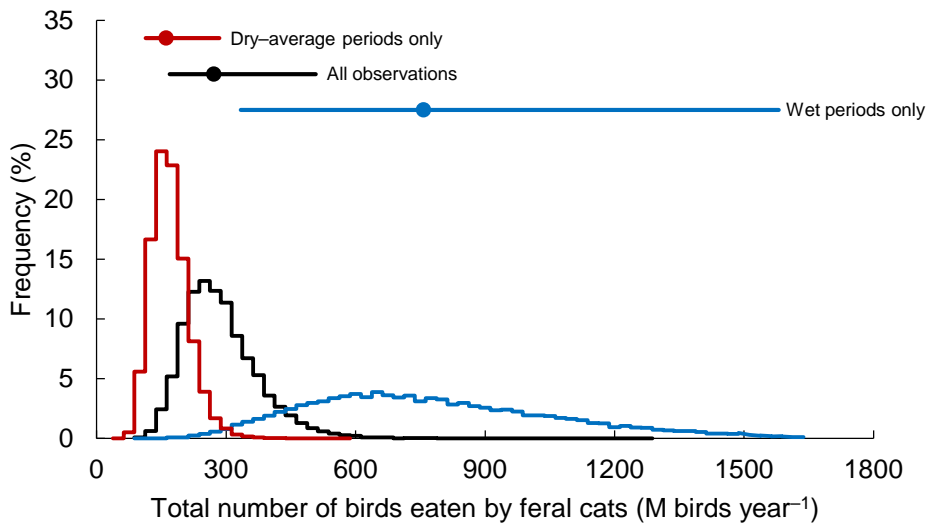


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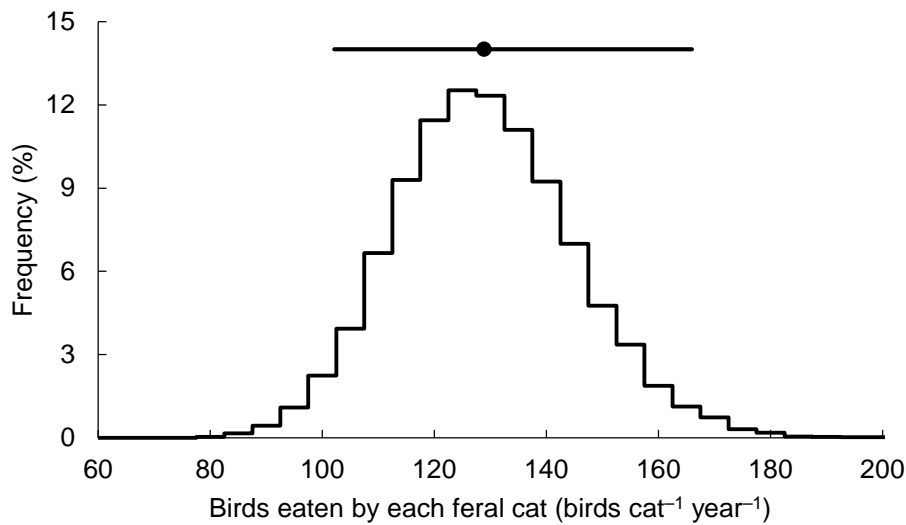
934 Figure 4. Model projections of (a) the frequency of birds in cat diets, and (b) the number of birds eaten
935 by cats each year, in natural environments throughout Australia. For (a), predictor variables in the

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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Figure 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).

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, ΔQAIC_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 ($\Delta\text{QAIC}_c < 2$) is shaded grey; models with very limited support ($\Delta\text{QAIC}_c > 5$), 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	ΔQAIC_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
<i>Owned cats</i>		
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
<i>Feral cats*</i>		
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)
<i>Feral cats in highly modified landscapes**</i>		
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%