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Sharing meals: predation on Australian mammals by the introduced European red fox compounds and complements predation by feral cats

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Abstract

Two introduced carnivores, the European red fox *Vulpes vulpes* and domestic cat *Felis catus*, have had, and continue to have, major impacts on wildlife, particularly mammals, across Australia. Based mainly on the contents of almost 50 000 fox dietary samples, we provide the first comprehensive inventory of Australian mammal species known to be consumed by foxes, and compare this with a similar assessment for cats.

We recorded consumption by foxes of 114 species of Australian land mammal (40% of extant species), fewer than consumed by cats (173 species). Foxes are known to consume 42 threatened mammal species (50% of Australia's threatened land mammals and 66% of those within the fox's Australian range). Reflecting the importance of mammals in their diet, foxes are known to consume a far higher proportion of Australian mammal species (40%) than of Australian birds (24%) and reptiles (16%).

Both foxes and cats were most likely to consume medium-sized mammals, with the likelihood of predation by foxes peaking for mammals of ca. 280 g and by cats at ca. 130 g. For non-flying mammals, threatened species had a higher relative likelihood of predation by foxes than non-threatened species. Using trait-based modelling, we estimate that many now-extinct Australian mammal species had very high likelihoods of predation by foxes and cats, although we note that for some of these species, extinction likely pre-dated the arrival of foxes. These two predators continue to have compounding and complementary impacts on Australian mammals. Targeted and integrated management of foxes and cats is required to help maintain and recover the Australian mammal fauna.

Key words: bat, diet, extinction, invasive species, marsupial, rodent, threatened species

1. Introduction

Introduced predators have been a major cause of animal extinctions globally, with particularly pronounced impacts on island-endemic species (Doherty et al. 2016). Australia has two widespread introduced mammalian predators, the European red fox *Vulpes vulpes* (hereafter fox), successfully introduced to south-eastern Australia from about the 1870s (Fairfax 2019), and the domestic cat *Felis catus* (hereafter cat), introduced in 1788 (Abbott 2008). Both of these predators have had a severe toll on its native wildlife since European colonisation in 1788 (Woinarski et al. 2014). Australia's distinctive mammal fauna has especially suffered over this period with 34 endemic land mammals (more than 10% of ca. 320 native land mammal species) now rendered extinct (Woinarski et al. 2019b), and a further 66 recognised as threatened, and many more species continue to decline (Stobo-Wilson et al. 2019, Woinarski et al. 2001).

There is compelling evidence implicating the fox in much of this loss and decline of Australian mammals (Woinarski et al. 2014), including: (i) strong spatio-temporal correlation of the contraction and decline of many mammal species with the historical spread of the fox (Short 1998, Abbott et al. 2014, Abbott 2011, Seebeck et al. 1990); (ii) persistence of some mammal species only in parts of Australia where the fox is absent (monsoonal northern Australia, Tasmania and other islands: Fig. 1) (Abbott et al. 2014); (iii) increases in some mammal species in areas where fox abundance has been reduced (Robley et al. 2014, Claridge et al. 2010, Dexter & Murray 2009, Dexter et al. 2007, Kinnear et al. 2002); (iv) significantly reduced success of re-introductions of mammals to areas with foxes, compared to areas without (Moseby et al. 2011); (v) autecological studies demonstrating that predation by foxes can cause high rates of mortality in some mammal species (Augee et al. 1996, Russell et al. 2003); and (vi) the strong relationship of body size with decline of Australian mammal species (the 'critical weight range' (35-5500 g): Burbidge and McKenzie 1989), with losses most evident for medium-sized species presumed to be within the preferred prey range of foxes (and cats). Due particularly to its severe impact on Australian mammals, the fox is listed as a Key Threatening Process under Australian legislation and that of some states (Department of the Environment Water Heritage and the Arts 2008). Foxes have impacts on mammal fauna across their extensive global range, but the impact of the fox on Australian mammals may be exceptional on a global scale. In a review based on International Union for Conservation of Nature (IUCN) Red List assessments, Doherty et al. (2016) reported that fox predation was considered a threat to 27 of the world's threatened mammal species, and had contributed to the extinction of 10 mammal species: all of these are (or were) Australian endemic species.

Although there is now broad recognition of the impacts of foxes on Australian mammals, there has been no previous comprehensive inventory of the mammal species known to be consumed by foxes in Australia. However, the national Threat Abatement Plan for foxes (Department of the Environment Water Heritage and the Arts 2008) listed 48 threatened Australian mammal taxa (including subspecies, collectively of 40 species) as 'affected' by the fox (albeit based on conjecture in some cases), with this tally comprising 56% of the Australian land mammal taxa then listed as threatened. Here, we provide the first comprehensive collation of all Australian mammals that have been reported as consumed by foxes, and we investigate the morphological and/or ecological characteristics that may render some species more or less likely to be consumed by foxes.

We also compare and contrast our review with a recent analysis of the mammal component of the diet of cats in Australia, and the methodology we adopt is similar to that of the previous study (Woolley et al. 2019). This allows us to identify points of difference and overlap in the mammalian composition of the diet of these two introduced predators, for which mammals form the bulk of the diet (Henry 1986, Doherty et al. 2015). Our interest is partly in the extent of resource partitioning between these two predator species, but more so to consider whether the impacts of fox predation compound (i.e., target the same group of prey species) or complement (affect different sets of species) the impacts of cat predation. This study also parallels comparable reviews of predation by foxes on Australian bird (Woinarski et al. in review) and reptile species (Stobo-Wilson et al. in press).

The objectives of our study are: (1) to tally the number (and proportion) of mammal species known to be consumed by an introduced predator (the fox) across a near-continental range; (2) to compare this tally, and the overlap in species complement, with that of another co-occurring introduced predator, the cat; and (3) to evaluate whether the relative likelihood of predation by foxes and by cats on native mammals is associated with morphological or ecological characteristics. We also (4) assess the number (and proportion) of threatened mammals known to be consumed by these two predators and whether mammal species known to be consumed by foxes are more likely to be undergoing population decline than those species not known to be consumed by foxes, and (5) use our trait-based modelling to retrospectively assess the relative likelihood of predation by foxes and by cats on the now extinct Australian mammal species. Such information can help evaluate the magnitude of the problem posed by introduced predators and help guide the direction of conservation management response (e.g., to where it may be more important to effectively control foxes than cats, and for which native mammal species predator control is most critical).

2. Methods

2.1. Australian mammal species consumed by foxes

We derived a list of Australian land mammal species from the comprehensive taxonomic review by Jackson and Groves (2015), and updated this following some recent taxonomic changes (see Supplementary material, Table S1). We included extinct, marine and introduced mammal species in the compilation but, unless otherwise stated, excluded them from analyses because our focus related to the conservation of extant native land mammals and all fox dietary studies in our collation post-dated Australian mammal extinctions within the fox's range (Woinarski et al. 2019b).

We noted the conservation status of every mammal species, as of October 2020, at the global level (as assessed by the IUCN: https://www.iucnredlist.org/) and national level (as recognised by the Australian Government's *Environment Protection and Biodiversity Conservation Act, 1999*: EPBC Act). We considered a species as threatened if it was listed as Vulnerable, Endangered or Critically Endangered at national or global levels. In some cases, mammal subspecies are listed as threatened under Australian legislation (39 subspecies of 24 species); however, we report only on predation at the species level because most fox predation records identified prey to species rather than subspecies. Hence, if a subspecies was listed as threatened, we nominally treat the species as threatened.

In some reporting and analysis of our results, we consider bats and all other (i.e., non-flying) mammals separately, because declines and extinctions of Australian mammals have been far less pronounced for bats than other mammal groups (Woinarski et al. 2014), and it is reasonable to assume that foxes will be less likely to hunt and kill bats than non-flying mammals, as is the case for cats (Woolley et al. 2019).

Many of the records we collated derived from 85 studies of the diet of foxes, many with multiple study sites and collectively widely spread across the fox's Australian range (Fig. 1). These studies were identified from systematic literature searches (using Web of Science and Scopus databases, with relevant search terms: for more detail see Fleming *et al*. in press) and through informal contacts with relevant practitioners, and included published and unpublished studies (Supplementary material, Table S2). Collectively these studies reported on the prey contents of 41 377 fox scats and 7 031 stomachs. Since the landmark study of Coman (1973), identification of mammal hair in predator scats or stomachs has been widely practised in Australia. As with the comparable recent assessment of Australian mammals consumed by cats (Woolley et al. 2019), in addition to fox dietary studies, we also searched the literature of autecological studies of Australian mammals, in which sources of mortality were determined, and extracted records where predation was reported to be by foxes.

2.2. Scavenging or predation

One caveat in this compilation is that some of the records from studies of fox faeces or stomachs may have arisen through consumption of carrion by foxes rather than as a result of foxes killing the prey, with foxes widely recognised as scavengers of carrion (Sutherland et al. 2011, Read & Wilson 2004). In most of the dietary studies we collated, the authors did not state whether a dietary item was taken as carrion or not. However, given that there are definitive records of fox predation on young-at-foot of one of the largest Australian mammal species, the eastern grey kangaroo *Macropus giganteus* (average adult mass ca. 40 kg) (Banks et al. 2000), evidence that fox control can lead to increased abundance of this species (Banks et al. 2000) and evidence of foxes chasing adult kangaroos (Meek & Wishart 2017), we make the assumption that at least some of the observed consumption of large Australian mammal species by foxes is attributable to predation (especially of subadults). Conversely, there are also records of foxes killing mammals but then not consuming them (Short et al. 2002). This makes for some terminological nuance, but we generally refer to 'fox-consumed' animals in this paper, with the implication, unless otherwise stated, that this consumption aligns with predation.

2.3. Comparison with cats

Woolley et al. (2019) provided a comprehensive assessment of predation by cats on the Australian mammal fauna, and our aim is not to revisit that assessment, but rather to contextualise predation of Australian mammals by foxes with that by cats. There are several issues that influence this comparison, and hence merit some minor re-consideration of the treatment, tallies and analyses given in Woolley et al. (2019). First, there have been some recent taxonomic changes in the Australian mammal fauna (e.g., Cremona et al. 2020), and these are included here. Second, in our analyses of fox diet (see below), we use a different (and updated) offset term for the number of records for mammal species, and to best match the fox analysis, we also now use that offset term for cat analyses. Third, cats occur across the entire Australian mainland, Tasmania and about 100 islands whereas – although extensive – the fox's Australian range is a subset of that of the cat (Fig. 1). In response, we tally the numbers of mammal species consumed by cats both across their entire range, and also considering only the subset of mammals that occur within the fox's range, with the latter analysis providing a comparative assessment of the diet of the two predators in areas of their co-occurrence. Fourth, some records of cat predation on Australian mammals derive from pet cats, a component of the cat population that has no fox equivalent. We note that Woolley et al. (2019) undertook analyses of traits of non-flying mammal species consumed by cats, with models including and excluding records from pet cats, and found no notable difference in model outcomes. We also assume that if a mammal species is susceptible to predation by a pet cat it is also susceptible to predation by a feral cat, and we recognise that the toll taken by pet cats is part of the overall predation burden imposed by this introduced species on Australian mammals. Hence, we include (and explicitly note, where relevant) predation records from pet cats in our comparisons with consumption of mammals by foxes. Fifth, whereas there are definitive records of foxes killing (and regulating the abundance of) the largest Australian land mammal species (see section 2.2), the largest Australian mammal species known to be killed by cats are ca. 4 kg (Fancourt 2015, Fleming et al. 2020). However, some mammal species larger than this have been reported in cat dietary samples, with at least some of this consumption likely to be from carrion. In the analysis (below) comparing fox diet with cat diet, we take two approaches to this issue: (i) we consider mammal species larger than 4 kg that have been reported as cat-eaten to be consumed as carrion (i.e., reflecting lack of evidence that cats kill larger mammal species); and (ii) all mammal species reported as consumed by cats were considered to be killed by the cat (i.e., as for our treatment of foxes).

2.4. Analysis

We classified every mammal species to four predation classes: those known to be eaten by foxes but not cats (FX); by both foxes and cats (FC); by cats but not foxes (XC); and those not known to be eaten by either predator (XX). We used a likelihood ratio test to assess whether there was a significant difference in the frequency distribution of species between these groups. We used analysis of variance (ANOVA) to test whether there was a difference in abundance or distribution (the number of Atlas of Living Australia (ALA) records; see Supplementary material, Table S3), and sampling effort (the number of fox (or cat) dietary studies within the species' distributional range) between these four predation classes. This analysis assessed, in part, whether the absence of records of a mammal species being reported as consumed by a fox (or cat) likely reflects a sampling bias.

To examine whether predation was associated with morphological or ecological characteristics of mammal species, we undertook separate analyses for non-flying mammals and for bats. Using generalised linear models (GLMs), with the binomial error family, we modelled whether a species was recorded as consumed by a fox (yes/no) or cat (yes/no) against all possible combinations of species' traits. The traits used here were chosen to align with those used in previous analysis of the mammal species eaten by cats (Woolley et al. 2019), and in turn because they have previously been considered as factors that may have influenced the extent of mammal decline in Australia (e.g., McKenzie et al. 2007, Burbidge et al. 2008). For non-flying mammals, the predictor variables included in the model selection process related to adult body mass, diel activity (diurnal or nocturnal), aquatic habitat use (yes/no), saxicoline habitat use (yes/no), den type (arboreal, hollow logs, ground, shallow burrow/scrape, deep burrow/soil crevices or caves/rock crevices), diet (herbivore, omnivore or carnivore) and mean rainfall within the extant distribution of the species (see Table S3 for further descriptions of traits). We initially considered but ultimately excluded an arboreal trait, as preliminary analysis highlighted the trait was strongly correlated with both den type and mean rainfall. Traits were scored using information in Van Dyck and Strahan (2008) and Woinarski et al. (2014). We recognise that other traits, such as odour, coloniality or aggressiveness, may also influence the likelihood of a fox or cat consuming a mammal species, but we considered that attributing such traits to be too subjective.

Recognising that phylogeny may often be an important determinant of species' behavioural and ecological characteristics (Fritz & Purvis 2010), we trialled including a random intercept for family and genus to account for an influence of phylogeny on whether a species was consumed or not. To evaluate the need for this random intercept we compared the Akaike Information Criterion corrected for small sample size (AICc; Burnham and Anderson 2002) value of our most complex model (including all traits) fitted as a generalised linear mixed model (GLMM), against the AICc value of the most complex model fitted as a generalised linear model (GLM) without a random effect. The GLM models that did not include a random effect were the most strongly supported models for both the fox and cat dataset (ΔAICc >4), therefore we did not include a random effect in any further models and exclusively used GLMs.

To account for potential sampling bias, we included the number of ALA records for each extant mammal species (either the total number of records or the number within only the distributional range of the fox) and the number of fox or cat dietary studies within each species' distributional range as 'offset' terms, which were stipulated *a priori* for inclusion in all candidate models. We note that the number of ALA records is an imperfect surrogate (with some potential biases: Table S3) of the abundance or distribution of Australian mammal species, but note also that more direct measures (e.g., estimates of total population size) are unavailable for most species. All analyses were conducted in the computer program R (R Core Team 2017). Prior to modelling, we followed the protocol for data exploration provided by Zuur et al. (2010). Continuous explanatory variables were centred and standardised by deducting the mean and dividing by twice the standard deviation (Gelman 2008). We $\log_{10}$-transformed body mass, mean annual rainfall and the number of ALA records, and allowed the effect of body mass to be 'hump-shaped' by adding a quadratic term, stipulating its inclusion in a model only with the linear term (i.e., body mass^2 + body mass). As our collation identified records of fox predation on all of the aquatic mammals within the range of the fox (5 species), we excluded this trait from the fox-eaten analyses. To identify the traits of mammal species that are cat-eaten, models were run both including and excluding species with body mass >4 kg known to be consumed by cats but for which there were no definitive predation records (following Woolley et al. 2019).

Following the analytical pathway used for cat predation (Woolley *et al*. 2019), for bats (77 extant species) the only traits included were body mass and whether or not the species was known to roost in caves (Table S3), on the basis that cave-roosting species may be more readily captured by foxes

(Dwyer 1964) (and by cats) than species that roost in tree hollows or canopies. We similarly incorporated the number of ALA records and number of cat or fox dietary studies within each species' distributional range as offset terms in all candidate models.

To consider model uncertainty, we took a model-averaging approach which incorporated predictions of multiple candidate models weighted according to AICc. We examined several competing models simultaneously to identify the top set of models (95% confidence model set; see supplementary material Table S5 and Table S6), and these models were averaged to obtain parameter estimates (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 (RVI) ≥0.73 (equivalent to an AIC_c 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 identify the most influential traits and visualise variable effects.

We used parameter estimates averaged from the top set of fox- and cat-eaten models (Table S5 and Table S6, respectively, to predict the relative likelihood of predation for each non-flying mammal species by each predator. Note that this relative likelihood estimate controls for both the abundance or distribution of the species (number of ALA records) and the number of predator diet studies within each species' distributional range, so does not indicate the frequency of species in fox (or cat) dietary samples.

2.5. Extinct, threatened and declining mammal species

We tallied the number of threatened mammal species known to be consumed by foxes and/or by cats. To assess whether predation has an association with the current population trends of mammal species, we calculated the proportion of species with 'decreasing', 'stable', 'unknown' or 'increasing' population trends, as given in the most recent IUCN conservation status assessments (https://www.iucnredlist.org/), for each of the predation classes FX, FC, XC and XX, and tested for variation in trend categories between these predation classes using χ^2 test. For this assessment, we omitted species with 'unknown' trends and those that did not have Red List assessments, and we pooled the small number of species (<5) attributed an 'increasing' trend with those with a 'stable' trend.

From the trait-based models described above for non-flying mammals, we predicted the retrospective relative likelihood of predation (by foxes and cats) for now extinct mammal species. For this assessment we used the former range of the now extinct species to determine whether a species occurred within the distributional range of the fox (i.e., we excluded a small set of extinct species whose Australian range was restricted to areas beyond the current distribution of the fox). Note that the timing of extinction of some Australian mammal species may have pre-dated the arrival of the fox within the species' range. To identify such species, we matched the likely extinction date given in Woinarski et al. (2019) for every extinct Australian mammal species to the historical spread of the fox given in Fairfax (2019). We used binomial GLMs to explore whether threatened and extinct non-flying mammal species had a greater predicted likelihood of predation by the fox (species outside the fox's range were given a 0 risk of predation by the fox) and/or cat compared to species that are not threatened. As there were only two predictor variables in this instance (likelihood of cat predation and likelihood of fox predation) we ranked candidate models using AIC_c. The model with the lowest AIC_c by ≥2 AIC units was identified as the best model.

3. Results

3.1. Native terrestrial mammal species consumed

We collated records of consumption by foxes of 114 (108 non-flying, 6 bat) native land mammal species in Australia (Table S1). This represents 40% of the 289 extant Australian land mammal species (49% of non-flying species and 8% of bats), and 55% of the 206 native land mammal species within the distributional range of the fox (see Supplementary material, Table S4). The fox-consumed species included representatives of 18 of the 20 families of non-flying mammals, with the only exceptions being two families represented in Australia by single species beyond the range of the fox (Soricidae and Hypsiprymnodontidae).

The tally of fox-consumed species is fewer than the 173 native land mammal species (149 non-flying species, 24 bats) reported as consumed by cats (60% of the Australian native mammal fauna), although 25 of those mammal species consumed by cats occur only beyond the range of the fox. Eleven native land mammal species were recorded as consumed by foxes but not cats; and 72 species by cats but not foxes. The lower tally of mammal species reported to be consumed by foxes than by cats is notwithstanding an appreciably larger number of dietary samples in our collation for foxes (48 408) than for cats (12 279) (Woolley et al. 2019); however, we note that predator dietary studies formed only part of our record compilation. For cat tallies, records that derived only from pet cats added only a small proportion of non-flying mammal species (eight of the 149 species reported as cat-consumed), but a majority of the bat species (15 of 24 species).

In total, 101 native land mammal species are known to be consumed by both cats and foxes, and 105 species (within the distributional range of the fox) by neither predator (Fig. 2). The proportional tallies in the predator classes FC, FX, XC and XX were significantly non-random ($\chi^2_{3,\ n=289}$ = 104.3, $p<0.001$), with greater than expected numbers of FC and XX species, relative to species reported as consumed by one predator only (FX= 11 species; XC= 72 species). Mammal species that were not reported as consumed by either predator had significantly fewer ALA records (mean 850 ALA records; ANOVA: $F_{3,\ 285}$ =7.01, p <0.001), and fewer predator diet studies within their distributional range (mean 31 studies; ANOVA: $F_{3,\ 285}$ =25.8, p <0.001) relative to mammals that were only consumed by foxes (mean 4 218 ALA records; 73 diet studies), only consumed by cats (mean 2 943 ALA records; 52 diet studies), and consumed by both predators (mean 16 498 ALA records; 94 diet studies). This strong influence of sampling effort and species' abundance or distributional range on whether or not there were predation records justified the inclusion of the number of ALA records and of predator diet studies for each mammal species as offset terms in the GLMs.

3.2. Traits associated with fox and cat consumption of mammal species

Body mass was the best predictor of a mammal species being recorded as fox-eaten (body mass^2 RVI: 0.86; see Supplementary material, Table S5). Model averaging showed that medium-sized mammals (peaking at ca. 280 g) had the highest likelihood of being recorded as fox-eaten (Fig. 3a). Notwithstanding this relationship, we found consumption by foxes from the smallest non-flying mammal (long-tailed planigale *Planigale ingrami*, mass 4 g), to the largest (red kangaroo *Osphranter rufus*, average adult mass ca. 40 kg). Other than mass, no other traits that we considered (e.g., diet, habitat use) were significantly associated with variation among species in fox consumption (RVI <0.73; Table S5).

Body mass and mean rainfall were the best predictors of a mammal being recorded as cat-eaten (body mass^2 RVI: 1.00; rainfall RVI: 0.90; see Supplementary material, Table S6). Cats were also more likely to consume medium-sized mammals, but with a slightly narrower preference for smaller body size (peaking at ca. 136 g; Fig. 3a; see Supplementary material, Fig. S1a). Additionally, cats were more likely to consume mammals that occur in areas of lower rainfall (Fig. 3b; Fig. S1b). When considering only those mammal species that occur within the distributional range of the fox, body mass was the only significant predictor of mammal consumption by cats (Fig. 3a). For models that included all of those mammal species >4 kg, for which there were records of cat consumption, as cat-killed, and only those mammal species that occur within the distributional range of foxes, no traits significantly predicted mammal species that were more likely to be killed by cats (all models within 2 AIC of null model). In the variant of this model that considered mammals across the cat's entire range, only rainfall had a clear effect (RVI ≥0.73), with mammal species occurring in lower rainfall areas more likely to be cat-consumed. Henceforth, and following Woolley et al. (2019), we only report the results from models that did not consider species >4 kg as cat-killed.

Based on model predictions derived from the considered traits, the Australian non-flying mammal species with highest relative likelihood of being consumed by foxes are the itjaritjari *Notoryctes typhlops*, kakarratul *Notoryctes caurinus* and platypus *Ornithorhynchus anatinus* (Table 1). However, we note that these three species have behavioural features that may constrain predation by foxes, with the platypus mostly living in water and the two *Notoryctes* species mostly underground. Of the 20 non-flying mammal species with the highest likelihood of being consumed by foxes, all have been recorded as fox-eaten and seven are considered threatened. The non-flying mammal species that have highest relative likelihood of being consumed by cats are the crest-tailed mulgara *Dasycercus cristicauda,* kowari *Dasyuroides byrnei,* and plains mouse *Pseudomys australis*. Of the 20 non-flying mammals with the highest relative likelihood of being eaten by cats, 17 species have been recorded as cat-eaten and 11 are considered threatened (Table S1). Five non-flying mammals were identified in the 20 species with highest relative likelihood of being consumed by foxes and cats (itjaritjari, kakarratul, kowari, crest-tailed mulgara and brush-tailed mulgara *Dasycercus blythi*).

There were far fewer bat species recorded as consumed by foxes (six species) relative to cats (24 species; Fig. 2). Larger bat species were more likely to be consumed by foxes (Fig. 3d; Table S7). In contrast, we found no significant predictor for bat species most likely to be consumed by cats.

3.3. Extinct, threatened and declining mammal species

The non-flying mammals consumed by foxes include 40 threatened species (57% of the 70 non-flying threatened land mammals in Australia, and 73% of the threatened non-flying mammals within the fox's range; Table S3), fewer than the 48 threatened non-flying mammal species reported as consumed by cats (69% of the threatened non-flying mammals). Thirty-five threatened non-flying mammal species have been reported to be consumed by both predators, and 53 species (76% of all threatened non-flying mammals) by at least one of these two predators. There are records of five threatened non-flying species consumed by foxes but not cats (water mouse *Xeromys myoides*, yellow-bellied glider *Petaurus australis*, long-footed potoroo *Potorous longipes*, dusky hopping-mouse *Notomys fuscus* and New Holland mouse *Pseudomys novaehollandiae*), and 13 threatened non-flying species consumed by cats but not foxes (Table S1). The proportion of threatened bat species known to be consumed by cats and foxes was much lower than for non-flying mammals: of the 14 threatened bat species, two were reported as consumed by both foxes and cats, three by cats alone, and nine by neither species (Table S1).

Of 125 land mammal species for which population trends are given in Red List assessments, almost half (62) are considered to be decreasing, and only three are considered to be increasing. We found no significant association between predation class (i.e., FC, FX, XC and XX) and population trend class for Australian mammals (χ^2_3 =4.1, p>0.05; Fig. 2).

There were records of predation by foxes on two now-extinct Australian mammal species (eastern hare-wallaby *Lagorchestes leporides* and crescent nail-tailed wallaby *Onychogalea lunata*: Table S1), however there is compelling historical inference that foxes also killed many other now extinct mammals (e.g., Short 1998, Short & Calaby 2001, Abbott et al. 2014). From our models linking fox- and cat-predation records with traits of extant non-flying mammal species, we predicted the relative (retrospective) likelihood of predation (by foxes and cats) for extinct mammal species (Table 2). The white-footed rabbit-rat *Conilurus albipes*, Carpentarian rabbit-rat *Conilurus capricornensis* and lesser bilby *Macrotis leucura* had the highest relative likelihood of fox predation, however we note that extinction of two of these species likely pre-dated the arrival of foxes within their range. The northern pig-footed bandicoot *Chaeropus yirratji*, Nullarbor barred bandicoot *Perameles papillon* and desert bandicoot *Perameles eremiana* had the highest relative likelihood of cat predation.

From predicted values, threatened non-flying mammal species (including extinct species) had a greater relative likelihood of predation by both foxes (mean relative likelihood ± standard error; 0.63 ± 0.03) and feral cats (0.69 ± 0.03) than non-threatened species (foxes: 0.49 ± 0.03; cats: 0.61 ± 0.02). Based on GLMS the relative likelihood of predation by foxes better predicted whether a species was threatened, than the relative likelihood of cat predation (AIC_C increased by 4.09).

4. Discussion

We have identified records of the introduced fox consuming 114 species of extant Australian land mammal. This represents 40% of Australia's land mammal fauna and 55% of those species occurring within the Australian range of the fox. The predation pressure imposed by the fox adds to that of the cat, with these two introduced predators now known, collectively, to consume 184 extant Australian mammal species. Most of the 105 extant species not yet reported to be consumed by foxes or cats (36% of the Australian land mammal fauna) are either bats (61 species), which have been relatively under-studied, or rare or range-restricted non-flying species, again which tend to be relatively under-studied. Hence, the tally of native mammal species known to be fox- or cat-consumed is likely to increase with more targeted dietary or autecological studies. We emphasise that our focus is on the complement of Australian native land mammal species consumed by foxes, and by cats; and we do not seek here to quantify population-level impacts of such predation, which would require much more detailed information on predator densities, prey density, the numbers of prey individuals taken, and the reproductive capacity of prey species. Furthermore, we acknowledge that although cats and foxes co-occur extensively across Australia, there may be nuanced but significant local interactions between these two species that influence their combined predation pressure (e.g., Marlow *et al*. 2015).

The proportional tallies of mammal species reported here as fox-consumed are appreciably higher than comparable proportions found in recent collations for other vertebrate groups: foxes are known to consume 11% of species in the Australian reptile fauna (16% of those species within the fox's range) (Stobo-Wilson et al. in press), and 18% of the Australian non-vagrant bird fauna (24% of species occurring within the fox's range) (Woinarski et al. in review). This higher proportional tally of Australian mammal species consumed by foxes probably reflects the higher proportion of mammals than other vertebrate groups in fox diet generally (Sutherland et al. 2011), including in Australia (Robley et al. 2014, Triggs et al. 1984). However, it may also be influenced in part by the widespread use of hair analysis in predator dietary studies in Australia, allowing for ready identification to species of most mammal prey in fox scats and stomachs, although not always reliably so (Lobert et al. 2001). No comparable techniques for identification of bird and reptile species in dietary samples have been or are currently widely used in predator studies in Australia or elsewhere. However, 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.

Foxes consume a diverse subset of Australia's non-flying land mammals, across the entire size range of that fauna, across all habitats within the distributional range of the fox, across almost all families, and including nocturnal and diurnal, arboreal and ground-dwelling species. The only mammal trait, of those we considered, that was significantly associated with the likelihood of fox predation was body mass, with medium-sized mammals most likely to be consumed. Cat predation was also significantly more likely for medium-sized mammals, albeit with the peak likelihood of predation at lower body mass than for foxes (130 g vs 280 g, respectively), although this prey size relationship for cats was not retained when larger mammal species were presumed to be killed, rather than scavenged, by cats. The tendency for foxes to overlap substantially with cats in the mammalian composition of their diet, but to consume slightly larger mammals than do cats, is consistent with results from a previous study that collated dietary information across a set of 14 Australian sites where the two predators co-occurred (Murphy et al. 2019). It is also consistent with recent comparable analyses of Australian birds and reptiles that showed a similar overlap in prey body mass, but preference of foxes for larger species than those taken by cats (Stobo-Wilson et al. in press, Woinarski et al. in review). The consistency of these results indicates some partitioning in diet between these two species across their extensive shared range, plausibly related to the slightly larger size of the fox (average adult male mass 6.5 kg, cf. cat 5.3 kg) (Van Dyck & Strahan 2008) some differences in their foraging behaviours (Henry 1986), and possibly also to differences in skull morphology and biting power (Woinarski et al. 2019a, Fleming et al. 2020). This preference by foxes for medium-sized mammal species may also be a reflection of foraging efficiency, with medium-sized species potentially providing more energy per unit effort of prey capture and handling than smaller and larger species (Carbone et al. 2007).

The pattern we have identified, that medium-sized Australian mammals have the highest likelihood of predation by cats and by foxes, does not demonstrate impact. However, it is consistent with many previous studies that have reported that medium-sized ('critical weight range': 35-5500 g) Australian mammals represent a disproportionately large share of Australian extinct and declining mammal species, with introduced predators considered to be a major factor in such decline (e.g., McKenzie et al. 2007, Burbidge & McKenzie 1989). Our finding that species with a high likelihood of predation by cats and, especially, foxes were also more likely to be threatened further indicates that this predation pressure represents a considerable conservation impact.

However, we found no relationship between the current population trends of mammal species and whether or not the species was known to be consumed by foxes, cats, or both. This result may seem counter-intuitive, however, we interpret it to be a consequence of the success of some recent predator control programs (primarily using predator exclosure-fencing and lethal baiting), which have led to the reintroduction or in situ recovery (i.e., stable or increasing population trends) of many threatened Australian mammal species known to be killed by cats and foxes and susceptible to population decline as a result of this predation (Legge et al. 2018, Kanowski et al. 2018, Moseby et al. 2018, Dexter & Murray 2009).

In contrast to such recent successes, many Australian mammals were rendered extinct before conservation efforts could save them. Our results provide novel inferential support for predation by cats and foxes as contributing factors for the extinction of many Australian native mammal species. From models derived from the traits associated with predation-risk for extant mammals, we predicted that many now-extinct mammal species would have had very high relative likelihood of predation. In some cases (e.g., white-footed rabbit-rat, lesser bilby) there was a very high likelihood of predation by both predators; for others, the likelihood of predation was much higher for one predator than the other (e.g., eastern hare-wallaby *Lagorchestes leporides* by the fox; desert bandicoot, lesser stick-nest rat *Leporillus apicalis* by the cat). However, we note that the extinction of many of the species listed in Table 2 likely pre-dated the spread of foxes (but not cats) to their former range.

We found relatively few records of consumption of bat species by foxes, and notably fewer than for consumption of bats by cats. This result is probably due to a combination of factors, including relatively fewer autecological studies of Australian bats compared to many non-flying mammal species, the morphological indistinctiveness of many Australian bat species that renders their specific identification challenging in carnivore dietary samples, bats being a relatively minor dietary item (especially for foxes) because they cannot readily be caught, and that a relatively high proportion (33%) of Australian bat species occur only in areas outside the fox's range. Furthermore, an unusually high proportion of our collated records of bat consumption by cats derived from instances of pet cats catching bats, with their owners then taking the relatively intact dead bat to museums for identification: of 24 Australian bat species reported as killed by cats, records of 15 were sourced solely from such pet cat kills (Woolley et al. 2019).

Across parts of their Australian range, foxes are subject to management programs that aim to reduce their impacts on livestock and on some threatened mammal species (Saunders et al. 1995, Department of the Environment Water Heritage and the Arts 2008, Dexter & Murray 2009, Marlow et al. 2015b). The demonstration here of the wide range of native Australian mammals that are consumed by foxes provides further evidence of the ongoing value of such programs, and indicates that expansion of such programs (e.g., eradication of fox populations on more of the Australian islands on which they occur (e.g., Rout *et al*. 2014), expansion of predator exclosures for translocated threatened mammal species, increased regional-scale intensive baiting programs to reduce fox density) is likely to provide benefit to many more Australian mammal species. Such programs should be integrated with management of other potentially interacting invasive species (including cats) (Doherty & Ritchie 2017).

Competing Interests Statement

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

Abbott, I. (2008) The spread of the cat, *Felis catus*, in Australia: re-examination of the current conceptual model with additional information. *Conservation Science Western Australia,* **7,** 1.

Abbott, I., D. Peacock & J. Short, (2014) The new guard: the arrival and impacts of cats and foxes. In: *Carnivores of Australia: past, present and future*: 69. A. S. Glen & C. R. Dickman (Eds.). CSIRO Publishing, Collingwood.

Abbott, I. J. (2011) The importation, release, establishment, spread, and early impact on prey animals of the red fox *Vulpes vulpes* in Victoria and adjoining parts of south-eastern Australia. *Australian Zoologist,* **35,** 463.

Augee, M. L., B. Smith & S. Rose (1996) Survival of wild and hand-reared ringtail possums (*Pseudocheirus peregrinus*) in bushland near Sydney. *Wildlife Research,* **23,** 99.

Banks, P. B., A. E. Newsome & C. R. Dickman (2000) Predation by red foxes limits recruitment in populations of eastern grey kangaroos. *Austral Ecology,* **25,** 283.

Barton, K. (2018) Package "MuMIn" Title Multi-Model Inference. *See https://cran. r-project. org/web/packages/MuMIn/MuMIn. pdf*.

Burbidge, A. A. & N. L. McKenzie (1989) Patterns in the modern decline of Western Australia's vertebrate fauna: causes and conservation implications. *Biological Conservation,* **50,** 143.

Burbidge, A. A., N. L. McKenzie, K. E. C. Brennan, J. C. Z. Woinarski, C. R. Dickman, A. Baynes, G. Gordon, P. W. Menkhorst & A. C. Robinson (2008) Conservation status and biogeography of Australia's terrestrial mammals. *Australian Journal of Zoology,* **56,** 411.

Burnham, K. P. & D. R. Anderson (2002) *Model selection and multimodel inference: a practical information-theoretic approach*. Berlin: Springer.

Carbone, C., A. Teacher & J. M. Rowcliffe (2007) The costs of carnivory. *PLoS biology,* **5,** e22.

Claridge, A. W., R. B. Cunningham, P. C. Catling & A. M. Reid (2010) Trends in the activity levels of forest- dwelling vertebrate fauna against a background of intensive baiting for foxes. *Forest Ecology and Management,* **260,** 822.

Coman, B. J. (1973) The diet of red foxes, *Vulpes vulpes* L., in Victoria. *Australian Journal of Zoology,* **21,** 391.

Cremona, T., A. M. Baker, S. J. B. Cooper, R. Montague-Drake, A. M. Stobo-Wilson & S. M. Carthew (2020) Integrative taxonomic investigation of *Petaurus breviceps* (Marsupialia: Petauridae) reveals three distinct species. *Zoological Journal of the Linnean Society*.

de Sousa, L. L., S. M. Silva & R. Xavier (2019) DNA metabarcoding in diet studies: Unveiling ecological aspects in aquatic and terrestrial ecosystems. **1,** 199.

Department of the Environment Water Heritage and the Arts, (2008) Threat abatement plan for predation by the European red fox. Department of the Environment, Water, Heritage and the Arts, Canberra.

Dexter, N., P. Meek, S. Moore, M. Hudson & H. Richardson (2007) Population responses of small and medium sized mammals to fox control at Jervis Bay, southeastern Australia. *Pacific Conservation Biology,* **13,** 285.

Dexter, N. & A. Murray (2009) The impact of fox control on the relative abundance of forest mammals in East Gippsland, Victoria. *Wildlife Research,* **36,** 252.

Doherty, T. S., R. A. Davis, E. J. B. Etten, D. Algar, N. Collier, C. R. Dickman, G. Edwards, P. Masters, R. Palmer & S. Robinson (2015) A continental-scale analysis of feral cat diet in Australia. *Journal of Biogeography,* **42,** 964.

Doherty, T. S., A. S. Glen, D. G. Nimmo, E. G. Ritchie & C. R. Dickman (2016) Invasive predators and global biodiversity loss. *Proceedings of the National Academy of Sciences,* **113,** 11261.

Doherty, T. S. & E. G. Ritchie (2017) Stop jumping the gun: a call for evidence-based invasive predator management. *Conservation Letters,* **10,** 15.

Dwyer, P. D. (1964) Fox predation on cave-bats. *Australian Journal of Science,* **26,** 397.

Fairfax, R. J. (2019) Dispersal of the introduced red fox (*Vulpes vulpes*) across Australia. *Biological Invasions,* **21,** 1259.

Fancourt, B. A. (2015) Making a killing: photographic evidence of predation of a Tasmanian pademelon (*Thylogale billardierii*) by a feral cat (*Felis catus*). *Australian Mammalogy,* **37,** 120.

Fleming, P., H. Crawford, A. Stobo-Wilson, S. Dundas, S. Dawson, J.-M. Stuart, J. O'Connor, J. Speed, M. Gentle, J. Riley, J. Turpin, E. Thompson, E. Ritchie, R. Palmer, T. Newsome, C. Dickman, G. Saunders & J. Woinarski (in press) The diet of the introduced red fox Vulpes vulpes in Australia: analysis of temporal and spatial patterns. *Mammal Review*.

Fleming, P. A., H. M. Crawford, C. H. Auckland & M. C. Calver (2020) Body size and bite force of stray and feral cats—are bigger or older cats taking the largest or more difficult-to-handle prey? *Animals,* **10,** 707.

Fritz, S. A. & A. Purvis (2010) Selectivity in mammalian extinction risk and threat types: a new measure of phylogenetic signal strength in binary traits. **24,** 1042.

Gelman, A. (2008) Scaling regression inputs by dividing by two standard deviations. *Statistical Methods,* **27,** 2865.

Henry, J. D. (1986) *Red Fox: the Catlike Canine*. Washington, DC: Smithsonian Institution Press.

Kanowski, J., D. Roshier, M. A. Smith & A. Fleming, (2018) Effective conservation of critical weight range mammals: reintroduction projects of the Australian Wildlife Conservancy. In: *Recovering Australian threatened species: a book of hope*: 269. S. Garnett, P. Latch, D. Lindenmayer & J. Woinarski (Eds.). CSIRO Publishing, Clayton.
Kinnear, J., N. R. Sumner & M. L. Onus (2002) The red fox in Australia—an exotic predator turned biocontrol agent. *Biological Conservation,* **108,** 335.
Legge, S. M., J. C. Z. Woinarski, A. A. Burbidge, A. Palmer, J. Ringma, J. Radford, N. Mitchell, M. Bode, B. Wintle, M. Baselar, J. Bentley, P. Copley, N. Dexter, C. R. Dickman, G. Gillespie, B. Hill, C. Johnson, P. Latch, M. Letnic, A. Manning, E. E. McCreless, P. Menkhorst, K. Morris, K. Moseby, M. Page, D. Pannell & K. Tuft (2018) Havens for threatened Australian mammals: the contributions of fenced areas and offshore islands to protecting mammal species that are susceptible to introduced predators. *Wildlife Research,* **45,** 627.
Lobert, B., L. Lumsden, H. Brunner & B. Triggs (2001) An assessment of the accuracy and reliability of hair identification of south-east Australian mammals. *Wildlife Research,* **28,** 637.
Marlow, N. J., N. D. Thomas, A. A. E. Williams, B. Macmahon, J. Lawson, Y. Hitchen, J. Angus & O. Berry (2015a) Cats (Felis catus) are more abundant and are the dominant predator of woylies (Bettongia penicillata) after sustained fox (Vulpes vulpes) control. *Australian Journal of Zoology,* **63,** 18.
Marlow, N. J., N. D. Thomas, A. A. E. Williams, B. Macmahon, J. Lawson, Y. Hitchen, J. Angus & O. Berry (2015b) Lethal 1080 baiting continues to reduce European Red Fox (*Vulpes vulpes*) abundance after more than 25 years of continuous use in south-west Western Australia. *Ecological Management & Restoration,* **16,** 131.
McKenzie, N. L., A. A. Burbidge, A. Baynes, R. N. Brereton, C. R. Dickman, G. Gordon, L. A. Gibson, P. W. Menkhorst, A. C. Robinson, M. R. Williams & J. C. Z. Woinarski (2007) Analysis of factors implicated in the recent decline of Australia's mammal fauna. *Journal of Biogeography,* **34,** 597.
Meek, P. D. & J. Wishart (2017) Camera trap evidence of red fox (*Vulpes vulpes*) predation attempts on adult macropods. *Pacific Conservation Biology,* **23,** 302.
Moseby, K., P. Copley, D. C. Paton & J. L. Read, (2018) Arid Recovery: a successful conservation partnership. In: *Recovering Australian threatened species: a book of hope*: 259. S. Garnett, P. Latch, D. Lindenmayer & J. Woinarski (Eds.). CSIRO Publishing, Clayton.
Moseby, K., J. Read, D. Paton, P. Copley, B. Hill & H. Crisp (2011) Predation determines the outcome of 10 reintroduction attempts in arid South Australia. *Biological Conservation,* **144,** 2863.
Murphy, B. P., L. A. Woolley, H. M. Geyle, S. M. Legge, R. Palmer, C. R. Dickman, J. Augusteyn, S. C. Brown, S. Comer, T. S. Doherty, C. Eager, G. Edwards, D. A. Fordham, D. Harley, P. J. McDonald, H. McGregor, K. Moseby, C. Myers, J. Read, J. Riley, D. Stokeld, G. J. Trewella, J. M. Turpin & J. C. Z. Woinarski (2019) Introduced cats (*Felis catus*) eating a continental mammal fauna: the number of individuals killed in Australia. *Biological Conservation,* **237,** 28.
R Core Team, (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
Read, J. L. & D. Wilson (2004) Scavengers and detritivores of kangaroo harvest offcuts in arid Australia. *Wildlife Research,* **31,** 51.
Richards, S. A. (2005) Testing ecological theory using the information-theoretic approach: examples and cautionary results. *Ecology,* **86,** 2805.
Robley, A., A. Gormley, D. Forsyth & B. Triggs (2014) Long-term and large-scale control of the introduced red fox increases native mammal occupancy in Australian forests. *Biological Conservation,* **180,** 262.
Rout, T. M., R. Kirkwood, D. R. Sutherland, S. Murphy & M. A. McCarthy (2014) When to declare successful eradication of an invasive predator? *Animal Conservation,* **17,** 125.

Russell, B. G., B. Smith & M. L. Augee (2003) Changes to a population of common ringtail possums (*Pseudocheirus peregrinus*) after bushfire. *Wildlife Research,* **30,** 389.

Saunders, G., B. Coman, J. Kinnear & M. Braysher (1995) *Managing vertebrate pests: foxes*. Canberra: Australian Government Publishing Service.

Seebeck, J. H., A. F. Bennett & A. C. Dufty, (1990) Status, distribution and biogeography of the eastern barred bandicoot, *Perameles gunnii*, in Victoria. In: *Management and conservation of small populations*: 21. T. W. Clark & J. H. Seebeck (Eds.). Chicago Zoological Society, Brookfield, Illinois.

Short, J. (1998) The extinction of rat-kangaroos (Marsupialia: Potoroidae) in New South Wales, Australia. *Biological Conservation,* **86,** 365.

Short, J. & J. H. Calaby (2001) The status of Australian mammals in 1922 - collections and field notes of museum collector Charles Hoy. *Australian Zoologist,* **31,** 533.

Short, J., J. E. Kinnear & A. Robley (2002) Surplus killing by introduced predators in Australia—evidence for ineffective anti-predator adaptations in native prey species? *Biological Conservation,* **103,** 283.

Stobo-Wilson, A., B. Murphy, S. Legge, H. Chapple, S. Dawson, C. Dickman, T. Doherty, P. Fleming, M. Gentle, T. Newsome, R. Palmer, M. Rees, E. Ritchie, J. Speed, J.-M. Stuart, E. Thompson, J. Turpin & J. Woinarski (in press) Reptiles as food: predation of Australian reptiles by introduced red foxes compounds and complements predation by cats. *Wildlife Research*.

Stobo-Wilson, A. M., B. P. Murphy, T. Cremona & S. M. Carthew (2019) Contrasting patterns of decline in two arboreal marsupials from Northern Australia. *Biodiversity and Conservation,* **28,** 2951.

Sutherland, D. R., A. S. Glen & J. Paul (2011) Could controlling mammalian carnivores lead to mesopredator release of carnivorous reptiles? *Proceedings of the Royal Society of London B: Biological Sciences,* **278,** 641.

Triggs, B., H. Brunner & J. M. Cullen (1984) The food of fox, dog and cat in Croajingalong National Park, south-eastern Victoria. *Australian Wildlife Research,* **11,** 491.

Van Dyck, S. & R. Strahan (2008) *The Mammals of Australia,* Third edn. Sydney: Reed New Holland.

Woinarski, J. C., S. M. Legge & C. R. Dickman (2019a) *Cats in Australia: companion and killer*. CSIRO Publishing.

Woinarski, J. C. Z., M. F. Braby, A. A. Burbidge, D. Coates, S. T. Garnett, R. J. Fensham, S. M. Legge, N. L. McKenzie, J. L. Silcock & B. P. Murphy (2019b) Reading the black book: the number, timing, distribution and causes of listed extinctions in Australia. *Biological Conservation,* **239,** 108261.

Woinarski, J. C. Z., A. A. Burbidge & P. L. Harrison (2014) *The Action Plan for Australian Mammals 2012*. Melbourne: CSIRO Publishing.

Woinarski, J. C. Z., D. J. Milne & G. Wanganeen (2001) Changes in mammal populations in relatively intact landscapes of Kakadu National Park, Northern Territory, Australia. *Austral Ecology,* **26,** 360.

Woolley, L.-A., H. M. Geyle, B. P. Murphy, S. M. Legge, R. Palmer, C. R. Dickman, J. Augusteyn, S. Comer, T. S. Doherty, C. Eager, G. Edwards, D. K. P. Harley, I. Leiper, P. J. McDonald, H. W. McGregor, K. E. Moseby, C. Myers, J. L. Read, J. Riley, D. Stokeld, J. M. Turpin & J. C. Z. Woinarski (2019) Introduced cats (*Felis catus*) eating a continental fauna: inventory and traits of Australian mammal species killed. *Mammal Review,* **49,** 354.

Zuur, A. F., E. N. Ieno & C. S. Elphick (2010) A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution,* **1,** 3.

Tables

Table 1. The 20 non-flying mammal species predicted to be most likely consumed by foxes, given each mammal species' unique suite of traits. For each mammal species, the likelihood of being eaten is predicted by generalised linear models considering only species that occur within the distributional range of foxes, holding abundance (number of ALA records) and research effort (number of diet studies) constant. Values provided are predicted estimates of the relative likelihood of being fox-eaten and 95% confidence intervals (95% CI). * indicates those species that were also identified within the 20 species with highest relative likelihood of predation by feral cats considering all mammal species (see Supplementary material Table S5 for equivalent list of mammal species with highest relative likelihood of predation by cats). Acronyms for predator categories: FC known to be consumed by foxes and by cats; FX known to be consumed by foxes but not cats; XC known to be consumed by cats but not foxes; XX not known to be consumed by either foxes or cats.

Rank	Common name	Scientific name	Relative likelihood of fox predation	95% CI	Predator category	Threatened
1	Itjaritjari*	*Notoryctes typhlops*	0.94	0.54–1.00	FC	No
2	Platypus	*Ornithorhynchus anatinus*	0.94	0.54–1.00	FC	No
3	Kakarratul*	*Notoryctes caurinus*	0.93	0.53–0.99	FC	No
4	Numbat	*Myrmecobius fasciatus*	0.92	0.48–0.99	FC	Yes
5	Squirrel glider	*Petaurus norfolcensis*	0.90	0.63–0.98	FC	No
6	Brush-tailed phascogale	*Phascogale tapoatafa*	0.89	0.63–0.98	FC	No
7	Koala	*Phascolarctos cinereus*	0.89	0.37–0.99	FC	Yes
8	Leadbeater's possum	*Gymnobelideus leadbeateri*	0.89	0.63–0.98	FC	Yes
9	Yellow-bellied glider	*Petaurus australis*	0.89	0.62–0.98	FX	Yes
10	Sugar glider	*Petaurus breviceps*	0.89	0.63–0.98	FC	No
11	Krefft's glider	*Petaurus notatus*	0.89	0.62–0.98	FC	No
12	Grassland melomys	*Melomys burtoni*	0.88	0.60–0.98	FC	No
13	Kowari*	*Dasyuroides byrnei*	0.88	0.59–0.98	FC	Yes
14	Crest-tailed mulgara*	*Dasycercus cristicauda*	0.88	0.59–0.98	FC	No
15	Water-rat, Rakali	*Hydromys chrysogaster*	0.88	0.60–0.97	FC	No
16	Boodie, Burrowing bettong	*Bettongia lesueur*	0.88	0.60–0.97	FC	Yes
17	Common ring-tailed possum	*Pseudocheirus peregrinus*	0.88	0.58–0.97	FC	No
18	Brush-tailed mulgara*	*Dasycercus blythi*	0.88	0.60–0.97	FC	No
19	Fawn-footed melomys*	*Melomys cervinipes*	0.88	0.58–0.97	FC	No
20	Western ring-tailed possum	*Pseudocheirus occidentalis*	0.87	0.58–0.97	FC	Yes

Table 2. Predicted (retrospective) estimates of the relative likelihood of predation by foxes and cats (considering only those species within the distribution of the fox and all species) for the 32 extinct non-flying Australian mammal species, given each mammal species' unique suite of traits. For each mammal species, the likelihood of being eaten is predicted by generalised linear models considering only species that occur within the distributional range of foxes (other than the model shown in the last column, which is for all species), holding abundance (number of ALA records) and research effort (number of diet studies) constant. 95% confidence intervals (95% CI). Bolded values indicate relative likelihood predation estimates within each group greater than or equal to that of the top 25% of extant species. * indicates species whose extinction likely pre-dated the arrival of foxes to its former range. For none of the species in this Table did extinction pre-date the arrival of cats.

Common name	Scientific name	Relative likelihood of fox predation (95% CI)	Relative likelihood of cat predation in fox range (95% CI)	Relative likelihood of cat predation (95% CI)
White-footed rabbit-rat *	*Conilurus albipes*	**0.89 (0.60-0.98)**	**0.98 (0.78-1.00)**	**0.90 (0.78-0.96)**
Carpentarian rabbit-rat *	*Conilurus capricornensis*	**0.89 (0.60-0.98)**	**0.98 (0.78-1.00)**	**0.89 (0.78-0.95)**
Yallara, Lesser bilby	*Macrotis leucura*	**0.89 (0.60-0.98)**	0.93 (0.70-0.99)	**0.92 (0.75-0.98)**
Short-tailed hopping-mouse *	*Notomys amplus*	**0.88 (0.57-0.97)**	0.93 (0.72-0.98)	**0.92 (0.79-0.97)**
Broad-cheeked hopping-mouse *	*Notomys robustus*	**0.88 (0.57-0.97)**	0.93 (0.72-0.98)	**0.92 (0.79-0.97)**
Long-tailed hopping-mouse *	*Notomys longicaudatus*	**0.87 (0.56-0.97)**	0.94 (0.73-0.99)	**0.94 (0.80-0.98)**
Long-eared mouse *	*Pseudomys auritus*	**0.86 (0.57-0.97)**	0.89 (0.63-0.97)	**0.88 (0.75-0.95)**
Darling Downs hopping-mouse *	*Notomys mordax*	**0.86 (0.56-0.97)**	0.85 (0.55-0.97)	**0.85 (0.70-0.93)**
Gould's mouse *	*Pseudomys gouldii*	**0.86 (0.56-0.97)**	0.87 (0.60-0.97)	**0.87 (0.73-0.94)**
Large-eared hopping-mouse *	*Notomys macrotis*	**0.85 (0.56-0.96)**	0.87 (0.59-0.97)	**0.87 (0.73-0.94)**
Blue-grey mouse *	*Pseudomys glaucus*	0.84 (0.54-0.96)	0.82 (0.51-0.95)	0.84 (0.69-0.93)
Lesser stick-nest rat	*Leporillus apicalis*	0.81 (0.60-0.92)	**0.96 (0.83-0.99)**	**0.94 (0.81-0.98)**
Broad-faced potoroo *	*Potorous platyops*	0.80 (0.64-0.91)	0.88 (0.70-0.96)	0.81 (0.64-0.91)
Nullarbor dwarf bettong *	*Bettongia pusilla*	0.80 (0.60-0.92)	0.94 (0.76-0.99)	**0.90 (0.71-0.97)**
Desert rat-kangaroo	*Caloprymnus campestris*	0.80 (0.57-0.92)	**0.95 (0.68-0.99)**	**0.93 (0.69-0.99)**
Desert bettong	*Bettongia anhydra*	0.79 (0.60-0.91)	0.92 (0.70-0.98)	**0.87 (0.66-0.96)**
Eastern hare-wallaby	*Lagorchestes leporides*	0.75 (0.58-0.87)	0.72 (0.47-0.88)	0.64 (0.44-0.80)
Liverpool plains striped bandicoot *	*Perameles fasciata*	0.74 (0.47-0.90)	**0.96 (0.83-0.99)**	**0.92 (0.78-0.98)**
Pig-footed bandicoot, Southern pig-footed bandicoot	*Chaeropus ecaudatus*	0.74 (0.46-0.90)	**0.96 (0.83-0.99)**	**0.94 (0.78-0.98)**
Yirratji, Northern Pig-footed bandicoot	*Chaeropus yirratji*	0.74 (0.46-0.90)	**0.97 (0.82-1.00)**	**0.95 (0.79-0.99)**
Desert bandicoot	*Perameles eremiana*	0.74 (0.46-0.90)	**0.97 (0.83-1.00)**	**0.95 (0.78-0.99)**
Marl *	*Perameles myosorus*	0.74 (0.46-0.90)	**0.96 (0.83-0.99)**	**0.93 (0.78-0.98)**

Nullarbor barred bandicoot	*Perameles papillon*	0.74 (0.46-0.90)	**0.97 (0.82-1.00)**	**0.95 (0.78-0.99)**
South-eastern striped bandicoot *	*Perameles notina*	0.73 (0.44-0.90)	**0.95 (0.77-0.99)**	**0.92 (0.71-0.98)**
Crescent nailtail wallaby	*Onychogalea lunata*	0.72 (0.44-0.90)	0.65 (0.21-0.93)	0.62 (0.29-0.86)
Kuluwarri, Central hare-wallaby	*Lagorchestes asomatus*	0.71 (0.42-0.90)	**0.95 (0.73-0.99)**	**0.92 (0.67-0.98)**
Toolache wallaby	*Notomacropus greyi*	0.65 (0.44-0.82)	0.26 (0.11-0.49)	0.25 (0.14-0.42)
Christmas Island shrew	*Crocidura trichura*	NA	NA	0.36 (0.09-0.76)
Bramble Cay melomys	*Melomys rubicola*	NA	NA	0.82 (0.66-0.92)
Maclear's rat	*Rattus macleari*	NA	NA	0.79 (0.64-0.89)
Bulldog rat	*Rattus nativitatis*	NA	NA	0.78 (0.58-0.90)
Thylacine	*Thylacinus cynocephalus*	NA	NA	0.02 (0.00-0.07)

Figures

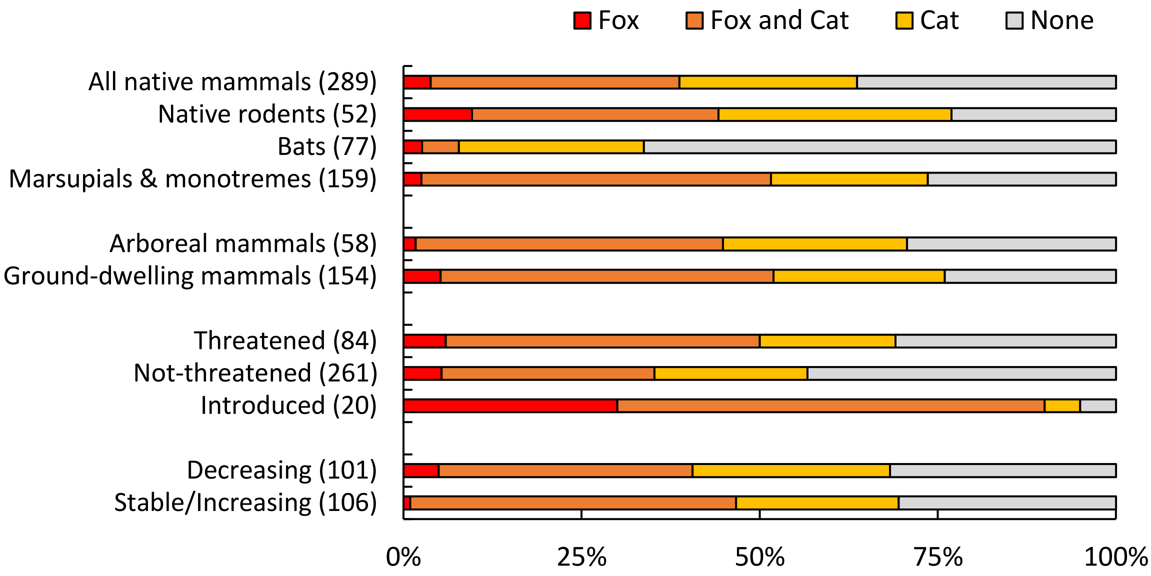
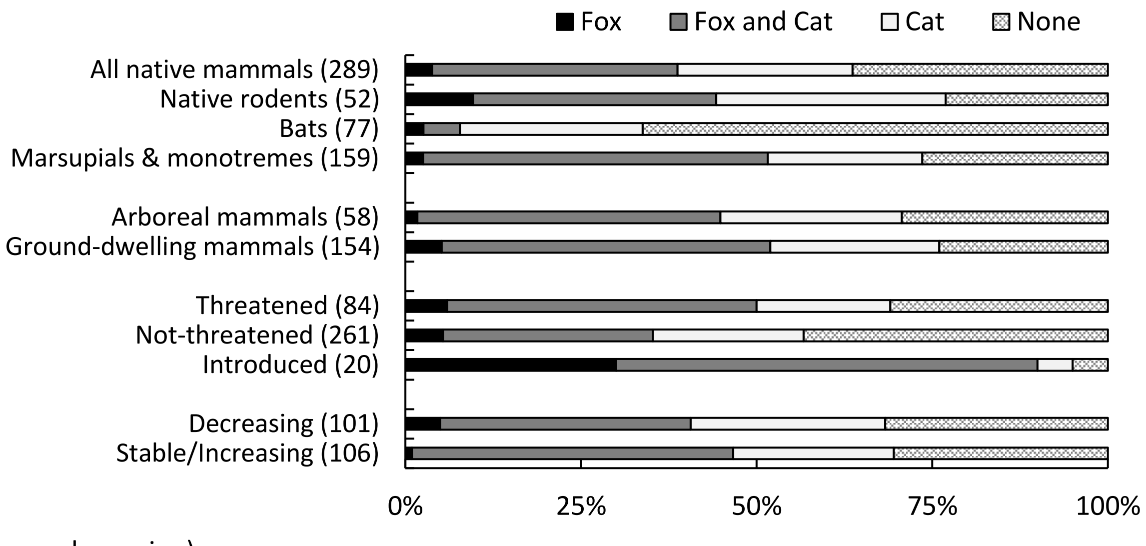


Figure 2. Breakdown of the proportion of extant Australian mammal species within the four predation classes shown for broad taxonomic groups and conservation status. Predator classes are: only fox-eaten (red); fox- and cat-eaten (orange), only cat-eaten (yellow) and not-eaten by either species (grey). The number of species within each category is presented in brackets.



(grey-scale version)

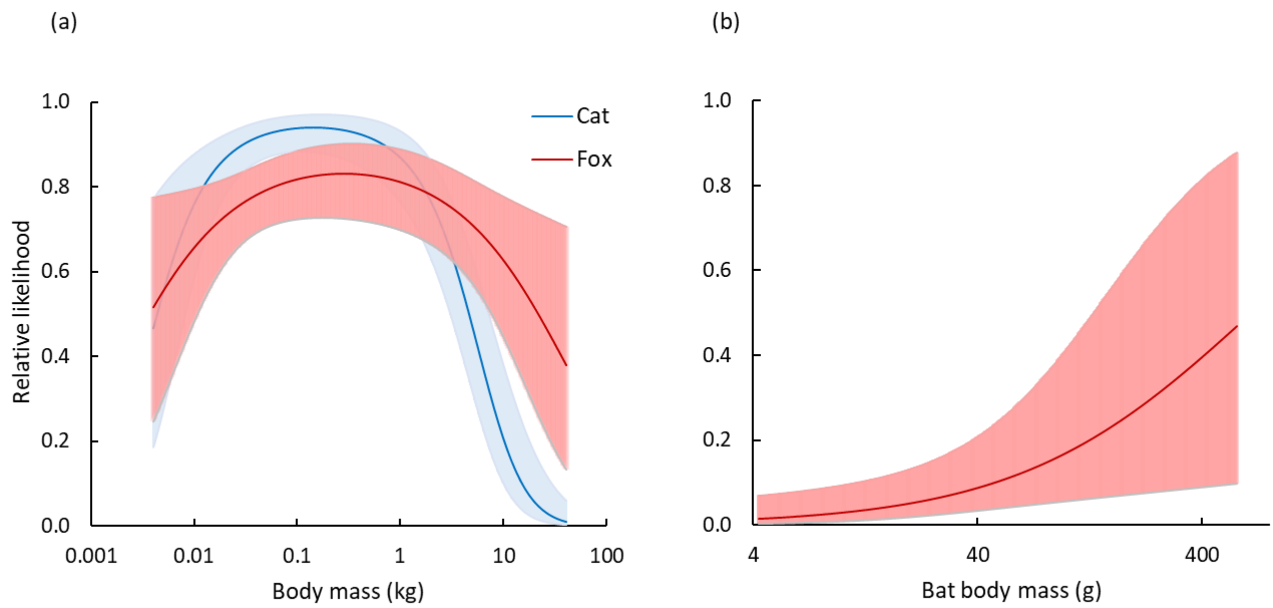


Figure 3. The relative likelihood of a non-flying mammal species being consumed by (a) a fox (red) or cat (blue) in relation to the species' body mass; and (b) the relative likelihood of a bat species being consumed by a fox in relation to the species' body mass. All relationships shown are based on models that *consider only mammals that occur within the range of the fox*. Values are derived from the optimal logistic regression model, offsetting for the number of ALA records recorded for each mammal species either within the distributional range of the fox or the total number of ALA records, and the number of fox or cat diet studies that have been undertaken within each mammal species' distributional range. Solid lines represent fits to the model's predicted values, shaded areas indicate 95% confidence intervals.

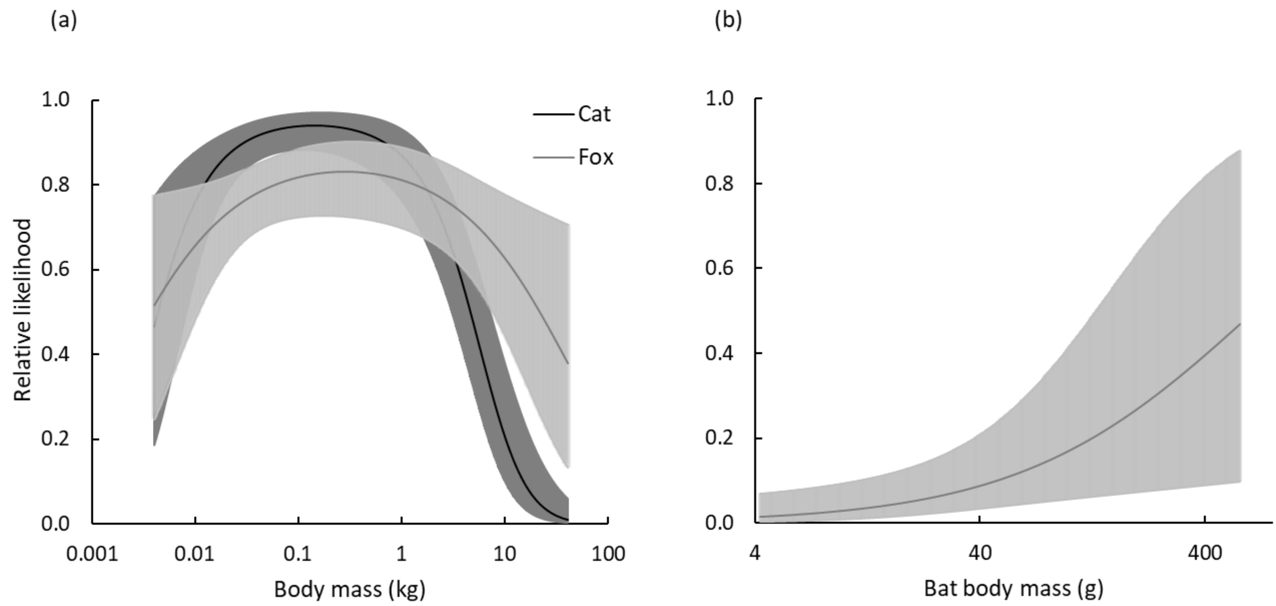


Figure 3 (grey-scale version). The relative likelihood of a non-flying mammal species being consumed by (a) a fox (light grey) or cat (dark grey) in relation to the species' body mass; and (b) the relative likelihood of a bat species being consumed by a fox in relation to the species' body mass. All relationships shown are based on models that *consider only mammals that occur within the range of the fox*. Values are derived from the optimal logistic regression model, offsetting for the number of

ALA records recorded for each mammal species either within the distributional range of the fox or the total number of ALA records, and the number of fox or cat diet studies that have been undertaken within each mammal species' distributional range. Solid lines represent fits to the model's predicted values, shaded areas indicate 95% confidence intervals.

Supplementary Material

Table S1. List of Australian mammal species detailing whether each species occurred beyond the distributional range of the fox, whether the species has been reported as cat- and/or fox-eaten, the source/s for such records, the current IUCN listing for each species (as of September 2020), and the categorisation of each species for each of the ecological traits used for modelling the probability of predation.

Table S2. Complete list of sources used to provide records of mammal species in fox diet.

Table S3. Mammal traits used as explanatory variables in the modelling; non-flying mammal models included all variables except 'cave roost'; bat models included only 'body mass' and 'cave roost'. Mean and range is shown for continuous variables; the most common category is shown for categorical variables.

Table S4. Tallies of extant Australian land mammal species reported as consumed by foxes and cats.

Table S5. Best candidate models (95% confidence model set) used to test the effects of predictor variables on records of fox predation considering only those non-flying mammals that occur within the distributional range of the fox. ΔAIC_C is a measure of change in the Akaike Information Criterion with correction for small sample size; Akaike w_i is the probability of model *i* is the best model. All models include the offset terms for the number of ALA records for each mammal species (records were limited to the distributional range of foxes), and the number of fox diet studies that have occurred within the distributional range of each species. For definitions of variables see Table 1.

Table S6. Best candidate models (95% confidence model set) used to test the effects of predictor variables on records of cat predation considering (a) only those non-flying mammals that occur within the distributional range of the fox and (b) all species. ΔAIC_C is a measure of change in the Akaike Information Criterion with correction for small sample size; Akaike w_i is the probability of model *i* is the best model. All models include the offset terms for the number of ALA records for each mammal species and the number of cat-diet studies that have occurred within the distributional range of each species. For definitions of variables see Table 1.

Table S7. Complete candidate model set used to test the effects of predictor variables on records of (a) fox predation and (b) cat predation considering only Australian bat species that occur within the distributional range of the fox, and (c) cat predation including all extant bat species. ΔAIC_C is a measure of change in the Akaike Information Criterion with correction for small sample size; Akaike w_i is the probability of model *i* is the best model. All models include the offset terms for the number of ALA records for each mammal species (records were limited to the distributional range of foxes for fox-eaten models), and the number of fox- or cat-diet studies that have occurred within the distributional range of each species. The grey highlighted model is the null hypothesis model and bold text indicates the most supported models (ΔAIC ≤ 2). For definitions of variables see Table 1.

Table S8. The 20 non-flying mammal species predicted to be most likely to be consumed by feral cats considering (a) only those species that occur within the distributional range of the fox, and (b) all species, given each mammal species' unique suite of traits. For each mammal species, the relative likelihood of being eaten is predicted by generalised linear models, holding abundance (number of ALA records) and research effort (number of diet studies) constant. Values provided are predicted estimates of the relative likelihood of being cat-eaten and 95% confidence intervals (95% CI).

Figure S1. The relative likelihood of a mammal species being consumed by cats in relation to the species' (a) body mass, and (b) mean annual rainfall across the species' extant range, for all non-flying mammal species. Relationships shown are based on models that *include those species that occur outside the range of the fox*. Values are derived from the optimal logistic regression model, to model the respective relationships all other continuous variables were held at fixed median levels, offsetting for the total number of ALA records, and the number of cat diet studies that have been undertaken within each mammal species distributional range. Solid lines represent fits to the model's predicted values, shaded areas indicate 95% confidence intervals.