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Compilation and traits of Australian bird species killed by cats

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Abstract. House cats *Felis catus* have contributed to the extinction of many bird species on islands, but their impact on continental bird faunas is less well resolved. Here, we compile and analyse a comprehensive record of all bird species known to be killed by feral cats at a continental scale. From published studies and unpublished data, we document predation by feral and pet cats on 357 bird species in Australia, including 338 Australian (non-vagrant) native bird species (=45.6% of the 741 Australian native bird species, excluding vagrants). This tally included 24 species listed as threatened or extinct by the IUCN (40% of the 58 non-vagrant Australian species listed as threatened), and 71 of the 117 bird species (61%) listed as threatened under Australian legislation (or species with one or more subspecies so listed). These tallies are substantially larger than reported in previous reviews. We provide the first continental-scale attempt to model bird species' traits that are associated with likelihood of being killed by cats, and use such modelling to attempt to redress some inevitable biases in compilation of predation records on birds. We conclude that the likelihood of being killed by a cat was highest for bird species that are restricted to islands, are of intermediate body mass (ca. 60-300 g), and nest and forage on the ground, and least likely for bird species occurring mostly in rainforests and wetlands. We also identify a set of bird species most likely to be threatened by cat-predation and hence most likely to benefit from enhanced management of cats. This study does not specifically evaluate the impact of cats on bird populations or on the conservation of Australian birds, but our results suggest that such impact may be much more pervasive than previously documented.

Running head: Australian bird species killed by cats

Additional key words: diet, invasive predator, modelling, threatened species

Introduction

Cats *Felis catus* are versatile predators that largely employ an 'ambush' hunting strategy (Bradshaw 1992; Turner and Meister 1988) to capture and kill a very wide range of animal species from small invertebrates to vertebrates up to at least 4 kg (Bonnaud et al. 2011; Fancourt 2015). Predation by introduced cats has been a major cause of extinction for many species, with such impact particularly pronounced for island-endemic vertebrates (Blackburn et al. 2004; Blackburn et al. 2005; Doherty et al. 2016; Medina et al. 2011; Nogales et al. 2013) and for mammals in Australia (Woinarski et al. 2015). In contrast, the impacts of predation by cats on continental bird faunas is less well resolved, although cats are known to kill hundreds of millions to billions of birds annually in continental settings (Blancher 2013; Dauphiné and Cooper 2009; Loss et al. 2013), with such predation shown to be a major source of bird mortality (Loss et al. 2012, 2015).

In a recent paper, Woinarski et al. (in press) concluded that about one million birds are killed in Australia per day by cats. However that study provided no information on the extent to which this toll fell equitably or otherwise across bird species. Here, we complement that previous paper by reporting on the Australian bird species known to be killed by cats, and seek to identify bird species, or groupings of species, that are most likely to be subject to cat predation.

First introduced to Australia in the late eighteenth century (Abbott 2008), cats are now almost ubiquitous across the Australian mainland and also occur on many Australian islands (Legge et al. 2017). There have been two notable listings of Australian bird species known to have been preyed upon by cats. An extensive survey of pet-owners in south-eastern Australia reported records of pet cats killing (or capturing) individuals of 186 bird species (Paton 1990; Paton 1991; Paton 1993), although the full list associated with that study has never been formally published. More recently, Doherty et al. (2015) aggregated information from 70 published and unpublished studies, widely spaced across Australia, of the diet of feral cats. That review compiled cat-predation records for 123 bird species, including 113 native species, of which two species were listed by the IUCN as threatened (Malleefowl *Leipoa ocellata* and Southern Rockhopper Penguin *Eudyptes chrysocome*). Another recent but more speculative compilation relating to the possible detrimental effects of feral cats on Australian biodiversity listed 40 threatened Australian bird taxa (including subspecies) that 'may be affected by predation by feral cats', although in many of these cases this implication was not based on any definite records of such predation (Department of the Environment 2015).

As recognised by their authors, the lists of bird species reported as preyed upon by cats in these previous compilations have some substantial biases and incompleteness (Table 1). Paton's set of studies were based on cat-owners' records in urban and rural areas of south-eastern Australia, and hence bird species that are readily identified by the public were more likely reported by respondents, and bird species that are more common and widespread in this region were likely to have contributed most to the cat-killed tallies. The compilation by Doherty et al. (2015) was more geographically representative, but was also likely to include more common and widespread bird species, and species for which partly-digested prey items are readily identifiable to species. Rare and restricted bird species are less likely to be reported as cat-prey in these data sets, but it is possible that such species have a higher *per capita* rate of being preyed upon by cats, and hence suffer more conservation impact, than those bird species that – because of their abundance or wide distributions – are more likely to be reported in cat dietary studies.

In the current study, we build on these important preceding compilations through inclusion of records from many additional and more diverse sources in order to provide a continental-scale compilation of bird species for which there are records of individual birds killed by cats, noting also the threatened bird species in this compilation. We then examine, across all Australian bird species, for relationships between records of cat predation and bird species' ecological, morphological and other traits. We then model these relationships to rank species according to their likelihood of being killed by cats, with and without controls for a measure of bird abundance and range. Our modelling at continental scale seeks to diminish the bias due to cat predation being more likely to have been recorded for bird species that are common in areas with higher human population density. This bias may be particularly important to try to redress because a recent continental-scale assessment of predation by feral cats in Australia (Woinarski et al. in press) reported that the modelled rate of predation of birds (i.e. no. individual birds killed km^{-2} y^{-1}) by cats was highest in arid and semi-arid areas remote from most human population centres, and hence bird species in those relatively under-studied areas may be most at risk from cat predation.

Methods

Terminology. Note that for convenient shorthand here we use the expression 'bird species killed by cats', or variants. We recognise that it is individuals, rather than species, that are killed; but repeated use of that correct wording is unduly cumbersome.

Compilation of cat-predation database

We sought records of birds being killed by cats from many diverse sources. The most notable of these included:

- cat dietary studies (including and extending all sources used in Doherty et al. (2015));
- a small number of largely anecdotal records compiled in the Handbook of Australian and New Zealand and Antarctic Birds series (Higgins 1999; Higgins and Davies 1996; Higgins and Peter 2002; Higgins et al. 2006; Higgins et al. 2001; Marchant and Higgins 1990, 1993), the compendium of all information then available about Australian birds, in which sources of bird mortality (including "street urchins" and "horseless carriages") are occasionally provided;
- autecological studies of bird species, where these provided information on causes of mortality (e.g. Smith and Saunders 1986);
- unpublished records from the Australian Bird and Bat Banding Scheme of reported causes of mortality or injury to banded birds (340 records of cat-killed birds of 124 species);
- unpublished records from all Australian museums (372 specimen records of cat-killed birds of 110 species); and
- compilations of injured wildlife reported by veterinarians, where the cause of injury was reported (Dowling et al. 1994).

A total of 86 published sources (including reports and theses) with records of Australian birds being killed by cats are included in this compilation (Appendix B); augmented by a further 18 unpublished studies that provided information on contents of a total of 1571 cat stomachs or scats (Appendix A). About ten of the published sources are largely secondary, but the distinction between primary and secondary sources was not always clear in the literature. Although some published or unpublished records of birds being killed by cats clearly indicated the subspecies of birds being consumed, most did not, so our compilation is at species level only.

We include cases of birds known to be injured (but not necessarily killed and consumed) by cats. We include records of cats consuming eggs and nestlings, in the few cases where the bird species was identified. Some of the dietary records may be a result of cats scavenging on dead birds (perhaps especially in the case of larger bird species), but in many cases it is impossible to determine whether items reported in a cat's stomach or scat are a result of predation or scavenging. In general, cats prefer hunting live prey to scavenging, but they are known to consume carrion (Doherty et al. 2015; Molsher et al. 2017).

Some of the literature we searched incidentally included records of cats killing birds of species that occur in Australia, but for which the reported predation occurred outside Australia. We noted these records (in Appendix B), but we have not attempted to review literature of cat-predation beyond Australia, and we do not include these records in our analyses or tallies. Some sources also noted that cat-predation was inferred, rather than being supported by definitive evidence. Such records are noted in Appendix B as inferred predation, but are also not included in our tallies or modelling.

This compilation does not differentiate between predation by pet or feral cats because a substantial proportion of the primary sources that we examined did not make this distinction. Furthermore, there is a continuum from, at one extreme, pet cats that are not allowed outside (for which all food is provided by their human owners) to, at the other extreme, feral cats in natural environments remote from humans.

Bird species traits

Our listing of Australian bird species was from the recent comprehensive data base of Garnett et al. (2015): these include species occurring on the Australian mainland and islands, including Australia's overseas territories. That source also categorised some of these species as vagrant, and unless otherwise indicated, such species are omitted from analyses here. The threatened status of every bird species as at January 2017 was also included in our database, at both global level (i.e. by the IUCN) and national level (as recognised by Australia's *Environment Protection and Biodiversity Conservation Act, 1999*). Note that the Australian legislation allows listing of subspecies as threatened; in this study, we report killing by cats only at the species level, but if a cat is known to kill one subspecies of a particular bird species, it is reasonable to assume that it is likely to also kill another subspecies of that species.

For every bird species, we tallied the number of different sources that reported predation by cats. We also condensed this to a binary variable – whether there were or were not confirmed records of cat-predation in Australia for that species in our collated database. We also compiled a set of ecological, morphological and other variables for every Australian bird species (Table 2), with traits included based largely on results from previous studies that have indicated some factors associated with the likelihood of a bird species being preyed upon by cats, including body mass, nest site and foraging substrate (Dickman 1996; Kutt 2012; Lepczyk et al. 2004; Paltridge et al. 1997). Our scoring for these factors was mostly derived from the comprehensive database of traits of Australian birds (Garnett et al. 2015), although some were simplified from that source to provide tractability in the modelling (see Appendix C). We could not readily derive, and hence do not include in modelling, information about some additional traits that may also differentially affect the likelihood of a bird species being preyed upon by cats. For example, scent may be important for some mammalian predators, and some bird species (e.g. Ground Parrots *Pezoporus wallicus*) are considered particularly detectable to mammalian predators because of their strong scent (Mattingley 1918). Likewise, bird species that have conspicuously marked plumage may also be more readily detected by hunting cats; some bird species may be characteristically more wary than others; and some bird species may respond vigorously and pugnaciously to attempted attacks.

For every bird species, we also included two variables that relate to their abundance, distribution and the extent to which the species has been subject to research. The variables were: (i) the number of observations reported in the two Atlases of Australian Birds (1977 to 1981, and 1998 to 2001) combined. This value will tend to be higher for species that are more widespread and abundant, with substantial distributions overlapping that of major human population centres (i.e. where most observers reside). For idiosyncratic reasons, the Atlas tallies do not include any records from oceanic islands; and (ii) the number of individual birds banded, a measure of targeted research effort, which again is likely to be higher for species that are more widespread and abundant, with substantial distribution overlapping that of major human population centres, but may also be high for some rarer and more restricted species that have happened to have been subject to intensive research programs. Given that there is more information available, including more targeted studies, for species with higher values for these variables, it is likely that species with high values for these variables will be more likely to have documented records of being killed by cats than would otherwise similar bird species that have low values for these variables (i.e. are rarer, more restricted or less studied), even though their *per capita* rate of predation by cats may be comparable. In analyses (below) we seek to redress this bias.

Analysis

As one approach to considering the extent to which our compilation of diverse sources redresses potential bias arising from common and widespread bird species being particularly likely to be reported in cat dietary studies, we compared the abundance and distributional extent of the set of bird species recorded as killed by cats in the Doherty et al. (2015) compilation, the set of additional bird species recorded here as killed by cats, and the set of bird species that have not yet been reported to be killed by cats, using Kruskal-Wallis analysis of variance.

Our principal analysis modelled the presence/absence of cat-predation records for Australian bird species against all possible combinations of bird species' traits using generalized linear models (GLM's) (binomial logistic regression) run in R version 3.3.2 (R Core Team 2016). The predictor variables considered in the model selection process comprised *body mass*, *ground foraging*, *ground nesting*, *preferred habitat*, aggregation at *waterholes*, use of *urban* areas and *island*-endemicity (Table 2: italics indicate name used in reporting of modelling results). We log-transformed body mass and allowed the effect of body mass to be non-linear by introducing a quadratic term, stipulating its inclusion in a model only with the linear term. All continuous variables were standardised by dividing by two times the standard deviation (Gelman 2008).

To consider model uncertainty, we took a model averaging approach to the analysis which incorporates estimates from multiple candidate models weighted according to Akaike Information Criterion with correction for small sample size (AIC_c) (Burnham and Anderson 2002). In this way, we examined several competing models simultaneously to identify the top set of models (95% confidence model set). These top models were averaged to obtain parameter estimates and predictions were generated based on full model-averaged coefficients obtained from summed Akaike weight (R package MuMIn: Barton 2016). The *abundance*-distribution factor (Table 2) was used as an offset variable, and stipulated *a priori* for inclusion in all candidate models.

To identify a single optimal model for the purpose of visualisation of variable effects (R package visreg: Breheny and Burchett 2016), relative variable importance values (*w+*), defined as the sum of Akaike weights for all models containing a given predictor variable, were used to identify only highly influential variables (*w+* ≥ 0.73, equivalent to an AIC difference of 2 which is widely used to assess a 'clear' effect: Richards (2005)) for inclusion in the optimal model. Optimal model validation was conducted by calculation of Variance Inflation Factors (VIF) (car package: Fox and Weisberg 2011) to test for multicollinearity among predictor variables, the dispersion statistic to test the fit of the distribution, Cook's distances to check for observations with disproportionally high influence, and adjusted McFadden Pseudo R^2 (pscl package: Jackman 2015) to estimate the deviance explained by the model. Pearson residuals were plotted against fitted values, as well as included and excluded covariates, to check for homogeneity, independence and model fit. For categorical variables with more than two levels (i.e. *preferred habitat* and *ground nesting*), we used the 'glht' function (R package multcomp: Hothorn et al. 2008) to identify significant differences among categories.

To answer the question: 'what is the relative likelihood that a cat will prey upon a bird species?' predictions (P_{cat}) were generated by offsetting the abundance variable: for this question, bird species that are more common are likely to rank highly. To answer the question 'among all bird species, what is the relative likelihood of an individual bird being killed by a cat?' abundance was held constant at the mean when generating predictions (P_{bird}). This question relates to a bird species' relative *per capita* rate of predation by cats – for example, a rare species for which 20% of individuals are killed by cats per year would rank higher than a very common species for which only 10% of individuals are killed by cats per year. This prediction is the likelihood of an individual of a bird species being killed by cats (relative to all other bird species), given its ecological and other traits. Note that it is not an explicit probability of an individual of that bird species being killed by cats over any particular time period.

The modelling was repeated with the dependent variable being the number of separate sources reporting cat-predation (rather than whether or not there were any cat-predation records for a bird species in our compilation). The same predictor variables as used above in the binary analysis (Table 2) were considered in the model selection process for number of sources. To model this count data we used negative binomial GLM's and predictions were generated from model-averaged coefficients obtained from a top 95% confidence model set (R package MuMIn: Barton 2016). This parallel analysis recognises that there are somewhat different biases in each approach: for example, use of only presence/absence of predation records treats a bird species that may have had only a single and unsual record of cat predation as equivalent to a species with numerous records indicating cat predation on that species occurs frequently; whereas use of number of sources reinforces the bias that species that are common, much-studied and occur in areas overlapping human population centres are likely to be more frequently recorded as cat-predated, even if the incidence of such cat predation is actually comparable to rare species occurring in remote areas.

Results

Collation

We collated records in Australia of 339 native bird species (of which one species was a vagrant to Australia), with this tally comprising 45.6% of the 741 Australian native bird species, excluding vagrants (Appendix B). Cat predation was also stated in our sources as presumed or implied in Australia, or reported elsewhere, for a further 56 native bird species (of which three are vagrants to Australia). Our compilation also includes 18 introduced bird species reported as killed by cats in Australia (Appendix B). These tallies represent major advances from the previous compilations, of cat predation records on 113 Australian native bird species reported by Doherty et al. (2015), and on 186 bird species (native and introduced) reported by (Paton 1990; Paton 1991; Paton 1993)

Our compilation includes records of cat predation in Australia for 75 bird species listed as extinct or threatened by the IUCN or (with one or more subspecies listed as threatened) under Australia's *Environment Protection and Biodiversity Conservation (EPBC) Act* 1999 (Appendix B). This includes one extinct species (Paradise Parrot *Psephotus pulcherrimus*), and 23 species listed as threatened by the IUCN (40% of the 58 IUCN-listed threatened bird species occurring (other than as vagrants) in Australia). Our collation includes records of cat predation for 71 of the 117 bird species (i.e. 61%) that are listed as threatened species under the EPBC Act or have one or more subspecies so listed. Again, these tallies represent major advances from the previous compilations, notably of cat predation on two threatened Australian bird species recorded by Doherty et al. (2015).

Bird species reported to be killed by cats in Doherty et al. (2015) were more widespread and abundant (mean 6624 Atlas records per species; s.e. 768), and more likely to have been well-studied (mean of 11084 individuals banded; s.e. 2466), than the additional bird species recorded as killed by cats in the current compilation (mean of 2247 Atlas records (s.e. 253); mean of 4234 individuals banded (s.e. 1182)): i.e. our inclusion of more diverse sources served to capture cat-predation records of more rare and restricted bird species than the previous compilation. However, both sets of species were also more widespread and common, and more likely to have been studied, than bird species for which we could locate no records of being killed by cats (mean of 895 Atlas records (s.e. 100); mean of 1988 individuals banded (s.e. 346)). The differences among these three groups of species (i.e. recorded in previous compilation as cat-predated, newly recorded here as cat-predated, or with no records of cat predation) were highly significant ($H=119.1$, $p<0.0001$ for Atlas records; $H=93.7$, $p<0.0001$ for numbers of birds banded).

Modelling

A 95% confidence set of logistic regression models for extant native birds generated eight models from summed AIC_c weights. All predictor variables other than *urban* and *waterholes* were highly influential (Tables 3, 4).

For the optimal model containing only highly influential variables, VIF was less than 1.3, suggesting that any collinearity among variables was unlikely to affect statistical inference (Zuur et al. 2010). Further model validation techniques confirmed no dispersion issues, Cook's distances were <0.1, residuals were unbiased and homoscedastic, and adjusted McFadden Pseudo R^2 of 0.16 indicated good model fit (McFadden 1974).

From the optimal model (Akaike weight w_i = 0.35), the relative likelihood of a bird species being preyed upon by cats was higher for bird species that forage on the ground, are of medium size (ca. 60-300 g) and are island endemics. Bird species that nest in Australia on the ground were more likely to be preyed upon by cats than were bird species that were non-breeding visitors ($p < 0.001$), and those that typically nest in Australia >1 m above ground ($p<0.01$) (Fig. 1). *Preferred habitat* was also associated with likelihood of being killed by a cat, with bird species primarily occurring in rainforests/mangroves being less likely to be killed by cats than those associated with grasslands ($p<0.05$), shrublands/heathlands ($p< 0.05$), and open forests/woodlands ($p<0.001$); coastal/marine bird species also had a relatively high likelihood of being killed by cats.

Based on modelling of traits, the bird species that cats are most likely to prey upon are mostly widespread and common species that forage (and/or nest) on or near the ground. These include species such as Masked Lapwing *Vanellus miles,* Australasian Pipit *Anthus novaeseelandiae,* Superb Fairy-wren *Malurus cyaneus*, Common Blackbird *Turdus merula*, Silver Gull *Chroicocephalus novaehollandiae*, Yellow-rumped Thornbill *Acanthiza chrysorrhoa* and Striated Pardalote *Pardalotus striatus* (Appendix D).

When bird abundance is held constant to provide predictions of the *per capita* likelihood of a bird species being preyed upon by cats, the ordering of bird species is very different (Appendix E). Reflecting the strong influence of the *island*-endemicity variable in the models, the species with highest predicted *per capita* likelihood of being preyed upon by cats are island endemic species, including several that are now extinct. With the small set of island-endemic species and the island variable excluded, the 40 bird species with highest predicted *per capita* likelihood of being preyed upon by cats is listed in Table 5, and values for all species given in Appendix F. Species with highest modelled *per capita* likelihood of cat predation included many relatively localised, uncommon and little-studied species, with some consistent groupings, notably of quail-thrush *Cinclosoma* spp., button-quail *Turnix* spp., and some ground-dwelling pigeons.

Results from modelling that used, as the dependent variable, the number of documented sources of cat predation per bird species were consistent with modelling using only presence/absence of cat predation records: detailed results are presented in Appendix G.

Discussion

Our compilation greatly increases the number of Australian bird species, and number of threatened bird species, known to be preyed upon by cats. This is largely because we use a far more diverse set of primary sources than the previous national compilation (Doherty et al. 2015), whose sources were largely restricted to studies that focused on feral cat diet (rather than also including reports of factors involved in bird mortality) and hence tended to include mostly common and widespread bird species. Notwithstanding our extensive search of the literature, our results also indicate that our compilation may retain some bias against recording predation by cats on less common and more localised bird species.

Our results are largely consistent with previous studies that have reported that a very broad range of bird species are preyed upon by cats, and that particular traits render some bird species more susceptible to such predation (Dickman 1996; Kutt 2012; Lepczyk et al. 2004; Paltridge et al. 1997). Our models indicate that predation by cats is most likely for bird species that nest and forage on the ground and occur mostly in relatively open habitats (rather than rainforests and mangroves). A preference by cats for bird species that forage and/or nest on the ground has been reported previously in Australia (Paltridge et al. 1997; Paton 1991) and elsewhere (Dunn and Tessaglia 1994; Lepczyk et al. 2004; Mead 1982).

Our demonstration that bird species' preferred habitat also influences the likelihood of a bird species being preyed upon by cats may have several explanations. Our analysis may not have completely overcome marked unevenness in the information base arising because there have been few studies of the ecology and diet of cats in rainforest and mangrove habitats (Doherty et al. 2015). The relative lack of such studies may itself be because these comprise only a small proportion of Australia's continental area. To some extent, this bias can be redressed through information derived from autecological studies of bird species associated with these closed forest habitats. Although there are notable autecological studies of some Australian rainforest and mangrove bird species (Frith and Frith 1995; Heinsohn et al. 2009; Laurance and Grant 1994; Noske 1996, 2001), few report rates and causes of mortality. The relatively low likelihood of predation by cats predicted here for bird species associated with rainforests and mangroves may be real rather than an artefact of sampling unevenness. The likelihood of cat predation on birds is probably low in closed forest environments because cat density is relatively low in such environments (Legge et al. 2017), and/or because characteristics of the understorey of these environments may reduce cat hunting efficiency, and/or because many bird species in these environments are canopy-dwellers. We cannot readily partition the relative influence of these potential explanations, and more research on the abundance and impacts of cats in these environments is warranted. The relatively higher likelihood of cat depredation for birds occurring in coastal/marine habitats than for birds in freshwater wetland habitats is probably because cats kill many seabirds that nest colonially on land, whereas most freshwater wetland birds are offered some protection from cat predation by the water itself.

We also demonstrate that predation by cats is most likely for bird species of intermediate body mass (ca. 60-300 g). Bird body size has been linked with likelihood of cat predation in previous studies: for example, in north-eastern Queensland, Kutt (2012) found that cat predation was selective for birds in the 10-50 g range, Dickman (1996) proposed that feral cats on the Australian mainland prefer birds up to 200 g, and Paton (1991) considered that most birds taken in urban and peri-urban areas of south-eastern Australia were <100 g. Cats' preferred bird size range may be difficult to circumscribe neatly, given that the presence of large birds in cat diets may represent consumption of their carrion or take of chicks or eggs.

We found no indication that the likelihood of cat predation was higher for bird species that aggregate at water sources, in contrast to such preference being reported for some studies in arid Australia (Paltridge et al. 1997). This difference may be because our assessment was continental in scope, and aggregations of bird species at water sources are largely a phenomenon of arid and semi-arid areas.

Although there were relatively few island-endemic bird species in our data set (24 species), these few island-endemic species are strongly associated with relatively high predation risk, with the 18 bird species with highest predicted likelihood of predation by cats all being island-endemic species (Appendix E). The susceptibility of island-endemic species, including bird species, to be killed by cats is well established, with island endemic bird species contributing disproportionately to all known bird extinctions, in large part due to introduced cats (Blackburn et al. 2005; Doherty et al. 2016; Medina et al. 2011; Nogales et al. 2004). Furthermore, where cats are present on Australian islands, their densities are, on average, an order of magnitude higher than on comparable areas of the mainland (Legge et al. 2017), and such elevated densities of cats could contribute to the greater likelihood of island birds being killed by cats. Furthermore, cats on Australian islands typically consume a higher proportion of birds in their diet than do cats in comparable mainland areas (Doherty et al. 2015; Woinarski et al. in press).

The models allowed us to estimate the likelihood of predation by cats for every Australian bird species (Table 5; Appendices E, F), with control of many biases in our documentation. To our knowledge, there are no comparable estimates of predation risk for entire continental bird faunas elsewhere. These predicted values provide a general indication of the types of birds that may be most detrimentally affected by cat predation, with high *per capita* likelihood of cat predation particularly for island endemic, ground-nesting, ground-foraging and medium-sized species. Given their high predicted rates of *per capita* cat-predation, we consider there may be particular cause for conservation attention for all island-endemic bird species, ground-dwelling pigeons and doves (*Phaps, Petrophassa, Geophaps* spp.), quail-thrush *Cinclosoma* spp., quail *Coturnix* spp., Plains-Wanderer *Pedionomus torquatus* and button-quail *Turnix* spp (Table 5). Appropriate management responses may include as enhanced management of cats in areas important for these bird species, monitoring of population trends for these species and autecological studies. Although some of these species are recognised to be of conservation concern, many have not hitherto been considered as meriting particular conservation attention.

Our models included only a small number of traits, and some of these were greatly simplified from original sources, so we may well have lost much of their ecological nuance. Our models also did not include some traits (such as conspicuousness of plumage, and wariness) that may influence the likelihood of a bird species being preyed upon by cats but were not readily parameterised. Although challenging to parameterise, inclusion of appropriate measures for these characteristics could in future help refine our modelling and improve its predictive power.

Records of predation by cats, or the predicted likelihoods of such predation, do not necessarily correspond to conservation impact or consequences to the population viability of any bird species. Impacts may also be influenced by the relative abundance of a bird species, the relative abundance of cats, the relative availability of other prey to cats, a bird species' reproductive output and life history, the array of other threats, and the interaction of other factors (such as fire regime, habitat fragmentation and livestock grazing) that may serve to increase or decrease the severity of predation impacts (Graham et al. 2013; Leahy et al. 2015; McGregor et al. 2015; McGregor et al. 2014; McGregor et al. 2016). Notwithstanding these caveats, the predicted values reported here of relative *per capita* likelihood of being killed by cats for every Australian bird species are probably more robust indicators of the potential threat of cat depredation to individual bird species than is a simple documentation of whether or not there are predation records reported.

Given the now near-pervasiveness of cats across the Australian landscape, including many islands and almost all conservation reserves (Legge et al. 2017), and that cats kill on average ca. 377 million Australian birds per year (Woinarski et al. in press), our demonstration here that many more Australian bird species (particularly threatened species) are preyed upon by cats than previously recognised suggests that there is an urgent need to undertake more intensive studies of the impacts of cat predation on the population viability of at least those bird species most likely to be susceptible. Our results also support recent management initiatives to increase the currently very small proportion of Australia that is free of cats (either on islands or within fenced predator-exclosures) and the area in which cats are intensively controlled (Commonwealth of Australia 2015).

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Table 1. Real or potential biases in documentation of records of cat predation, and constraints on modelling.

Potential bias	Response in this study to reduce bias
Studies of cat-predation will tend to report records of predation of more common and widespread bird species, and those occurring in areas in and around human population centres	We included information on predation from many diverse sources, including autecological studies of birds, rather than simply collations of cat diet; our modelling includes an offset for abundance, to allow derivation of a *per capita* estimate of predation risk
Observations of cat predation on birds will be biased towards larger and more distinctive birds	We included information on predation from many diverse sources, including autecological studies of birds, rather than simply collations of cat diet. The bias due to some bird species being more conspicuous or more easily identified mostly relates to the minority of records here that derive from pet-owners' reports
Observations of cat predation on birds will be biased towards bird species that have been the subject of intensive autecological studies	This bias was not entirely circumvented in our compilation or modelling. However, there are relatively few autecological studies of Australian bird species that include documentation of different sources of mortality, and our compilation used very diverse sources in addition to reports from autecological studies.
There have been relatively few studies of birds or cats in mangroves and rainforest habitats.	This bias was not entirely circumvented in our compilation or modelling, but other studies (Legge et al. 2017) indicate that cat density is likely to be relatively low in closed forest habitats.
There will be fewer records of cat predation on birds that became extinct soon after European settlement	This bias was not entirely circumvented in our compilation or modelling, but modelling indicated high predation risk for many extinct bird species anyway
Eggs and nestlings will be under-represented in samples because these may be quickly digested and unidentifiable in cat samples	This bias was not entirely circumvented in our compilation or modelling, but is unlikely to introduce any systematic bias for or against particular bird species
Larger birds may be included in cat samples but these may represent carrion rather than predation	This bias was not circumvented in our compilation or modelling, but our inclusion of predation information arising from assessments of causes of mortality within autecological studies of birds may redress this concern
Cats may kill birds but not consume them ('surplus kill'), and these killed birds will not be present in dietary samples	This factor should not introduce any major bias among bird species – i.e. although colonial bird species may be more likely to be

	subject to ‘surplus killing’ this should not affect our analysis, which is based on any records of bird species being killed rather than the tally of numbers of individuals being killed
Consumption of a single individual of a large bird species may satiate cats, whereas it may require many small birds to satiate cats	Not a bias *per se* – simply recognises that more individuals of smaller bird species may be taken by cats than of larger birds

Table 2. Bird traits used in modelling. Note that we also used information presented in Garnett et al. (2015) to categorise bird species as vagrant or not, extinct or extant, native or introduced, and threatened or not.

Parameter	Coding	Source	Comment
Body *mass*	Adult body mass (g)	Garnett et al. (2015)	Note that cat-predation records may relate to predation on much smaller chicks, or eggs
Preferred *habitat*	Categorical (as either 1=grassland, 2=shrubland/heathland, 3=woodland/open forest, 4=rainforest/mangrove, 5= freshwater, or 6=coastal/marine)	Simplified from Garnett et al. (2015) (see Appendix C)	
Urban use	Categorical (as 0=not reported to use urban habitats; 1=reported to use urban habitats)	Garnett et al. (2015)	
Island endemic	Categorical (as 0=not endemic to islands, or 1=endemic to islands)	Garnett et al. (2015)	
Waterholes	Categorical (as 0=typically does not aggregate to drink at waterholes; 1= often aggregates to drink at waterholes)	Derived anew from information presented in HANZAB series	
Abundance and distributional extent	Continuous	Garnett et al. (2015)	This parameter was a log-transformed measure of the total number of observational records of a species in two Atlases of Australian Birds (1977 to 1981, and 1998 to 2001). Note that the Atlas index did not include any records from oceanic islands, and may have some bias towards species occurring mostly in or near areas of higher human population density.
Extent of research effort	Continuous	Australian Bird and Bat Banding Scheme	The number of individual birds banded (per species) was included in preliminary models as an indicator of study effort, but this variable included extremely high values for an idiosyncratic set of species, so was excluded from models described here
Ground-foraging	Continuous, varying from 0 (does not feed on the ground) to 3 (feeds entirely on the ground)	Simplified from Garnett et al. (2015) (see Appendix C)	
Ground-nesting	Categorical (as either 0=not nesting in Australia, 1= typically nesting in shrubs, trees or other sites >1 m above ground; or 2=typically nesting on the ground or within 1 m of it)	Simplified from Garnett et al. (2015) (see Appendix C)	

Table 3. Best candidate models (95% confidence model set) used to test the effects of predictor variables on records of cat-predation. AICc is the Akaike Information Criterion with correction for small sample size; ΔAICc is a measure of change in AICc relative to the best model; Akaike weight w_i is the probability that model *i* is the best model. When present in candidate models, body mass includes both linear and quadratic terms. All models include the offset for abundance. For definitions of variables see Table 2.

Model	**ΔAICc**	$\boldsymbol{w_i}$
Ground foraging + ground nesting + habitat + island + body mass	0.00	0.35
Ground nesting + habitat + island + body mass	1.46	0.17
Ground foraging + ground nesting + habitat + island + body mass + waterholes	1.92	0.13
Ground foraging + ground nesting + habitat + island + body mass + urban	1.97	0.13
Ground nesting + habitat + island + body mass + waterholes	3.07	0.08
Ground nesting + habitat + island + body mass + urban	3.37	0.06
Ground foraging + ground nesting + habitat + island + body mass + waterholes + urban	3.91	0.05
Ground nesting + habitat + island + body mass + waterholes + urban	5.02	0.03

Table 4. Relative importance values (w_+) of predictor variables. For definitions of variables see Table 2.

Variable	w_+
Island	1.00
Habitat	1.00
Ground nesting	1.00
Body mass	1.00
Body mass^2	1.00
Ground foraging	0.76
Urban	0.29
Waterholes	0.27

Table 5. The 40 bird species with highest relative *per capita* likelihood of being killed by cats (P_{bird}). These results derive from modelling, across all non-vagrant bird species, of the relationship between presence/absence of cat-predation records and bird traits, with bird abundance kept constant, and the small set of island-endemic species omitted. Values given in table are estimated value and 95% confidence interval (95% CI). *species extinct in Australia; **threatened species, or at least one subspecies listed as threatened

Common name	Scientific name	fit	95% CI
Spotted Quail-thrush**	*Cinclosoma punctatum*	0.794	(0.690-0.870)
Chestnut-backed Button-quail	*Turnix castanotus*	0.793	(0.689-0.868)
Painted Button-quail**	*Turnix varius*	0.792	(0.689-0.868)
Buff-breasted Button-quail**	*Turnix olivii*	0.792	(0.689-0.868)
White-quilled Rock-Pigeon	*Petrophassa albipennis*	0.792	(0.679-0.872)
Chestnut-quilled Rock-Pigeon	*Petrophassa rufipennis*	0.792	(0.678-0.873)
Partridge Pigeon**	*Geophaps smithii*	0.791	(0.677-0.872)
Brush Bronzewing	*Phaps elegans*	0.791	(0.676-0.872)
Squatter Pigeon**	*Geophaps scripta*	0.790	(0.675-0.872)
Chestnut Quail-thrush	*Cinclosoma castanotus*	0.789	(0.647-0.885)
Chestnut-breasted Quail-thrush	*Cinclosoma castaneothorax*	0.788	(0.646-0.883)
Sandstone Shrike-thrush	*Colluricincla woodwardi*	0.787	(0.685-0.863)
Red-backed Kingfisher	*Todiramphus pyrrhopygius*	0.787	(0.684-0.863)
Cinnamon Quail-thrush**	*Cinclosoma cinnamomeum*	0.786	(0.645-0.882)
Rufous Scrub-bird**	*Atrichornis rufescens*	0.784	(0.681-0.860)
Paradise Parrot*	*Psephotus pulcherrimus*	0.782	(0.672-0.863)
Southern Scrub-robin	*Drymodes brunneopygia*	0.776	(0.636-0.874)
Rufous Songlark	*Cincloramphus mathewsi*	0.776	(0.670-0.854)
Common Blackbird	*Turdus merula*	0.774	(0.673-0.851)
Western Ground Parrot**	*Pezoporus flaviventris*	0.772	(0.622-0.874)
Bush Stone-curlew	*Burhinus grallarius*	0.772	(0.651-0.860)
Eastern Ground Parrot	*Pezoporus wallicus*	0.771	(0.622-0.873)
Rufous Bristlebird**	*Dasyornis broadbenti*	0.769	(0.616-0.874)
Crested Bellbird	*Oreoica gutturalis*	0.768	(0.621-0.870)
California Quail	*Callipepla californica*	0.767	(0.650-0.853)
Stubble Quail	*Coturnix pectoralis*	0.767	(0.652-0.852)
Brown Quail	*Coturnix ypsilophora*	0.767	(0.652-0.852)
Banded Lapwing	*Vanellus tricolor*	0.766	(0.650-0.853)
Inland Dotterel	*Charadrius australis*	0.765	(0.651-0.850)
Night Parrot**	*Pezoporus occidentalis*	0.764	(0.641-0.855)
Spinifex Pigeon	*Geophaps plumifera*	0.764	(0.640-0.854)
Western Whipbird**	*Psophodes nigrogularis*	0.763	(0.618-0.865)
Eastern Bristlebird**	*Dasyornis brachypterus*	0.762	(0.618-0.865)
Plains-wanderer**	*Pedionomus torquatus*	0.762	(0.650-0.847)
Noisy Scrub-bird**	*Atrichornis clamosus*	0.762	(0.617-0.864)
Chirruping Wedgebill	*Psophodes cristatus*	0.761	(0.616-0.863)
Chiming Wedgebill	*Psophodes occidentalis*	0.760	(0.616-0.862)

Brown Songlark	*Cincloramphus cruralis*	0.760	(0.648-0.845)
Flock Bronzewing	*Phaps histrionica*	0.760	(0.634-0.852)
Rock Dove	*Columba livia*	0.760	(0.634-0.852)

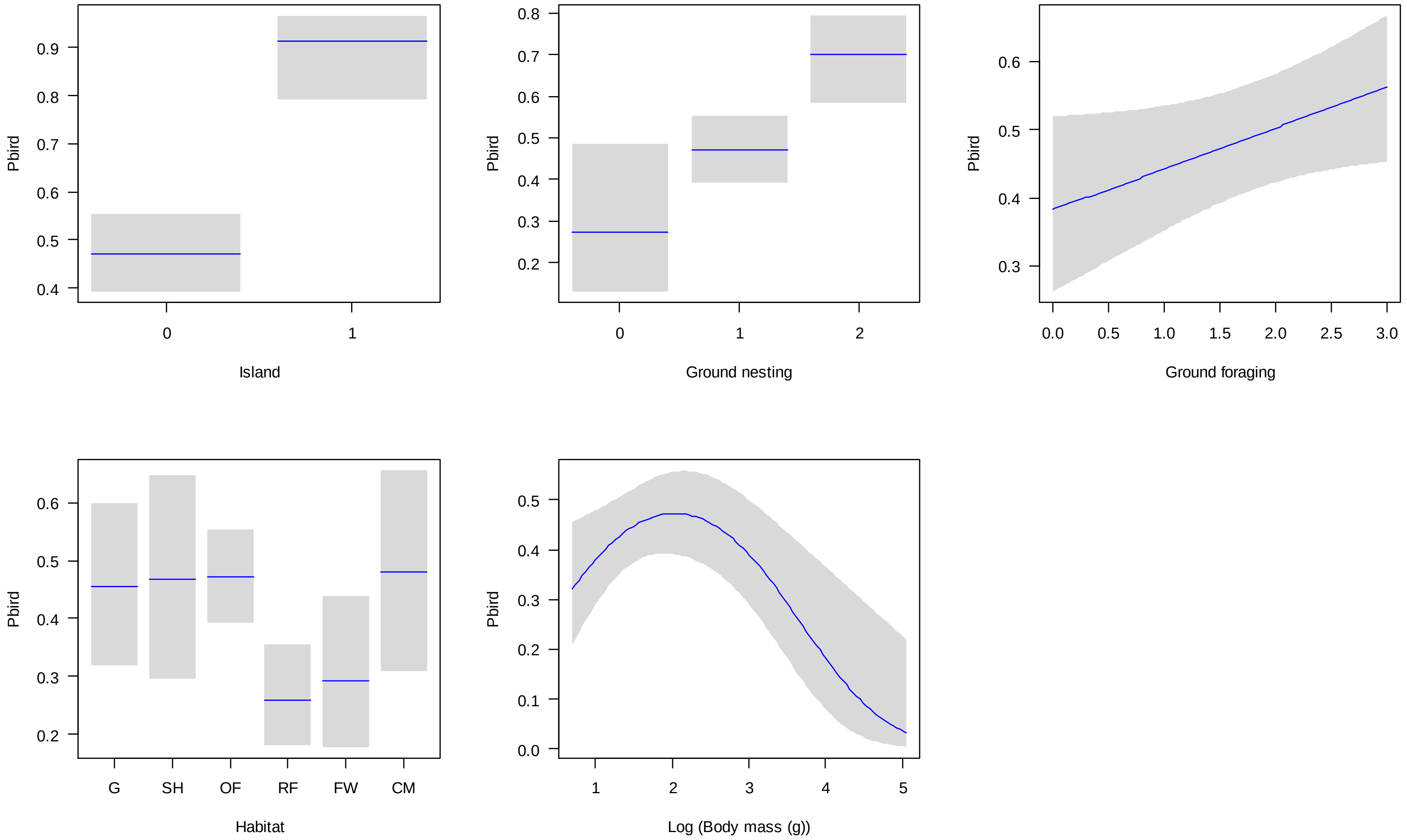

Figure 1. Relationships between the *per capita* likelihood of being preyed upon by a cat (P_{bird}) and key predictor variables (while holding all other variables at fixed median levels (continuous variables) and most common category (categorical variables) and offsetting for bird species abundance by holding

abundance constant at the mean), derived from the optimal logistic regression model. Continuous lines represent fits to the model's predicted values and grey area indicates 95% confidence interval of model fits. Codes for categorical variables: island (0=not endemic to islands, 1=endemic to islands); ground nesting (0=does not breed in Australia, 1=nests >1 m above ground, 2=nests <1 m from ground); habitat (G=grassland, SH=shrubland/heathland, OF=woodland/open forest, RF=rainforest/mangrove, FW=freshwater, CM=coastal/marine).