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Abstract

1. Mammals comprise the bulk of the diet of free-roaming domestic cats (*Felis catus*) in most parts of their global range. In Australia, predation by feral cats has been implicated in the extinction of many mammal species, and in the ongoing decline of many extant species.
2. Here, we collate a wide range of records of cat predation on Australian mammals and model species' traits associated with the relative likelihood of cat predation. We explicitly seek to overcome biases in such a continental scale compilation by excluding possible carrion records for larger species and accounting for differences in the distribution and abundance of potential prey species, as well as study effort across a species' range.
3. For non-volant species, the relative likelihood of predation by feral cats was greatest for species in an intermediate weight range (peaking at ca. 400 g), in lower rainfall areas and not dwelling in rocky habitats. Previous studies have shown the greatest rates of decline and extinction in Australian mammals to be associated with these traits. As such, we provide the first continental-scale link between mammal decline and cat predation through quantitative analysis.
4. Our compilation of cat (including feral and pet cats) predation records for most extant native terrestrial mammal species (151 species, or 52% of the Australian species' complement) is substantially greater than previously reported (88 species) and includes 50 species listed as threatened by the IUCN or under Australian legislation (57% of Australia's 87 threatened terrestrial mammal species). We identify the Australian mammal species most likely to be threatened by cat predation and hence most likely to benefit from enhanced mitigation of cat impacts.

Keywords: conservation, critical weight range, diet, feral cats, invasive predator

Running head: Australian mammals killed by cats

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Introduction

Introduced species often disrupt and challenge the conservation of biodiversity where they invade (Simberloff et al. 2013). Many species associated with humans have spread widely across the world, and some of these species constitute major threats to biodiversity in many locations where they have been introduced (Gurevitch & Padilla 2004). Where introduced, free-ranging domestic cats (*Felis catus*) have had a substantial impact on wildlife (Pimentel et al. 2005; Loss et al. 2013; Doherty et al. 2016), particularly on island-endemic vertebrates (Burbidge & Manly 2002; Medina et al. 2011; Woinarski et al. 2017a; Woinarski et al. 2017b), due at least in part to prey naiveté in the presence of an evolutionarily novel predator (Banks & Dickman 2007; McEvoy et al. 2008). The impact of cats on continental biodiversity is generally less well-established (Loss & Marra 2017). Many global studies have demonstrated that mammals comprise the dominant component of the diet of cats (Fitzgerald 1988; Bradshaw et al. 1996; Loss et al. 2013).

Since their introduction following European settlement of Australia in 1788, cats have spread pervasively and now occupy the entire continent and many islands including all islands larger than 400 km^2, except Dirk Hartog Island where cats were recently eradicated (Abbott et al. 2014; Legge et al. 2017). Relative to other continents, the impacts of cats on Australian wildlife are especially pronounced (Doherty et al. 2016; Woinarski et al. 2018), with cats having been implicated in the decline and extinction of many Australian species, particularly mammals (Johnson 2006; Woinarski et al. 2015; Radford et al. 2018). The extent of decline and extinction is greater for mammals than any other taxonomic group in Australia and many surviving Australian native mammal species are still declining rapidly (Ziembicki et al. 2013; Fisher et al. 2014; Woinarski et al. 2015).

Many of the detrimental impacts of cats on Australian mammals are well documented in localised autecological studies on mammal species (e.g., Gibson et al. 1994; Phillips et al. 2001; Glen et al. 2010; Mifsud & Woolley 2012; Fancourt 2014; Peacock & Abbott 2014), as well as cat dietary studies (e.g., Paltridge et al. 1997; Molsher et al. 1999; Read & Bowen 2001; Spencer et al. 2014; Doherty 2015; Stokeld et al. 2018). There has been one previous attempt to inventory mammal species known to be killed by cats in Australia (Doherty et al. 2015), with that compilation reporting that 88 Australian mammal species are consumed by cats. Here, we use a much larger and more diverse set of sources to revisit that inventory. We also compare our list of species known to be preyed upon by cats with the complementary list of species not yet known to be killed to consider whether any ecological factors and species' traits may influence the likelihood of predation, noting that many such traits have been previously associated with variation in the extent of decline among Australian mammal species (Dickman 1996; McKenzie et al. 2007; Burbidge et al. 2009; Johnson & Isaac 2009).

This study complements two recent papers that compiled records of predation by cats on 357 bird species (Woinarski et al. 2017a) and 258 reptile species (Woinarski et al. 2018) in Australia. As with the current paper, the former study also modelled traits that rendered species more likely to be killed by cats, finding that birds that nest or forage on the ground and are in the weight range 60-300 g are most likely to be killed by cats (Woinarski et al. 2017b). The current study also complements a paper reporting on the total number (and spatial variation) of mammals killed by cats in Australia (B. Murphy et al., submitted).

Our objectives are to: (i) provide a comprehensive list of mammal species known to be killed by cats for an entire continental area, Australia; (ii) assess whether any species' traits render mammal species more likely to be killed by cats; and (iii) predict which mammals are most likely to be preyed upon by cats and thus benefit from management interventions.

Methods

Collation

We derived a list of extant Australian mammal species from the comprehensive review by Jackson and Groves (2015), updated following some recent taxonomic accounts. We excluded several recently-recognised species where prior records of cat predation could not be unambiguously assigned to that species (e.g., *Acrobates pygmaeus*/*A. frontalis*), and kept the record as per the previously assigned species name (Appendix S1). We did not include extinct species, and non-native species were included in the compilation but excluded from analyses because our focus related to the conservation of Australian mammal species.

We included the conservation status of every mammal species, as at December 2018, at both the global level (as assessed by the International Union for Conservation of Nature, IUCN) and national level (as recognised by the Australian Government's *Environment Protection and Biodiversity Conservation Act, 1999,* EPBC Act). Although Australian legislation allows listing of subspecies as threatened, we report only on predation at the species level, as most of the cat predation records we compiled identified prey species rather than subspecies.

We compiled 107 studies of the diet of feral cats (Fig. 1), including published (Appendix S1) and unpublished studies (Appendix S2), reporting on the prey contents of 12,279 cat scats and stomachs. Since the landmark studies of Coman and Brunner (1972) and Brunner and Coman (1974), identification of mammal hair in predator scats or stomachs has been widely and reliably practised in Australia. However, hair diagnosis to species level is challenging among some closely-related taxa, and consequently some dietary studies did not distinguish between closely-related and morphologically similar mammal prey species. In addition to records from feral cat dietary studies, we also compiled information from all main Australian museums (for specimens in their collection reported as killed by cats), autecological studies of mammal species, compilations of injured wildlife (where cats (mostly pets) were known to be the cause of injury or mortality) brought to veterinarians (Appendix S1), and records from studies of the take of wildlife by pet cats. In our compilations, we noted whether records were attributable to feral cats (free-ranging and unreliant on humans) or pet cats (owned by and dependent on humans) (Appendix 1). We condensed all the aggregated information into a yes/no variable describing whether the mammal species had been recorded as eaten by feral cats, and a yes/no variable describing whether the species had been recorded as eaten by pet cats.

One potential shortcoming in this compilation is that some of the records in studies of cat faeces or stomachs may have arisen through consumption of the mammal as carrion rather than as a result of the cat killing the prey. This may be particularly the case for larger mammal species. However, we note that cats have been reported to hunt and kill Australian mammals at least as large as 4 kg (Fancourt 2015; Read et al. 2018), and cats preferentially kill their prey rather than scavenge (Paltridge et al. 1997). Furthermore, while it is improbable that cats kill adults of larger mammal species, they may take the smaller juveniles (Childs 1986; Read et al. 2018). Although there were some explicit records of carrion consumption reported in some studies, e.g., southern elephant seal (*Mirounga leonina*) (Jones 1977) and common wombat (*Vombatus ursinus*) (Brunner et al. 1991), in most of the cat dietary studies we collated the authors could not confirm whether a dietary item was taken as carrion or not. To address this issue, we excluded from analyses all records of mammal species >2 kg reported in cat dietary studies unless there was some definitive evidence of that species being killed by cats. We consider this a highly conservative filter, as it is likely that some excluded species were actually killed by cats.

Analysis

All else being equal, there is greater likelihood of a species being recorded as cat-predated if the species is common, widespread and well-studied. As a measure of these characteristics, we used the number of occurrence records for each mammal species reported in a recent review of the conservation status of Australian mammals (Woinarski et al. 2014). To assess the extent to which our large and diverse collection of sources redressed this species' abundance bias, we compared this number of records across the set of mammal species: (i) recorded as cat prey in the more limited compilation by Doherty et al. (2015); (ii) added to that source here; and (iii) not yet recorded as cat prey, using Kruskal-Wallis analysis of variance.

Initial collation of records showed that mammal species across a wide range of body mass are known to be predated by cats. Most non-volant Australian mammal species fall within smaller (<100 g) body mass categories and a high proportion of these have been recorded as feral cat prey. We explored this relationship further through modelling that also incorporated a range of other species' traits.

Our principal analysis involved modelling the presence/absence of cat-predation records for each Australian mammal species, as a function of all possible combinations of predictor variables (species' traits) using generalised linear models (binomial logistic regression) run in R version 3.5.1 (R Core Team, 2018). The traits considered for non-volant species (Table 2) were scored according to Van Dyck and Strahan (2008) and Woinarski et al. (2014). These traits were chosen for consistency with bird (Woinarski et al. 2017a) and reptile (Woinarski et al. 2018) studies using the same approach, and 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. 2009; Johnson & Isaac 2009; Fisher et al. 2014). We log-transformed body mass and rainfall and allowed for non-linear trends by including these variables as quadratic terms. We firstly modelled presence/absence of cat-predation records derived from feral cat records only, and secondly we modelled all records derived from both feral and pet cats.

Bats (78 species) were considered separately in our analyses, and the only traits included were body mass and whether or not the species is known to roost in caves (Table 2), due to the possibility that cave-roosting species may be more vulnerable to predation than species that roost in hollows in large trees. We modelled records for bats obtained from all sources, including museum and pet cat records, and also modelled records obtained only from feral cat dietary studies.

To consider model uncertainty, we took a model-averaging approach which incorporated estimates from multiple candidate models weighted according to the Akaike Information Criterion corrected for small sample size (AIC_c) (Burnham & Anderson 2003). We examined several competing models simultaneously to identify the best-supported models (95% confidence model set) and these models were averaged to obtain parameter estimates (R package MuMIn: Barton (2018)).

To identify a single optimal model for visualisation of variable effects, relative variable importance (*w+*: the sum of Akaike weights for all models containing a given predictor variable) was used to identify highly influential variables, i.e., those variables with $w+ \geq 0.73$, which is equivalent to an AIC_c difference of 2 which is widely used to assess a 'clear' effect (Richards 2005).

To redress potential biases in information availability, we included two offset variables in the models for non-volant species. To redress bias due to differences among species in abundance and range size, we offset for the number of post-1990 occurrence records of each species, derived from Woinarski et al. (2014). This offset was also included to redress bias introduced by the use of only presence/absence of predation records, which treats a mammal species with only a single and perhaps unusual record of cat predation as equivalent to a species with numerous records (thus indicating cat predation occurs frequently). We also recognise that mammal species are self-evidently more likely to have been reported as cat-predated if they occur in areas in which one or more cat dietary studies have been conducted. To redress this sampling bias we offset for the number of collated cat dietary studies within the extant range of each mammal species. Due to better model fit, the number of such dietary studies was used instead of the total dietary sample size (highly correlated (0.9), Appendix S4). A small proportion (eight of the 107) of the diet studies included in our compilation were conducted between 1977 and 1989, but all native prey species reported in these studies were also reported in studies post-1990 (Appendix S1), and therefore we consider that no temporal bias was introduced by inclusion of pre-1990 predation records.

To answer the question 'what is the relative likelihood, based on species' traits, that a mammal species will be preyed upon by a cat?', the two offsets (number of occurrence records and number of cat dietary studies within the species' range) were included in all candidate models and held constant at their mean when generating predictions (based on full model-averaged coefficients). We generated predictions based on feral cat predation records, as well as records from all cat (feral and pet cat) sources. This question relates to a mammal species' relative risk of predation by cats, i.e., the likelihood of a mammal species being preyed upon by cats relative to all other mammal species, based on its traits. Note that it is not an explicit probability of an individual of that mammal species being preyed upon by cats over any particular time period.

Results

Collation

Across all sources (from both feral and pet cats), we collated records of cat predation on 151 (24 volant, 127 non-volant) of the 288 extant native terrestrial mammal species in Australia (52%) (Table 1, Appendix S1). From feral cat dietary studies, predation records were collated for 127 mammal species (9 volant, 118 non-volant), and from pet cat sources (consisting of pet cat dietary studies, museum records, and veterinary sources) predation records were collated for 81 mammal species (20 volant, 61 non-volant) (Appendix S1). Fifteen volant and nine non-volant species records were obtained exclusively from pet cat dietary studies; the non-volant species recorded from studies of pet cats but not feral cats were: platypus (*Ornithorhynchus anatinus*), spotted-tailed quoll (*Dasyurus maculatus*), Woolley's antechinus (*Pseudantechinus woolleyae*), swamp antechinus (*Antechinus minimus*), subtropical antechinus (*Antechinus subtropicus*), koala (*Phascolarctos cinereus*), striped possum (*Dactylopsila trivirgata*), squirrel glider (*Petaurus norfolcensis*) and heath mouse (*Pseudomys shortridgei*).

A further 19 large (>2 kg) non-volant species were reported as consumed by cats, but not definitively recorded as being killed by them (i.e., they were confirmed or assumed to be consumed as carrion). Their inclusion increases the tally of cat consumption to 59% of extant native terrestrial mammal species (Appendix S1). Of this tally, representation was particularly high for non-volant species, with 146 (70%) Australian non-volant mammal species now known to be killed or consumed by cats (Appendix S1). Among the more speciose taxonomic groups, there was a high proportion of species with cat predation records for dasyurids (78% of 59 species), bandicoots and bilbies (73% of 11 species), possums (70% of 27 species), and rodents (65% of 52 species), with much lower representation among bats (31% of 78 species). Our compilation also included 14 introduced mammal species reported as consumed by cats, and one native marine species (southern elephant seal, although this record is undoubtedly of carrion) (Appendix S1). Fifty terrestrial mammal species (including 5 bat species) for which we have records of cat-predation are listed as threatened by the IUCN or (with one or more subspecies) under Australia's EPBC Act (Appendix S1), representing 57% of the 87 Australian terrestrial mammal species listed as threatened.

Most data sources did not provide measures of the relative numbers of individuals killed by cats, with the exception of museum records. The museum tallies are notable, in that they show relatively large numbers of some arboreal mammal species. However, these species' tallies may be influenced by a range of factors, such as cat-owners being unfamiliar with these prey species and hence taking them to museums for identification, and museums being disinclined to retain specimens of species already well-represented in collections. Across the eight museum collections examined, there were 801 specimens of 71 native mammal species (and a further 32 specimens of four introduced species) reported as killed by cats. Species with the most cat-killed museum specimens were the sugar glider

(*Petaurus breviceps*) (157 specimens), squirrel glider (*Petaurus norfolcensis*) (89), feather-tailed glider (*Acrobates pygmaeus*) (74), eastern barred bandicoot (*Perameles gunnii*) (47), brown antechinus (*Antechinus stuartii*) (37), long-nosed bandicoot (*Perameles nasuta*) (32), lesser long-eared bat (*Nyctophilus geoffroyi*) (30) and brush-tailed phascogale (*Phascogale tapoatafa*) (26).

Analysis

As expected from our more diverse and larger sourcing of data, mammal species reported as cat prey in Doherty et al. (2015) were more widespread and/or abundant (mean 3700 ± 658 [SE] occurrence records per species) than the additional mammal species recorded as cat prey in the current compilation (1931 ± 711). Species with no confirmed records of cat predation in our compilation had substantially fewer occurrence records (602 ± 286): i.e. they were rarer and/or more restricted. The differences in number of occurrence records among these three sets of species were significant ($H = 49.7$, $p < 0.001$).

Initial collation of records showed that mammal species across a wide range of body mass are known to be predated by cats (Fig. 2). Most non-volant Australian mammal species fall within smaller (<100 g) body mass categories and a high proportion of these have been recorded as feral cat prey. We explored this relationship further through modelling that also incorporated a range of other species' traits.

In models relating (non-volant) species' traits to the presence/absence of cat-predation records derived from feral cat sources, 16 models composed the 95% confidence set of logistic regression models when offsets were included to control for abundance/distribution and sampling bias. Habitat preference, den type and diet were removed from analyses due to collinearity with rainfall, saxicoline and body mass respectively, i.e., most of the variation in one of these variables was explained by their collinear counterpart, but body mass, rainfall and saxicoline provided better model fit. Body mass, rainfall and saxicoline were highly influential predictors (Table 3) of the likelihood of a species being reported as killed by feral cats and the optimal model containing these variables showed the relative probability of a non-volant mammal species being preyed upon by feral cats was greater for species with intermediate body mass (peaking at ca. 400 g), those occurring in lower rainfall zones, and those that are not saxicoline (Fig. 3).

When offsets were excluded, 7 models composed the 95% confidence set of logistic regression models relating (non-volant) mammal traits to whether or not a species had been reported as feral cat prey. Body mass, rainfall and saxicoline were highly influential predictors (Table 3, Fig. 3).

When all sources were included, i.e., from museum records, pet cat dietary studies and feral cat dietary studies, results were very similar (Table 3, Appendix S5). When carrion-consumed species were included in the models as positive cat consumption records, results were similar when offsets were included, but body mass was not influential when offsets were excluded (Appendix S6).

For bat species, the number of cat dietary studies in a species' range was the only important predictor of cat predation from all sources of predation records, as well as when reduced to only records from studies of feral cat diet ($w+ = 1.00$); cave roosting and body mass were not predictive ($w+ = 0.25$, 0.00 respectively for all sources, $w+ = 0.29$, 0.07 respectively for feral cat sources, derived from 95% confidence set of logistic regression models) (Fig. 4).

From full model-averaged predictions including offsets, and thus based on species' traits, the species with the greatest risk of cat predation included mulgaras (*Dasycercus* spp.), kowari (*Dasyuroides byrnei*), marsupial moles (*Notoryctes* spp.), many smaller dasyurids and medium- to large-sized rodents, amongst others (Table 4, Appendix S3): i.e., species occurring mainly in arid areas, not associated with rocky habitats and of intermediate body mass.

Discussion

Australian mammal species occurring in lower rainfall areas, that do not use rocky habitat refuges, and have a body mass in the 'critical weight range' (CWR), i.e., 35 - 5500 g (Burbidge & McKenzie 1989) have shown far greater rates of decline and extinction than species that do not have these traits (Dickman 1996; Paltridge et al. 1997; Burbidge & Manly 2002; McKenzie et al. 2007; Burbidge et al. 2009; Johnson & Isaac 2009; Radford et al. 2015). The studies previously reporting these patterns have largely speculated that predation by the introduced domestic cat and European red fox (*Vulpes vulpes*) may be responsible for the observed relationships. Here, we show from analysis of cat predation records that this speculation is reasonable, because mammal species with these traits are indeed those most likely to be killed by cats. Our compilation demonstrates that cats are now known to kill individuals from most species of Australia's diverse mammal fauna, and traits analysis associates this predation directly with the extremely high rates of mammal decline and extinction seen across the continent in recent history (Woinarski et al. 2015). Fifty threatened Australian mammal species are known to be killed by cats, and we show that many of these species have the greatest risks of predation by cats.

Our overall tally of cat predation records for 151 (52%) extant terrestrial native mammal species, excluding records for 19 larger species (>2 kg) conservatively assumed to be consumed as carrion, is substantially greater than the 88 species reported in a previous national compilation (Doherty et al. 2015). This is largely because we expanded and diversified our sources to include data from subsequent cat dietary studies, additional unpublished studies, autecological studies, museum records, and veterinary reports. Most of the 64 non-volant species for which we could locate no records of cat predation or consumption are rare or poorly-studied, or occupy restricted ranges (< 10,000 km^2) where few, if any, cat diet studies have been conducted, or are too large to be killed by cats. Given that cats overlap the range of all these species (Legge et al. 2017), it is likely that the lack of records of cat predation for all but the larger species is a sampling artefact and almost all are preyed upon by cats. We also note that cats may fatally injure or kill mammals that they do not consume (McGregor et al. 2015), and in this case dietary studies alone may result in an underestimate of total species killed by cats. Cats may also have indirect impacts on mammal populations through disease transmission. The cat is the sole primary host in Australia for toxoplasmosis (Hollings et al. 2013; Fancourt & Jackson 2014) and toxoplasmosis is now prevalent in many Australian mammal species (Canfield et al. 1990; Groenewegen et al. 2017).

Although the proportion of bat species reported as cat prey in this study (31%) is lower than that of non-volant species, our tally (24 species) is a substantial increase on the five bat species previously reported (Doherty et al. 2015). Recent global reviews indicate that the extent of cat predation on bats, and the impacts of such predation, may be greater than previously recognized (Ancillotto et al. 2013; Welch & Leppanen 2017). The clear relationship we found between cat predation and the number of cat dietary studies in a bat species' range suggests that further research would identify predation on many more Australian bat species. Furthermore, our tally is likely to be an underestimate given the many recent taxonomic changes to Australian bats (e.g., Reardon et al. 2014) render past records from cat dietary studies difficult to reconcile unambiguously with currently recognised species. Additionally, many Australian bat species are difficult to distinguish morphologically, especially within dietary samples, and thus most studies in our compilation reporting bat predation (64%) did not identify bats to species level. This problem of species' identification of bats from their remains in feral cat stomach and scat samples probably explains the relatively high proportion of bat species in our compilation that were recorded as pet cat prey, with such records typically being of intact animals that were more readily identifiable.

Our tallies of the number and proportion of Australian mammal (and threatened mammal) species known to be killed by cats cannot readily be compared with data from other continents, because there are no other continents with such a magnitude of cat dietary studies. However, we offer a novel, globally applicable approach for future comparison of geographic (dis)similarities in species' traits influencing vulnerability to predation, which could aid in informing the global prioritisation of species conservation efforts.

It is particularly noteworthy that the 'cat-preferred' weight range identified by our modelling when controlling for bias nearly matches the CWR for Australian mammal species exhibiting the greatest rates of decline and extinction (Burbidge & McKenzie 1989). Our relatively low modelled likelihood of cat predation on small mammal species, i.e., below the CWR (<35 g), is intriguing. As originally defined, the CWR concept considered that the smallest species exhibited relatively low rates of decline, not because they were less likely to be preyed upon, but rather because small mammal species had relatively high reproductive output and typically high densities, and so could sustain rates of predation that would cause population decline in less fecund larger species (Burbidge & McKenzie 1989; Johnson & Isaac 2009). However, our analysis suggests that cats are relatively more likely to select mammal species of intermediate body mass (Fig. 3). Some previous studies have also indicated that cats preferentially prey on species with intermediate body weight e.g., larger rodents (>25 g) have been shown to be preferred by feral cats in the MacDonnell Ranges, central Australia (McDonald et al. 2018). There is also some evidence that cats may exhibit individual preferences and specialise in hunting particular prey, sometimes of larger sizes (Gibson et al. 1994; Dickman & Newsome 2015). However, in our models run without controlling for abundance and study effort bias, confidence intervals are much broader across small body size classes (<35 g), indicating smaller mammals are more likely to be reported as preyed upon by cats (Fig. 3). Predictions generated from these models, and thus based on the likelihood of a cat encountering a mammal, predict a greater likelihood of cat predation on smaller species, consistent with other localised studies of cat diet selectivity (Kutt 2012; Read et al. 2018). This is also evident in the greater overall proportion of mammal prey species falling within smaller body mass categories, before the data were modelled to focus prediction on mammal traits and account for sampling bias (Fig. 2).

The modelled likelihood of cat predation was not strongly influenced by whether a mammal species was arboreal or not. Museum records confirmed that arboreal mammal species are often preyed upon by cats. This result contrasts markedly with a comparable analysis for Australian birds, which found that birds that nest or forage on the ground were more likely to be preyed upon by cats (Woinarski et al. 2017b). We consider that the lack of an association between cat predation records and whether a mammal species is arboreal or not is most likely because most Australian arboreal mammals tend to spend some time on the ground, and when on the ground many of them are relatively poor at evading predation attempts by cats. Furthermore, cats are adept climbers and may readily take arboreal mammals in trees (McComb et al. 2018).

The traits considered in our analysis are unlikely to encompass every species-specific characteristic determining the likelihood of being preyed upon by cats. For example, although the short-beaked echidna (*Tachyglossus aculeatus*) has records of cat predation, its defence of stout spines (a trait not included in our modelling) may render such outcomes relatively unlikely or uncommon (Fleming et al. 2014). Likewise, although records of predation are available for marsupial moles (*Notoryctes* spp.) and they were modelled here to be highly likely to be killed because they occur in low rainfall areas, are not saxicoline, and fall within the cat-preferred weight range, they spend most of their time underground and thus may rarely be encountered by cats (Paltridge 1998). Furthermore, very little is known about the distribution or abundance of marsupial moles (Burbidge & Woinarski 2016). Some behavioural traits unique to certain species could not be readily and consistently attributed across all species and therefore could not be included in our models. Overall, the position of the majority of species on our list of cat predation likelihood is plausible and consistent with predator-susceptibility assessments (Radford et al. 2018) and autecological studies. For instance, Pedler et al. (2016) found dramatic recovery of crest-tailed mulgara (*Dasycercus cristicauda*) after rabbit populations dropped severely due to biocontrol, resulting in substantial decline in cat populations and hence release of mulgaras from cat predation.

Although we did not include extinct species in our analyses, their inclusion would likely strengthen the model results reported here. Most of Australia's extinct mammal species occurred in arid and semi-arid habitats, were non-saxicoline, and/or were of intermediate body size, such as bandicoots, hare-wallabies, and conilurine rodents, comparable to the traits found here to be highly associated with likelihood of cat predation. Although cat predation likely played a role in many of these extinctions, there are no or few records of cat predation on almost all of these extinct species, as most disappeared prior to modern studies (Woinarski et al. 2015).

The traits of the cat itself partly explain why most native mammals are ideal prey. In Australian landscapes, cats are generally opportunistic predators that hunt most effectively in open habitats and prefer to take live prey smaller than their own body size (McGregor et al. 2015; Leahy et al. 2016; Read et al. 2018). Cats have a highly flexible diet, and although they may selectively hunt certain prey species, they can adapt readily to changing prey availability by prey-switching, and hence may prey on a wide range of mammal species present in their range (Yip et al. 2014; Dickman & Newsome 2015; Doherty et al. 2015). Most (78%) Australian mammals have a mean adult body mass of less than 3 kg and are generally accessible to cats when active. Furthermore, our analysis linking traits with the likelihood of cat predation on mammal species is consistent with other recent assessments of cat behaviour and abundance in Australia. For example, on at least the regional scale, feral cats are less abundant and probably hunt less effectively in rugged rocky areas (Hohnen et al. 2016); and in years of good rainfall, cats occur at appreciably greater densities in more arid areas (Legge et al. 2017), so mammal species associated with higher rainfall and/or rocky areas are less likely to be preyed upon by cats than are comparable species in non-rocky habitats and lower rainfall areas.

Our results reinforce the need for feral cat management to be prioritised for the conservation of many Australian mammal species, especially those within the CWR, those in the arid zone, and those that do not use rocky refuges. Many highly threatened mammals have been the subject of intensive management responses designed to limit or remove the pressure of predation by cats (and the other main introduced predator, the European red fox). Such management responses include translocations to predator-free islands, the establishment of predator-proof fenced exclosures, and broad-scale baiting to reduce numbers of cats and foxes (Algar et al. 2013; Legge et al. 2018), with many of these measures achieving at least local-scale recovery for some of these species (Moseby et al. 2011; Hayward et al. 2015; Anson 2017). National policy should include efforts to curb the impact of cats along the continuum of domestication, with community education and communication an important part of any management program (Denny & Dickman 2010; Loss et al. 2018; Crowley et al. 2019).

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Table 1. Collated tally of number of Australian mammal species reported as consumed or killed by feral and/or pet cats. The number of records is also given as a proportion of total Australian extant, native, terrestrial species (in brackets), i.e. 210, 78, 288 for non-volant, volant, and total mammal species respectively.

Record type	Non-volant (210)	Volant (78)	Total (288)
Consumed by cats (records from feral and pet cats; and including large-bodied species assumed to be consumed as carrion)	146 (70 %)	24 (31 %)	170 (59 %)
Killed (preyed upon) by cats (records from feral and pet cats)	127 (60 %)	24 (31 %)	151 (52 %)
- Killed by feral cats (records only from feral cat diet studies)	118 (56 %)	9 (12 %)	127 (44 %)
- Killed by pet cats (records only from pet cat diet studies, museums, veterinary records)	61 (29 %)	20 (26 %)	81 (28 %)

Table 2. Mammal traits used to model the effects of predictor variables on the presence/absence of cat predation records: non-volant mammal models included all except cave roost; bat models included only body mass and cave roost. Mean and range is shown for continuous variables, and most common category is shown for categorical variables.

Variable	Coding	Mean or most common category	Range
Abundance - distribution	Total number of confirmed occurrence records of a species over the period 1990-2014, derived from databases compiled in the Mammal Action Plan (Woinarski et al. 2014)	2182	0 - 33791
Number of studies	Total number of cat diet studies conducted within a species' extant range	8	0 - 85
Body mass	Mean adult body mass (g)	2760	4 - 40750
Saxicoline	Mostly inhabits rocky substrates (binary - yes/no)	No	
Rainfall	Mean annual rainfall centroid across species' extant range (mm)	970	150 - 2500
Aquatic	Uses aquatic environments (binary - yes/no)	No	
Ground foraging	Extent to which species forage on the ground: does not forage on the ground, sometimes forages on the ground, always forages on the ground	Always	
Activity	Diel activity pattern: diurnal, nocturnal, crepuscular	Nocturnal	
Habitat preference	Preferred habitat used: rainforest, tall eucalypt forest, woodland, shrubland/heathland, hummock grassland, tussock grassland, gibber plain	Woodland	
Den type	Den type used: open arboreal, dense arboreal cover, tree hollows, hollow logs, dense ground cover, open ground, shallow burrow/scrape, deep burrow/soil crevices, caves/rock crevices	Dense ground cover	
Diet	Diet type: carnivore, omnivore, herbivore, granivore	Herbivore	
Cave roost	For bats only: roosts in caves (binary - yes/no)	No	

Table 3. The relative importance (*w+*) of traits and number of models (N) containing the trait variable derived from modelling the effects of predictor variables on records of feral cat predation, or feral + pet cat predation, on non-volant native mammals, with inclusion and exclusion of offsets to account for abundance and sampling bias. Highly influential variables (*w+* ≥ 0.73) are indicated in bold. See Table 2 for variable definitions.

		Offsets included		*Offsets excluded*	
Records	Variable	*w+*	N	*w+*	N
Feral cats					
	Body mass	**1.00**	**16**	**1.00**	**7**
	Rainfall	**0.91**	**12**	**1.00**	**7**
	Saxicoline	**0.76**	**9**	**0.96**	**6**
	Aquatic	0.35	8	0.25	3
	Ground foraging	0.15	4	0.13	2
	Activity	0.10	4	0.11	2
Feral + pet cats					
	Body mass	**1.00**	**18**	**1.00**	**6**
	Rainfall	**0.86**	**13**	**1.00**	**6**
	Saxicoline	**0.76**	**10**	**1.00**	**6**
	Aquatic	0.47	8	0.31	3
	Ground foraging	0.15	5	0.12	2
	Activity	0.17	6	0.11	2

Table 4. The non-volant, extant, native mammal species with greatest relative likelihood (between 0 and 1) of being killed by feral cats, based on the species' traits. These predictions were generated from full model-averaged coefficients derived from modelling the relationship between the presence/absence of cat-predation records and mammal traits (offset by mean occurrence and the number of cat diet studies within a species' extant range). 'Lower' and 'Upper' are the limits of 95% confidence interval (CI). See Appendix S3 for complete listing of relative likelihood of feral cat predation on all mammal species.

* Threatened species, or at least one subspecies listed as threatened.

			95% CI	
Scientific name	Common name	Likelihood	Lower	Upper
*Dasycercus cristicauda**	Crest-tailed mulgara	0.930	0.629	0.991
*Dasyuroides byrnei**	Kowari	0.930	0.629	0.991
Dasycercus blythi	Brush-tailed mulgara	0.853	0.597	0.958
*Leporillus conditor**	Greater stick-nest rat	0.848	0.553	0.962
*Pseudomys australis**	Plains mouse	0.841	0.508	0.964
Notoryctes typhlops	Southern marsupial mole	0.836	0.404	0.975
*Perameles bougainville**	Western barred bandicoot	0.835	0.594	0.946
*Notomys fuscus**	Dusky hopping-mouse	0.814	0.466	0.956
Notomys cervinus	Fawn hopping-mouse	0.809	0.459	0.955
*Sminthopsis psammophila**	Sandhill dunnart	0.779	0.419	0.945
Rattus villosissimus	Long-haired rat	0.778	0.581	0.898
*Pseudomys fieldi**	Shark Bay mouse	0.772	0.489	0.923
*Phascogale calura**	Red-tailed phascogale	0.754	0.463	0.916
*Zyzomys pedunculatus**	Central rock-rat	0.747	0.398	0.930
Notomys mitchellii	Mitchell's hopping-mouse	0.737	0.496	0.889
*Myrmecobius fasciatus**	Numbat	0.732	0.257	0.956
*Parantechinus apicalis**	Dibbler	0.732	0.357	0.931
*Pseudomys shortridgei**	Heath mouse	0.727	0.532	0.862
*Bettongia lesueur**	Boodie	0.717	0.359	0.920
*Sminthopsis douglasi**	Julia Creek dunnart	0.713	0.500	0.861
Notomys alexis	Spinifex hopping-mouse	0.711	0.419	0.893
Pseudomys occidentalis	Western mouse	0.711	0.415	0.895
Notoryctes caurinus	Northern marsupial mole	0.703	0.294	0.931
Rattus sordidus	Canefield rat	0.682	0.486	0.830
Pseudomys gracilicaudatus	Eastern chestnut mouse	0.672	0.486	0.816
*Zyzomys palatalis**	Carpentarian rock-rat	0.667	0.350	0.882
Rattus tunneyi	Pale field-rat	0.665	0.471	0.816
Petaurus breviceps	Sugar glider	0.665	0.327	0.890
Petaurus norfolcensis	Squirrel glider	0.650	0.307	0.886
Phascogale tapoatafa	Brush-tailed phascogale	0.648	0.406	0.832
Dasykaluta rosamondae	Kaluta	0.639	0.347	0.855

Rattus fuscipes	Bush rat	0.639	0.428	0.807
Pseudantechinus woolleyae	Woolley's antechinus	0.628	0.269	0.886
*Conilurus penicillatus**	Brush-tailed rabbit-rat	0.601	0.347	0.810
*Phascogale pirata**	Northern brush-tailed phascogale	0.599	0.345	0.809
Antechinomys laniger	Kultarr	0.579	0.295	0.819
*Pseudomys fumeus**	Smoky mouse	0.578	0.384	0.751
Antechinus vandycki	Tasman Peninsula dusky antechinus	0.574	0.365	0.760
*Mesembriomys macrurus**	Golden-backed tree-rat	0.569	0.317	0.790
Antechinus flavipes	Yellow-footed antechinus	0.568	0.342	0.769

Figure legends

Fig. 1. Location of feral cat dietary studies, with circle size corresponding with sample size at each study site. Christmas Island (n = 187) and Macquarie Island (n = 756) are excluded from this figure.

Fig. 2. Number of non-volant terrestrial mammal species across body mass categories recorded as, or not recorded as, feral cat prey in Australia. Also shown are records of the number of species consumed as carrion, or assumed to be consumed as carrion, for large-bodied species >2 kg. Only feral cat predation records are included, i.e., excluding museum sourced records of predation and pet cat dietary studies (see Appendix 1). Dashed lines represent the body mass extent of the 'critical weight range' (CWR) for mammals, i.e., 35-5500 g (Burbidge & McKenzie 1989).

Fig. 3. Relationship between the relative likelihood of a non-volant mammal species being preyed upon by a feral cat (P_{cat}) and predictor variables derived from logistic regression when accounting for abundance and sampling bias. All variable relationships shown are highly influential and derived from the optimal logistic regression model while holding other explanatory variables constant (continuous variables at their median and categorical variables at their most common category). Continuous black lines represent model fit, grey bands represent the 95% confidence interval, and the dashed line represents the body mass extent of the 'critical weight range' for mammals, i.e., 35-5500 g (Burbidge & McKenzie 1989). See Table 2 for variable definitions.

Fig. 4. Relationship between predictor variables and the relative likelihood of a bat species being preyed upon by (A) feral cats or (B) all cats (P_{cat}), derived for each variable from the optimal logistic regression model while holding other variables at their mean (continuous variables) or most common category (categorical variable). Continuous black lines represent model fit and grey bands represent the 95% confidence interval. See Table 2 for variable definitions.

Supplementary legends

Appendix S1. List of Australian mammal species and cat predation records.

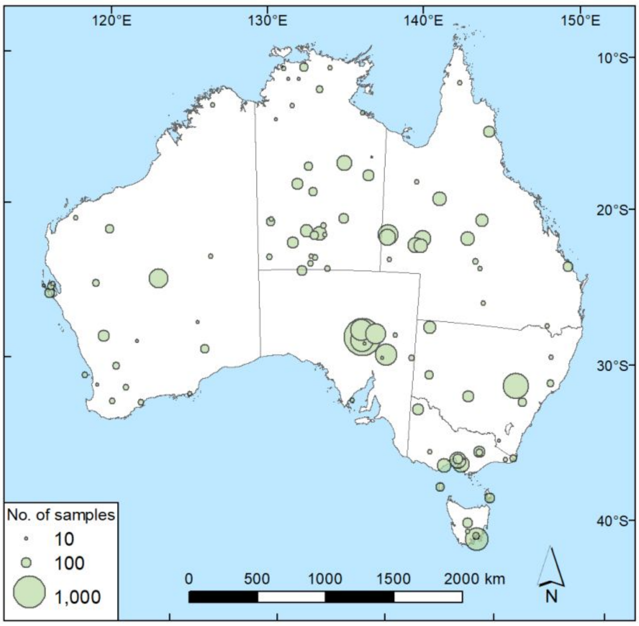
Appendix S2. Sources of unpublished information on records of mammal species in cat diet.

Appendix S3. List of non-volant mammal species ranked by their relative likelihood of being killed by feral cats, derived from modelling species traits against records of feral cat predation.

Appendix S4. Offset variables used to account for species abundance-distribution and sampling bias.

Appendix S5. All predation records. Regression relationships between highly influential predictor variables and the likelihood of a non-volant mammal species being killed by cats including all records from studies of feral cats and pet cats, i.e. including museum sourced records of predation and pet cat dietary studies.

Appendix S6. All consumption records. Regression relationships between highly influential predictor variables and the likelihood of a non-volant mammal species being consumed by cats including all records from studies of feral cats and pet cats, i.e. including museum sourced records of predation and pet cat dietary studies, as well as including records for all larger species (>2 kg) assumed to be attributed to carrion consumption.



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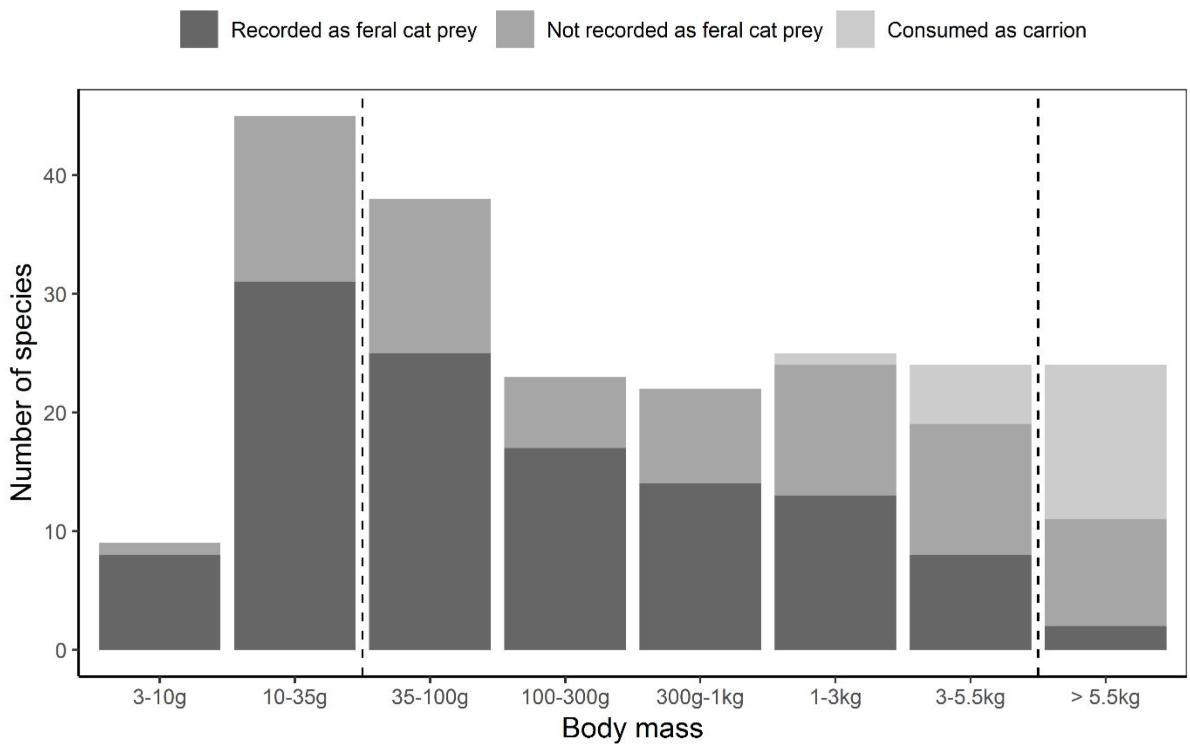

Fig. 2. Number of non-volant terrestrial mammal species across body mass categories recorded as, or not recorded as, feral cat prey in Australia. Also shown are records of the number of species consumed as carrion, or assumed to be consumed as carrion, for large-bodied species >2 kg. Only feral cat predation records are included, i.e., excluding museum sourced records of predation and pet cat dietary studies (see Appendix 1). Dashed lines represent the body mass extent of the 'critical weight range' (CWR) for mammals, i.e., 35-5500 g (Burbidge & McKenzie 1989).

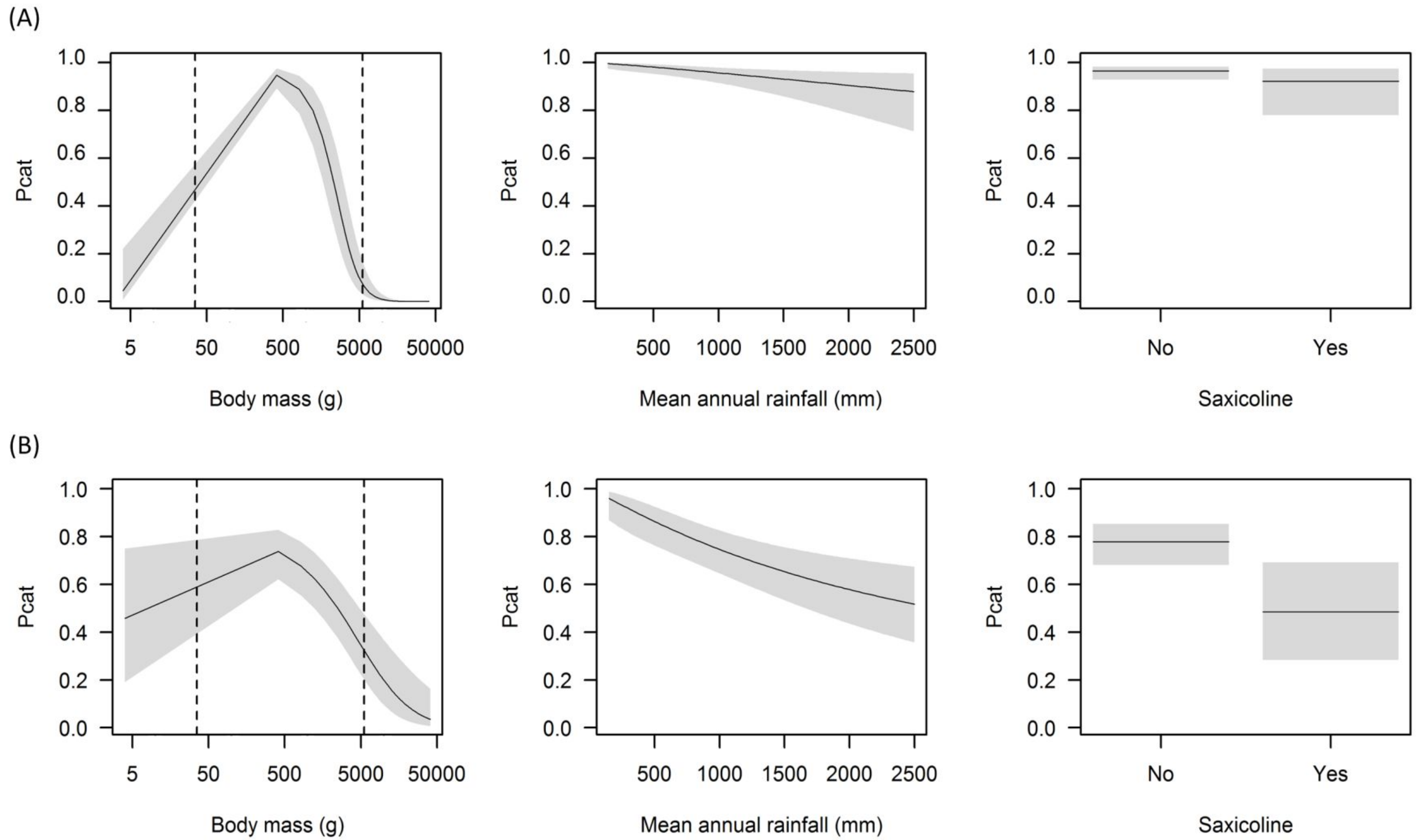

Fig. 3. Relationship between the relative likelihood of a non-volant mammal species being preyed upon by a feral cat (P_{cat}) and predictor variables derived from logistic regression (A) including and (B) excluding offsets for abundance and sampling bias. All variable relationships shown are highly influential and derived from the optimal logistic regression model while holding other explanatory variables constant (continuous variables at their median and categorical variables at their most common category). Continuous black lines represent model fit, grey bands represent the 95% confidence interval, and dashed lines represent the body mass extent of the 'critical weight range' for mammals, i.e., 35-5500 g (Burbidge & McKenzie 1989). See Table 1 for variable definitions.

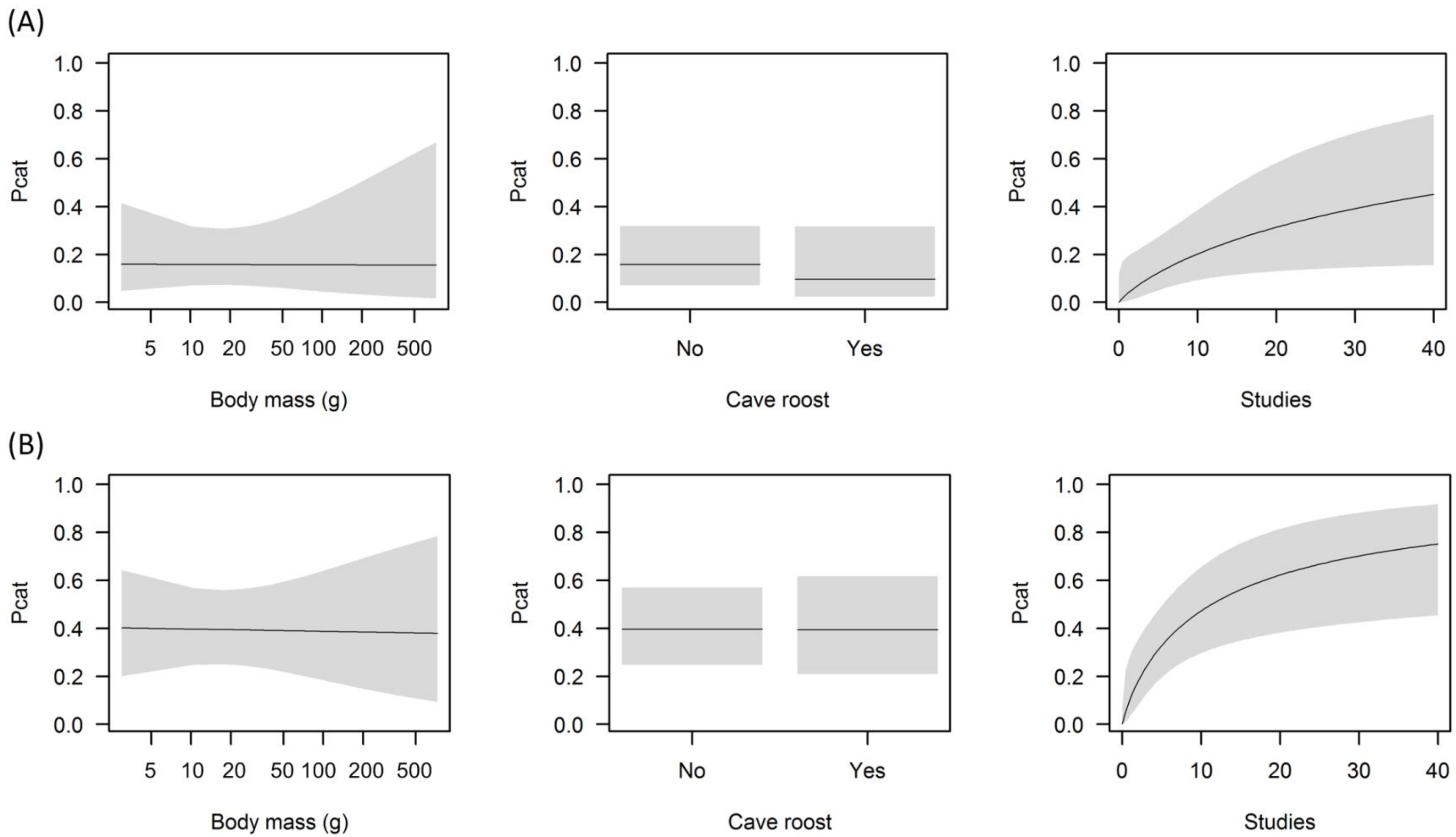

Fig. 4. Relationship between predictor variables and the relative likelihood of a bat species being preyed upon by (A) feral cats or (B) all cats (P_{cat}), derived for each variable from the optimal logistic regression model while holding other variables at their mean (continuous variables) or most common category (categorical variable). Continuous black lines represent model fit and grey bands represent the 95% confidence interval. See Table 1 for variable definitions.