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Compounding and complementary carnivores: Australian bird species eaten by the introduced European red fox *Vulpes vulpes* and domestic cat *Felis catus*

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Abstract

Two introduced carnivores, the European red fox *Vulpes vulpes* and domestic cat *Felis catus*, have had extensive impacts on Australian biodiversity. In this study, we collate information on consumption of Australian birds by the fox, paralleling a recent study reporting on birds consumed by cats. We found records of consumption by foxes on 128 native bird species (18% of the non-vagrant bird fauna and 25% of those species within the fox's range), a smaller tally than for cats (343 species, including 297 within the fox's Australian range, a subset of that of the cat). Most (81%) bird species eaten by foxes are also eaten by cats, suggesting that predation impacts are compounded. As with consumption by cats, birds that nest or forage on the ground are most likely to be consumed by foxes. However, there is also some partitioning, with records of consumption by foxes but not cats for 25 bird species, indicating that impacts of the two predators may also be complementary. Bird species ≥3.4 kg were more likely to be eaten by foxes, and those <3.4 kg by cats. Our compilation provides an inventory and describes characteristics of Australian bird species known to be consumed by foxes, but we acknowledge that records of predation do not imply population-level impacts. Nonetheless, there is sufficient information from other studies to demonstrate that fox predation has significant impacts on the population viability of some Australian birds, especially larger birds, and those that nest or forage on the ground.

Keywords: bird, introduced species, predation, threatened species

Introduction

Introduced predators have been a major cause of bird extinctions and declines globally (Blackburn *et al.* 2004, Szabo *et al.* 2012). The European red fox *Vulpes vulpes* (hereafter fox) and domestic cat *Felis catus* (hereafter cat) have had catastrophic impacts on Australian biodiversity, causing numerous extinctions and ongoing declines of many native animal species (Johnson 2006, Abbott, Peacock and Short 2014, Woinarski *et al.* 2019a). The Australian fox population derives from introductions in the 1870s, with subsequent spread across most of the mainland: it also now occurs on about 40 islands (Abbott *et al.* 2014). Cats were introduced from 1788 and spread rapidly to occupy the entire continent by the 1890s, and now also occurs on about 100 Australian islands (Abbott 2008b, Legge *et al.* 2018, Woinarski, Legge and Dickman 2019b).

Early observers reported on the impacts of these two predators on the Australian bird fauna, with severe and rapid decline of many native bird species mirroring the sequential spread of cats and foxes (e.g., Campbell 1915, Le Souef 1923, Abbott *et al.* 2014), although the separate and relative influence of these two predators has often been difficult to tease apart. Other evidence of the extent of predation and the impacts of cats (feral and pet) on Australian birds has been adduced in a series of recent publications (Woinarski *et al.* 2017a, Woinarski *et al.* 2017b, Legge *et al.* 2020).

There has been no such comparable review of the impacts of foxes on Australian birds, nor of the impacts of foxes on the bird fauna of any other continent. The impact of the fox on Australian birds may be exceptional. In a global review, Doherty *et al.* (2016) considered that the red fox had population-scale impacts on nine threatened bird species, and had contributed to the extinction of one bird species: all of these are (or were) Australian endemic birds. In part, this preponderance of impacts on birds in Australia is because the fox has been introduced to few other large land masses, at least relative to the cat. Nonetheless, heavy predation of birds by the red fox has been recorded elsewhere. For example, Sargeant, Allen and Eberhardt (1984) reported that foxes in mid-continental North America killed about 900,000 ducks annually, and Harding, Doak and Albertson (2001) attributed a 50% decline over five years in the population of the endangered California clipper rail *Rallus longirostris obsoletus* primarily to fox predation.

Several lines of evidence indicate that foxes have had, and continue to have, a significant detrimental impact on at least some components of the Australian bird fauna. Some bird species, such as the bush stone-curlew *Burhinus grallarius,* have disappeared from, or declined in, parts of their formerly extensive mainland ranges but have remained abundant on islands where foxes have not been introduced (Gates and Paton 2005), or in mainland areas beyond the current distributional range of the fox. Historical accounts have indicated a strong correlation between the spatio-temporal patterns of decline of some bird species and the spread of the fox in Australia (Abbott 2008a, Saunders, Gentle and Dickman 2010, Abbott 2011, Abbott *et al.* 2014). Furthermore, some experimental studies and management programs have demonstrated increases in the abundance and/or breeding success of some bird species in areas subjected to intensive lethal fox control (Dowling and Weston 1999, Wheeler and Priddel 2009, Kirkwood *et al.* 2014, Johnston 2016) or exclusion (Smith *et al.* 2020): for example, the abundance of the superb lyrebird *Menura superba* increased at sites exposed to 10 years of fox poison-baiting, but decreased at comparable sites without baiting (Claridge *et al.* 2010).

Other studies have reported that fox predation caused the rapid loss of individual breeding colonies of some Australian bird species including the gull-billed tern *Gelochelidon macrotarsa,* wedge-tailed shearwater *Ardenna pacifica* and flesh-footed shearwater *A. carneipes* (Higgins and Davies 1996, Abbott 2008a), and caused reduction in the population size of other breeding colonies, such as for the little penguin *Eudyptula minor* (Bourne and Klomp 2004, Wallis, King and Wallis 2017). Fox predation has also been demonstrated to cause marked reduction in breeding success of other ground-nesting bird species such as the hooded plover *Thinornis rubricollis* (Weston 2003) and malleefowl *Leipoa ocellata* (Priddel and Wheeler 1997).

Although there are now substantial areas in south-western and south-eastern Australia in which broad-scale and ongoing lethal control of foxes is implemented (Robley *et al.* 2009, Marlow *et al.* 2015), most areas within the distributional range of the fox have no effective management (due mostly to logistical challenges of control in remote locations), and foxes persist even in managed areas. Hence, the impacts of fox predation on Australian birds may be ongoing and extensive.

Here, we examine the extent and characteristics of fox predation on Australian bird species, and compare this predation with that by cats. This assessment follows the approach used by Woinarski *et al.* (2017b), who collated records of predation by cats on 338 native (and 19 introduced) bird species (ca. 46% of the Australian non-vagrant bird fauna and 61% of threatened bird species). Using trait-based modelling, Woinarski *et al.* (2017b) also demonstrated that predation by cats was more likely for Australian bird species that were island endemics, of intermediate size (ca. 60–300 g), and that nest and forage on the ground. Here, we aim to derive a comparable tally and assessment of characteristics of Australian birds known to be killed by foxes – to identify species that may be at most risk, to compare the number and characteristics of bird species killed by these two predators, and to determine whether their impacts are complementary (i.e., affecting different suites of birds) or compounding (i.e., both predators killing much the same set of bird species). Such information can be used to help describe the magnitude of the threat posed by foxes to the Australian bird fauna and to guide conservation management responses to the bird species for which impacts may be most profound.

Methods

Of foxes and cats

This study counterpoints predation of birds by two introduced predators, at a continental scale. As context, we briefly note some relevant traits of foxes and cats. Both species are highly opportunistic and generalist in their diet (Sutherland, Glen and Paul 2011). Cats (male weight 3.4–7.3 kg) are typically slightly smaller than foxes (4.7–8.3 kg) (Van Dyck and Strahan 2008), and there is some evidence that foxes take larger prey (Murphy *et al.* 2019); however, cats can take prey almost as large as themselves, up to a body mass of about 4 kg (Fleming *et al.* 2020). Cats are more adept climbers, and can take birds and their young from nests high in trees (Saunders 1991), but foxes occasionally climb trees to hunt prey (Mella *et al.* 2018). Foxes are more likely than cats to dig up prey, including birds nesting in underground tunnels (e.g., White 1918).

General approach

In general, the methodology, including analyses, follows that used by Woinarski *et al.* (2017b) for the comparable assessment of Australian bird species reported as killed by cats, with some differences described below. We note records of predation on vagrant birds (i.e., those with few or irregular records from Australia), but exclude vagrant species from analyses. Where stated, we also exclude seabirds from analyses because almost all terrestrial records for most seabird species in Australia are from breeding colonies on islands unoccupied by foxes. Following Woinarski *et al.* (2017b), we categorise bird species as threatened if, at the species or subspecies level, they are listed as Critically Endangered, Endangered or Vulnerable under Australian national legislation or by the International Union for the Conservation of Nature (IUCN), as at October 2020. We also note any confirmed records of predation by foxes on now extinct Australian birds, but exclude extinct birds from analyses as almost all Australian bird extinctions preceded the set of fox dietary studies that form the main component of our collation (Woinarski *et al.* 2019a).

Given our interest in comparisons between the sets of birds eaten by foxes and eaten by cats, we revisited the cat-eaten bird models given in Woinarski *et al.* (2017b). The compilation of bird species reported killed by cats (Woinarski *et al.* 2017b) included many records from studies of pet cats (e.g., Paton 1990), a component of the predator tally without equivalence for foxes. Consequently, we re-analysed birds eaten by cats to both include and exclude those bird species for which records of predation were only from pet cats (with these models described as 'all cats' and 'feral cats' respectively, in text below).

The comparison of inventories of birds eaten by cats and foxes is also influenced by the fox's more restricted distributional range in Australia. Although the two predators' extensive ranges overlap across most of Australia, there are areas (and hence bird species) where cats occur but not foxes (mainly the island of Tasmania and the northern Australian monsoon tropics; for fox distribution see supplementary material Fig. S1). Our interest is in the complete national tallies of birds eaten by cats and foxes, but also in the extent of dietary overlap or segregation in areas of their co-occurrence. To compare birds eaten by foxes and by cats within the range of both predator species, we ran analyses of bird species recorded as consumed by cats both with and without bird species that are restricted to areas outside the distributional range of the fox. Our fox predation models include only those bird species within the range of the fox.

Following Woinarski *et al.* (2017b), a set of morphological and ecological traits was used to characterise bird species (Table 1). Woinarski *et al.* (2017b) used two variables (the number of individual birds banded and the number of records in the two Atlases of Australian Birds) as indices of variation among bird species in distributional range, abundance and/or research effort. We instead accounted for variation in the distributional range and abundance of each bird species by tallying the number of records for each species in the national biodiversity distributional database, the Atlas of Living Australia (ALA; www.ala.org.au). For analyses of bird species recorded as fox prey, we used only the number of ALA records for each species recorded within the distributional range of the fox. To account for variation in research effort across the distributional range of each bird species, we tallied the number of fox and cat diet studies that have occurred within the distributional range of each bird species (Table 1).

Inventory of bird species reported as consumed by foxes

We collated records of bird species (including introduced species) reported in fox dietary samples from 79 studies, many with multiple study sites (comprising ca. 40,000 stomach samples or scats) widely spaced across the range of the fox in Australia (see supplementary material Fig. S1, Table S1). The number of fox dietary studies, and samples within them, is larger than the number of cat dietary studies used in the previous analysis of birds reported eaten by cats (ca. 60 studies, many with multiple study sites, with ca. 10,000 samples). We note that the set of fox dietary studies also has a somewhat different frequency distribution over time than that of cat dietary studies, reflecting in part an earlier interest in fox diet stimulated by concerns about predation on livestock – concern about the impacts of the two predator species on wildlife is generally more recent: this issue is detailed further in Figure S2, and we note that there has been no significant variation in the frequency of occurrence of birds in fox diets over the time period spanned by our collation of fox dietary studies (Fleming *et al.* 2021). As with the study of cat-eaten birds by Woinarski *et al.* (2017b), we also included records of fox predation on birds reported in autecological studies of bird species and records included in major compilations of information on Australian birds (e.g., Marchant and Higgins 1990). A listing of all sources from which records were extracted is given in supplementary material Table S2.

Consumption or predation?

Many of the records we collated were from fox stomach or scat samples, and hence do not necessarily demonstrate predation. Foxes scavenge from carrion, including birds (O'Connor *et al.* 2020), at typically higher rates than cats, although most of the carrion taken is typically of larger mammals rather than birds (Catling 1988). Conversely, foxes can also kill birds without then consuming them (Short, Kinnear and Robley 2002). As a convenience, we mostly refer to 'consumption' rather than 'predation' in this paper, but consider that consumption (of birds) by foxes mostly implies predation.

Analyses

We tallied the number of bird species recorded within four predation classes: those known to be consumed by foxes and cats (FC); by foxes but not cats (FX); by cats but not foxes (XC); and those not known to be consumed by either predator (XX). Prior to modelling of birds consumed by foxes and/or cats, we used an analysis of variance (ANOVA) to assess whether there was a significant difference in the number of ALA records and diet studies within each bird species' distributional range between these four predation classes.

All analyses were conducted in program R (R Core Team, 2017). Prior to modelling, we followed the protocol for data exploration provided by Zuur, Ieno and Elphick (2010). All continuous

Table 1. Bird traits used as explanatory variables in the modelling.

Variable	Variable type	Source	Notes
Adult body mass (kg)	Continuous	Garnett *et al.* (2015)	Note that fox-predation records may relate to predation on much smaller chicks, or eggs
Typical habitat	Categorical (grassland; shrubland/heathland; woodland/open forest; rainforest/mangrove; freshwater; coastal/marine)	Simplified from Garnett et al. (2015)	
Urban use	Binary (no, not reported to use urban habitats; yes, reported to use urban habitats)	Garnett et al. (2015)	
Island endemic	Binary (no, not endemic to islands; yes, endemic to islands)	Garnett et al. (2015)	Note that all island endemic birds occurred outside the distributional range of foxes, thus this variable was only included in models of birds eaten by feral cats.
Waterholes	Binary (no, typically does not aggregate to drink at waterholes; yes, often aggregates to drink at waterholes)	Derived anew from information presented in HANZAB series Garnett et al. (2015)	
Total number of ALA records	Continuous	Atlas of Living Australia (2020)	This variable was a $\log_{10}$-transformed measure of the total number of records of a species in the Atlas of Living Australia (ALA). Note that the Atlas records are typically biased towards species occurring mostly in or near areas of higher human population density.
Number of ALA records within fox distributional range	Continuous	Atlas of Living Australia (2020)	This variable was a $\log_{10}$-transformed measure of the number of observational records of a species in the ALA that occurred within the distributional range of the fox. Note that the Atlas records are typically biased towards species occurring mostly in or near areas of higher human population density.

Table 1. (Continued)

Variable	Variable type	Source	Notes
Number of cat diet studies	Continuous		The total number of cat diet studies recorded within the range of a species.
Number of fox diet studies	Continuous		The total number of fox diet studies recorded within the range of a species.
Ground-foraging	Ordered categorical, varying from 0 (does not feed on the ground) to 3 (feeds entirely on the ground).	Simplified from Garnett et al. (2015) (see Woinarski et al. 2017b)	
Ground-nesting	Categorical (NA, not nesting in Australia; no, typically nesting in shrubs, trees or other sites >1 m above ground; yes, typically nesting on the ground or within 1 m of it)	Simplified from Garnett et al. (2015) (see Woinarski et al. 2017b)	Note that birds that do not nest within Australia were excluded from final analyses such that there were only two levels of this variable.

explanatory variables were centred and standardised by deducting the mean and dividing by twice the standard deviation (Gelman 2008).

We used generalised linear models (GLMs), within the binomial error family, to identify bird species' traits that were associated with the relative likelihood of being consumed by foxes and cats. We modelled the presence/absence of records of consumption of Australian bird species (excluding vagrants) by foxes and cats against all possible combinations of bird species' traits. The predictor variables included in the model selection process were body mass, typical habitat, presence in urban areas, waterhole use, ground foraging, ground nesting and island-endemicity (with the island-endemic trait included only in models for cats, given that there is no overlap in the range of foxes and island-endemic birds) (Table 1). We used adult body mass, but recognise that for larger bird species, foxes may hunt selectively on the much smaller young (or eggs). Furthermore, we note that other traits of birds such as odour, behaviour and plumage conspicuousness may also influence the likelihood of predation by cats or foxes, but such traits are not straightforward to categorise, and we restrict our consideration to only those traits used in the companion study of Australian birds killed by cats (Woinarski *et al.* 2017b).

We included the total number of ALA records for each bird species and the number of diet studies within each bird species' distributional range as offset terms, which were stipulated *a priori* for inclusion in all candidate models. We $\log_{10}$-transformed body mass and the number of ALA records, 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 (i.e. body mass^2 + body mass). As our collation revealed no records of fox consumption on bird species that are non-breeding visitors to Australia, we did not have records for one level of the ground nesting trait (i.e., the level of 'does not nest in Australia'), and therefore excluded bird species that are non-breeding visitors from our analyses. This exclusion reduced the ground nesting trait to two levels: birds that typically nest on the ground or within 1 m of it, and birds that typically nest in shrubs, trees or sites >1 m above ground.

We developed a candidate set of models to explain whether birds were fox-eaten and whether birds were cat-eaten, including all combinations of the six explanatory (trait) variables, without interactions (i.e., 64 models). To account for model-selection uncertainty, we took a model averaging approach, incorporating estimates from multiple candidate models weighted according to the second-order form of Akaike's Information Criterion, corrected 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; R package MuMIn: Barton 2018). We identified highly influential variables by calculating relative variable importance, defined as the sum of Akaike weights for all models containing a given predictor variable. Variables with a relative variable importance ≥ 0.73 (equivalent to an AIC difference of 2 which is a common 'rule-of-thumb' used to indicate a significant effect: Richards 2005) were retained in the best model, which was used to visualise variable effects.

To identify bird species with greatest likelihood of predation by either the fox or feral cat, given each species' traits, we used parameter estimates averaged from the top set of models (specified above) to predict the likelihood of predation for each bird species by each predator. We then used binomial GLMs to explore whether threatened bird species had a greater predicted likelihood of predation by the fox and/or feral cat compared to non-threatened species. We ranked candidate models (including only the two predictor variables of likelihood of feral cat predation and likelihood of fox predation) using AIC.

We ran models of fox-eaten and cat-eaten birds for all combinations of with, and without seabirds, and with, and without birds that are non-breeding visitors to Australia. Additionally, we ran models of cat-eaten birds considering predation records from all cats and feral (i.e., not pet) cats only, and for all birds and only birds within the distributional range of foxes. Below we report the results from only those models excluding seabirds and non-breeding visitors, and excluding birds that have been reported as eaten by pet but not feral cats. Results from all other models are mostly consistent with those models, and their details are presented as supplementary material (see supplementary material Table S3). Note that the cat-eaten models may vary in minor detail from those presented in Woinarski *et al.* (2017b) as there have been some recent taxonomic changes for Australian birds, and we also use a different metric of distributional range.

Results

Tallies of fox-consumed and cat-consumed birds

Our collation revealed records of 128 Australian native bird species (17.7% of the Australian avifauna, excluding vagrants; 24.7% of bird species occurring in the fox's range) and eight introduced species in the diet of foxes (see supplementary material Table S4). These tallies are substantially smaller than the equivalent tallies for all cats (343 native bird species, of which 297 species are within the fox's distributional range, and 18 introduced species) and for feral cats only (287 native bird species, of which 247 are within the fox's distributional range, and 18 introduced species).

Our records of bird species consumed by foxes were derived from many sources (Table S1, S2). The dietary studies that examined fox stomachs (total of 5, 284 samples) provided far more records of birds identified to species (61 bird species) than did comparable but larger studies based on inspection of fox scats (19 species from a total of 32, 040 samples). Most of the birds identified from fox scats had distinctive plumage (e.g., crimson rosella *Platycercus elegans*, superb fairy-wren *Malurus cyaneus*, rainbow bee-eater *Merops ornatus*) that remained diagnostic even in scats, suggesting that bird species with less conspicuous or readily recognisable features may be overlooked or harder to identify in scat samples than in stomach samples.

One hundred and three Australian native bird species are known to be consumed both by foxes and cats (including pet and feral); 25 by foxes but not cats; 240 by cats but not foxes; and 356 by neither predator: i.e. there are records of predation by either or both predators for half of the Australian bird fauna (368/724 = 50.8%). The proportions of bird species consumed by both predators, and by neither predator, were significantly larger relative to those eaten by one predator species only than expected by chance ($\chi^2_{3,720} = 72.0$, $p<0.001$). Bird species that were not reported as consumed by either cats or foxes had significantly fewer ALA records (mean 15,853 ALA records; ANOVA: $F_{3,\ 720}=46.1$, $p<0.001$), and fewer predator dietary studies within their distributional range (mean 72 studies; ANOVA: $F_{3,720}=60.1$, $p<0.001$) than birds that were only consumed by feral cats (mean 55, 206 ALA records, 108 studies), birds that were only consumed by foxes (mean 82, 961 ALA records, 154 studies) and birds that were consumed by both predators (mean 160, 225 ALA records, 150 studies); this demonstrates some sampling bias and validates the inclusion of both the number of ALA records and the number of studies for each bird species as an offset term in the GLMs.

Compared to cats, there were relatively few threatened bird species for which we found records of fox predation. There were records of consumption by both foxes and cats for 14 threatened bird species (excluding extinct species), 55 species by cats but not foxes, and only one species (masked owl *Tyto novaehollandiae*) by foxes but not cats. The fox tally of 15 threatened species comprises 12% of Australia's 125 threatened birds and 22% of the 68 threatened birds within the fox's range. We found no records of predation by foxes or cats for 55 threatened bird species (44% of Australia's threatened bird species), with most of these species now being highly restricted or rare (and hence unlikely to be included in predator dietary samples, unless specifically targeted) or occurring only on islands beyond the range of either predator. Our collation included no confirmed records of fox predation on the 12 bird species that are now extinct in Australia, an unsurprising result given that 11 of these species were restricted to islands that have not been colonised by foxes: the exception is the paradise parrot *Psephotellus pulcherrimus*, for which predation by foxes is not considered a contributing factor in its extinction (Garnett, Szabo and Dutson 2011).

Modelling

When considering only those birds within the distributional range of the fox, model averaging showed those birds ≥3.4 kg (of which there are only 11 species including four introduced species) were more likely to be eaten by foxes, while birds <3.4 kg (487 species) were more likely to be eaten by cats than by foxes (Fig. 1a). Model averaging showed those bird species that nest on, or close to the ground, and those that spend more time foraging on the ground were more likely to be eaten both by foxes and feral cats (considering all birds and only those birds within the distributional

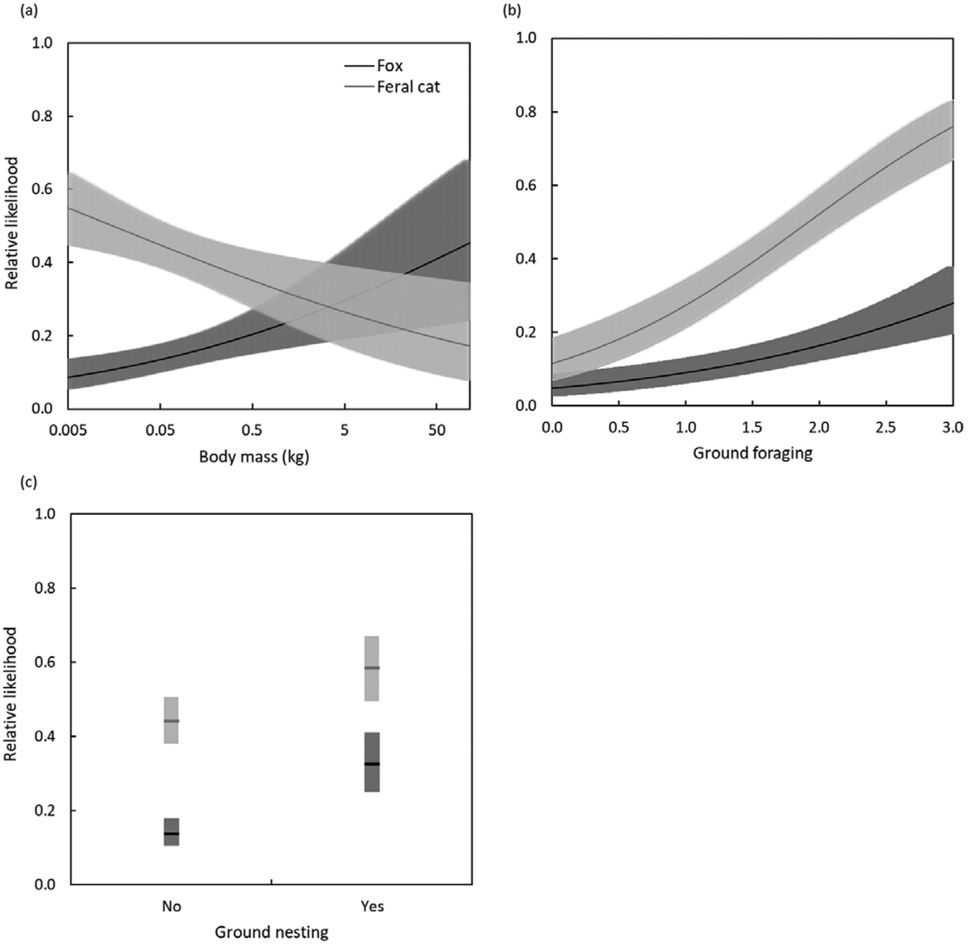

Figure 1. The relative likelihood of a bird species being consumed by a fox (dark grey) or a feral cat (light grey) considering only those species (other than vagrants, seabirds and non-breeding visitors) that occur *within the distributional range of the fox.* Relationships shown are for birds' (a) body mass, (b) ground foraging behaviour, and (c) ground nesting behaviour, with all continuous variables held at fixed median levels and categorical variables at the most frequent category, offsetting for the number of ALA records for each bird species within the distributional range of the fox, and the number of fox or cat diet studies that have been undertaken within each bird species distributional range. Values are derived from the optimal logistic regression model; solid lines represent fits to the model's predicted values and shaded areas indicate 95% confidence intervals.

range of the fox), relative to all other birds (Fig. 1; see supplementary material Table S5). Other traits were relatively inconsequential: for example, a bird species' preferred habitat was not a significant term in the models, suggesting that predation of birds by foxes occurred across habitat types.

When considering all birds (i.e., including those outside the distributional range of the fox), body mass was not a significant correlate of whether a bird was cat-eaten, but those bird species that occur mainly in rainforest/mangrove habitats, and freshwater habitats were less likely to be cat-eaten relative to birds that occur in grassland, shrubland/heathland, woodland/open forest, and coastal/marine habitats (see supplementary material Fig. S3). Bird species that are island endemics were also more likely to be cat-eaten when considering all birds.

Based on the model predictions, the Australian native bird species with the highest relative likelihood of predation by foxes mostly comprise larger species such as the superb lyrebird *Menura novaehollandiae* (adult mass 1.1 kg), Cape Barren goose *Cereopsis novaehollandiae* (5.4 kg) and Australian bustard *Ardeotis australis* (4.9 kg) (see supplementary material Table S6). Note that this assessment derives from modelling that controls for bird species' abundance and distribution, so this listing does not represent the birds most commonly eaten by foxes. Of the top 20 bird species with the highest relative likelihood of fox predation, five are threatened and 14 have been recorded as fox-eaten (Table S6). The bird species with the highest relative likelihood of predation by feral cats are smaller ground-dwelling birds and island endemics such as the Lord Howe woodhen *Hypotaenidia sylvestris* (although we note that cats have now been eradicated from Lord Howe Island) and New Zealand fantail *Rhipidura fuliginosa*. Of the 20 bird species with the highest relative likelihood of predation by feral cats, eight are listed as threatened, and only nine have been recorded as eaten by feral cats (see supplementary material Table S7). The bush stone-curlew was included in the 20 species with the highest relative likelihood of predation by both foxes and feral cats (Tables S6, S7). Based on GLMs the relative likelihood of predation by feral cats predicted whether a species was threatened (ΔAICc 29.8 from null model). Threatened species had a greater relative likelihood of predation by feral cats (mean relative likelihood ± standard error: 0.55 ± 0.02), but not foxes (0.22 ± 0.02), than non-threatened species (cats: 0.40 ± 0.01; foxes: 0.19 ± 0.01).

We repeated the modelling using different combinations of sets of birds (i.e., including or excluding seabirds, and including and excluding bird species occurring only outside the distributional range of the fox) and cats (i.e., including or excluding records from pet cats). These models were generally similar to those reported above (Table S3), with the most notable inconsistency being that bird body mass was a significant explanatory variable in some cat models, with a preference by cats for birds of intermediate body mass, as reported previously by Woinarski *et al.* (2017b).

Discussion

Two introduced mammalian carnivores, the fox and cat, now occur extensively across Australia. We show that, collectively, they have been recorded killing or consuming more than 50% of Australian bird species and that their predation on birds is both compounding and complementary. Both predators preferentially consume bird species that nest and forage on the ground, and there is a large overlap in species eaten. The most notable difference between the two predators is that birds eaten by foxes tend to be larger than those eaten by cats. Although no previous studies have noted this disparity between these two predators in preferred size of bird prey, the tendency for foxes to eat larger birds than for cats is consistent with the findings of previous Australian studies that foxes tend to consume larger mammals than do cats (Glen *et al.* 2011, Murphy *et al.* 2019).

Predator dietary studies formed a major component of our compilation. Notwithstanding that our aggregate of samples of fox diet was larger than of cat diet, we report appreciably fewer bird species known to be consumed by foxes than by cats (128 vs. 343 species, respectively), with this contrast accentuated for threatened bird species (15 species known to be eaten by foxes, 69 by cats). Part of the disparity in tallies is due to the more extensive Australian range of cats (7.7 million km^2

vs. ca. 6.3 million km^2 for foxes), encompassing some bird species occurring only beyond the distribution of foxes, including many threatened birds on islands. However, even when cat predation records were constrained to only those bird species within the range of foxes, we still found that more bird species are killed by cats. The larger number of bird species eaten by cats than by foxes is consistent with the size distribution of Australian birds: 97% of Australian bird species are smaller than 3.4 kg, the body mass that marks the divide between cat-preferred and fox-preferred birds.

That fewer bird species are known to be consumed by foxes than by cats is also broadly consistent with previous Australian studies that have shown birds to be a less important component of fox diet than of cat diet. For example, across 22 Australian sites where both predators co-occurred, Woinarski *et al.* (2017a) reported that birds occurred in 17% of fox dietary samples and in 29% of cat dietary samples.

Our results undoubtedly underestimate the actual number of bird species that are consumed by these predators. Most of the bird species for which we could find no records of predation by cats or foxes are relatively restricted or rare, so evidence of their consumption is less likely to have been reported in studies of predator diet. Information on the incidence and extent of predation for such species is more likely to come from targeted studies of the bird species themselves (e.g., through use of camera traps at nest sites, or radio telemetry) than from assessments of the contents of predator scats or stomachs (Priddel and Wheeler 1994, Dowling and Weston 1999, Goth and Vogel 2002). Furthermore, our results indicate that reporting of the contents of scats (the major source of our fox dietary information) has provided relatively little information on bird species consumed by foxes, probably because while remnants of feathers (or egg-shells) in scats show that birds have been eaten, those remnants are often insufficient evidence to identify the species eaten, and especially so for bird species that do not have conspicuous or diagnostic plumage. This constraint applies to cat scats also (Woinarski *et al.* 2017b). Recent developments in, and more widespread application of, genetic analysis in dietary sampling (e.g., de Sousa *et al.* 2019) may allow for more comprehensive assessment of the species consumed by Australian foxes.

We acknowledge some caveats in our study. Much of our information derives from birds detected in fox stomachs or scats, and such evidence does not prove that the birds in those dietary samples were killed by the fox that consumed them: some records, perhaps particularly of larger birds, may derive from carrion, although this is unlikely to be a significant component for birds, with most carrion consumed by foxes reported to be of large mammals (Catling 1988, Forbes-Harper *et al.* 2017). Conversely, foxes do not always eat what they kill (Macdonald 1977), sometimes killing many individuals without then consuming them (Short *et al.* 2002). We also recognise that the traits we used in our modelling may not match the features that render birds more susceptible to fox predation, or the cues used by foxes in their hunting of birds, which may include vocalisations, odour or plumage conspicuousness (Mattingley 1918). For example, previous studies have shown significant variation in the palatability of bird species and their eggs (Cotts 1946), with mammal predators (including cats) showing a consequential preference for eating more palatable bird species (Cotts 1953). Furthermore, body mass is an elastic metric, and adult body mass (as used by us) may not well match the size of individual birds killed by foxes. This is especially so for very large birds, such as the emu *Dromaius novaehollandiae* (adults weighing ca. 35 kg), for which predation by foxes is plausible for chicks but not adults. Nonetheless, we note valid records of fox predation on adult birds of moderately large size, such as the black swan *Cygnus atratus* (ca. 6 kg) (Abbott 2011). Our modelling results indicate that the likelihood of fox predation increases monotonically with the adult body mass of a species, but we acknowledge that some tempering in interpretation of this relationship is warranted at the upper extreme of bird size.

The most significant caveat in our study is that records of consumption of any bird species by foxes do not necessarily imply impacts on the population viability or conservation status of that prey species. Many bird species consumed by foxes may be abundant and some have high rates of reproductive output, such that they can tolerate high predation pressure – however, many Australian bird species have characteristically low reproductive rates (Woinarski 1985, Yom-

Tov 1987), so may not be resilient to the impact imposed by a new predator, let alone two new predators.

Our study reports that fewer Australian bird species are known to be consumed by foxes than by cats, with this difference particularly pronounced for threatened birds. We also found that threatened birds had a significantly higher relative likelihood of cat predation than non-threatened birds; fox predation did not predict whether a bird was threatened. Nonetheless, in some cases fox predation may have a more significant impact on some Australian birds than that by cats. Evidence suggests this may be particularly the case for ground-nesting birds, with many records in Australia of intensive predation by foxes on eggs and chicks, causing significant reduction in reproductive success and hence population viability, including for threatened bird species (Frith 1959, Weston 2003, Bourne and Klomp 2004). Pronounced impacts of fox predation on ground-nesting birds have also been reported on other continents (e.g., Tobajas *et al.* 2020).

Conclusions and management implications

Foxes and cats now co-occur across most of Australia, and in most habitats. Our results show that these two introduced predators share consumption of many Australian birds, but also show some partitioning of the bird fauna, and that birds comprise a more important part of cat diet than of fox diet. The similarities and differences in the bird component of the diet of these two predator species probably reflect nuanced differences in hunting behaviours and physiology (Glen *et al.* 2011, Glen 2014).

Management programs that reduce the abundance of foxes have been used effectively for conservation purposes in Australia, especially for the protection of threatened mammals (Kinnear *et al.* 2010) and some birds (Kirkwood *et al.* 2014). Our results indicate that such programs are also likely to benefit many native bird species, and that, in the absence of such control, foxes will exert an ongoing predation toll on Australian birds, that compounds and complements the toll taken by cats.

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Conflict of Interest Statement

None.

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Ethical standards

This study collated information collected through many previous studies, and did not itself undertake any activities affecting animals.

Supplementary Materials

To view supplementary material for this article, please visit http://dx.doi.org/10.1017/S0959270921000460.

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