Mammal Review

Mammal Review ISSN 0305-1838

REVIEW

Introduced cats *Felis catus* eating a continental fauna: inventory and traits of Australian mammal species killed

Leigh-Ann WOOLLEY* *NESP Threatened Species Recovery Hub, Research Institute for the Environment and Livelihoods, Charles Darwin University, Casuarina, NT 0909, Australia. Email: leigh-ann.woolley@cdu.edu.au*

Hayley M. GEYLE *NESP Threatened Species Recovery Hub, Research Institute for the Environment and Livelihoods, Charles Darwin University, Casuarina, NT 0909, Australia. Email: hayley.geyle@cdu.edu.au*

Brett P. MURPHY *NESP Threatened Species Recovery Hub, Research Institute for the Environment and Livelihoods, Charles Darwin University, Casuarina, NT 0909, Australia. Email: brett.murphy@cdu.edu.au*

Sarah M. LEGGE *NESP Threatened Species Recovery Hub, Centre for Biodiversity and Conservation Science, University of Queensland, St Lucia, Qld, 4072, Australia; Fenner School of Environment and Society, The Australian National University, Canberra, ACT 2602, Australia. Email: sarahmarialegge@gmail.com*

Russell PALMER *Department of Biodiversity, Conservation and Attractions, Locked Bag 104, Bentley Delivery Centre, WA, 6983, Australia. Email: russell.palmer@dbca.wa.gov.au*

Christopher R. DICKMAN *NESP Threatened Species Recovery Hub, Desert Ecology Research Group, School of Life and Environmental Sciences A08, University of Sydney, NSW 2006, Australia. Email: chris.dickman@sydney.edu.au*

John AUGUSTEYN *Queensland Parks and Wildlife Service, PO Box 3130, Red Hill, Qld 4701, Australia. Email: John.Augusteyn@des.qld.gov.au*

Sarah COMER *Department of Biodiversity, Conservation and Attractions, South Coast Region, Albany, WA 6330, Australia. Email: sarah.comer@dbca.wa.gov.au*

Tim S. DOHERTY *Centre for Integrative Ecology, School of Life and Environmental Sciences (Burwood Campus), Deakin University, Geelong, Vic 3220, Australia. Email: timothy.doherty@deakin.edu.au*

Charlie EAGER *Arkaba Conservancy, Flinders Ranges, SA 5434, Australia. Email: lodge@arkabaconservancy.com*

Glenn EDWARDS *Department of Environment and Natural Resources, Alice Springs, NT 0871, Australia. Email: Glenn.Edwards@nt.gov.au*

Dan K.P. HARLEY *Wildlife Conservation and Science Department, Zoos Victoria, PO Box 248, Healesville, Vic. 3777, Australia. Email: dharley@zoo.org.au*

Ian LEIPER *NESP Threatened Species Recovery Hub, Research Institute for the Environment and Livelihoods, Charles Darwin University, Casuarina, NT 0909, Australia. Email: ian.leiper@cdu.edu.au*

Peter J. MCDONALD *Department of Environment and Natural Resources, Alice Springs, NT 0871, Australia. Email: petermc@sprep.org*

Hugh W. MCGREGOR *NESP Threatened Species Recovery Hub, School of Biological Sciences, University of Tasmania, Private Bag 55, Hobart, Tas. 7001, Australia. Email: hugh.mcgregor@utas.edu.au*

Katherine E. MOSEBY *University of New South Wales, Kensington, NSW 2052, Australia. Email: k.moseby@unsw.edu.au*

Cecilia MYERS *Dunkeld Pastoral Co Pty Ltd, P.O. Box 50, Dunkeld, Vic 3294, Australia. Email: cecilia@dunkeldpastoral.com.au*

John L. READ *School of Earth and Environmental Sciences, University of Adelaide, Adelaide, SA 5000, Australia. Email: ecological67@gmail.com*

Joanna RILEY *School of Biological Sciences, University of Bristol, 24 Tyndall Ave, Bristol BS8 1TQ, UK. Email: joriley999@gmail.com*

Danielle STOKELD *Department of Environment and Natural Resources, Berrimah, NT 0828, Australia. Email: Danielle.Stokeld@nt.gov.au*
Jeff M. TURPIN *Department of Terrestrial Zoology, Western Australian Museum, 49 Kew Street, Welshpool, WA 6106, Australia. Email: jeff.m.turpin@gmail.com*
John C.Z. WOINARSKI *NESP Threatened Species Recovery Hub, Research Institute for the Environment and Livelihoods, Charles Darwin University, Casuarina, NT 0909, Australia. Email: john.woinarski@cdu.edu.au*

Keywords
Australia, conservation, critical weight range, diet, *Felis catus*, feral cats, invasive predator

*Corresponding author.

Submitted: 29 January 2019
Returned for revision: 28 February 2019
Revision accepted: 13 June 2019
Editor: DR

doi: 10.1111/mam.12167

ABSTRACT

1. Mammals comprise the bulk of the diet of free-ranging domestic cats *Felis catus* (defined as including outdoor pet cats, strays, and feral cats) in most parts of their global range. In Australia, predation by introduced 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 predation by cats (including feral and pet cats) on Australian mammals and model traits of extant, terrestrial, native mammal species 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, throughout each species' range.
3. For non-volant species, the relative likelihood of predation by 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 predation records for most extant, terrestrial, native 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 predation by cats (mulgaras *Dasycercus* spp., kowari *Dasyuroides byrnei*, many smaller dasyurids and medium-sized to large rodents, among others) and hence most likely to benefit from enhanced mitigation of cat impacts, such as translocations to predator-free islands, the establishment of predator-proof fenced exclosures, and broad-scale cat poison baiting.

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 throughout the world, and some of these species constitute major threats to biodiversity in many locations where they have been introduced (Gurevitch & Padilla 2004). Where free-ranging domestic cats *Felis catus* (defined as including outdoor pet cats, strays, and feral cats) have been introduced, they 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, 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).

Since their introduction following European settlement of Australia in 1788, cats have spread pervasively. Cats 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): cats have been implicated in the decline and extinction of many Australian species, particularly mammals (Johnson 2006, Woinarski et al. 2015, Radford et al. 2018). Consistent with many global studies that have demonstrated that mammals comprise the dominant component of the diet of cats (Fitzgerald 1988, Bradshaw et al. 1996, Loss et al. 2013), the extent of decline and extinction is greater for mammals than for 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 in cat diet studies (e.g. Paltridge et al. 1997, Molsher et al. 1999, Read & Bowen 2001, Spencer et al. 2014, Doherty 2015, Stokeld et al. 2018). The one previous attempt to create an inventory of mammal species known to be killed by cats in Australia (Doherty et al. 2015) documented 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, in order 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. Like 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). This study also complements a paper reporting on the total number (and spatial variation) of mammals killed by cats in Australia (Murphy et al. 2019).

Our objectives are to: (1) provide a comprehensive list of mammal species known to be killed by cats for an entire continental area, Australia; (2) assess whether any species' traits render mammal species more likely to be killed by feral and pet cats; and (3) predict which mammals are most likely to be preyed upon by cats and thus may benefit most 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. For several recently recognised species where prior records of predation by cats could not be unambiguously assigned to that species (e.g. *Acrobates pygmaeus*/*Acrobates frontalis*), we kept the records 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 native Australian mammal species.

We included the conservation status of every mammal species, as of December 2018, at both the global level (as assessed by the International Union for Conservation of Nature, IUCN) and the 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 data from 107 cat dietary studies (Fig. 1), including published (Appendix S1) and unpublished studies (Appendix S2), reporting on the prey contents of 12279 cat scats and stomachs. Since the landmark studies of

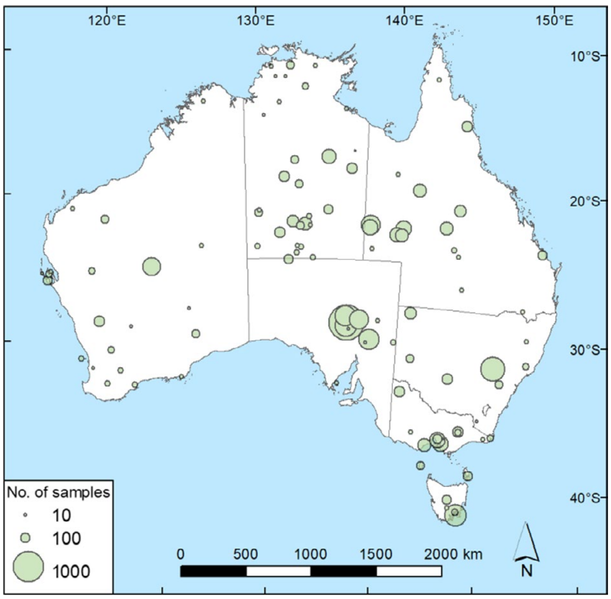

Fig. 1. Location of cat diet studies, with circle size corresponding with sample size at each study site. Christmas Island (n = 187) and Macquarie Island (n = 756) are excluded from this figure. [Colour figure can be viewed at wileyonlinelibrary.com]

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 diet studies did not distinguish between closely related and morphologically similar mammal prey species. In addition to records from cat diet studies, we also compiled records from all main Australian museums (for specimens in their collection reported as killed by cats, assumedly pet cats), records of injured wildlife (where cats – mostly pets – were known to be the cause of injury or mortality) brought to veterinarians, records from autecological studies of mammal species, and records from studies of the take of wildlife by pet cats (Appendix S1). In our compilations, we noted whether records were attributable to feral cats (free-ranging and not reliant on humans) or pet cats (owned by and dependent on humans; Appendix S1). We condensed all the aggregated information into a binary yes/no variable describing whether the mammal species had been recorded as eaten by all cats (including feral cats and pet cats), feral cats, or 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 explicit records of carrion consumption were included 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 diet studies we collated, the authors could not confirm whether a dietary item was taken as carrion or not. To address this issue, we assumed that all mammal species weighing > 2 kg and reported in cat diet studies had been taken as carrion, 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 a 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 that were: (1) recorded as cat prey in the more limited compilation by Doherty et al. (2015); (2) added to that source here; and (3) not yet recorded as cat prey, using Kruskal–Wallis analysis of variance.

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 1) 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. First, we modelled presence/absence of recorded predation by all cats (feral and pet cats) and second, we modelled records only from feral cats (i.e. from sources including feral cat diet studies and feral cat predation records from autecological studies, and excluding pet cat sources from pet cat diet studies, museum, and veterinarian records).

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 1), because cave-roosting species may be more vulnerable to predation than species that roost elsewhere. We modelled records for bats obtained from all cat (feral and pet cats) sources, and also modelled records obtained only from feral cat sources.

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 $w+ \geq 0.73$, equivalent

Table 1. Mammal traits used to model the effects of predictor variables on the presence/absence of records of predation by cats: non-volant 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

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 the species forages 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	

to an AIC_c difference of two, 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 (indicating that predation by cats 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 diet studies has been conducted. To redress this sampling bias, we offset for the number of collated cat diet studies within the extant range of each mammal species. Due to better model fit, the number of such diet studies was used instead of the total dietary sample size (these parameters were highly correlated [0.9]; Appendix S4). A small proportion of the diet studies (eight of the 107) 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 feral cat?', the two offsets (number of occurrence records and number of cat diet 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 records of predation by feral cats. This question relates to a mammal species' relative risk of predation, i.e. the likelihood of a mammal species being preyed upon by feral cats relative to the likelihood for all other mammal species, based on species' traits. It is not an explicit probability of an individual of that mammal species being preyed upon by feral cats over any particular time period.

RESULTS

Collation

Across all sources, we collated records of predation by all cats (feral and pet cats) on 151 (24 volant, 127 non-volant) of the 288 extant native terrestrial mammal species in Australia (52%; Table 2, Appendix S1). From feral cat sources (including feral cat diet studies and autecological studies), predation records were collated for 127 mammal species (9 volant, 118 non-volant), and from pet cat sources (including pet cat diet studies, museum and veterinarian records), predation records were collated for 81 mammal species (20 volant, 61 non-volant; Table 2, Appendix S1). Fifteen volant and nine non-volant species records were obtained exclusively from pet cat diet 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 (Table 2, 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 (Table 2, Appendix S1). Among the more speciose taxonomic groups, there was a high percentage 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); representation among bats was lower (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 five bat species) for which we have records of predation by cats are listed as threatened by the IUCN or in Australia's EPBC Act (one or more subspecies; 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, a major exception was 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, 801 specimens of 71 native mammal species (and a further 32 specimens of four introduced species) were reported as killed by cats. The species with the most cat-killed individuals among the 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): they were rarer and/or more restricted. The differences in

Table 2. Collated tally of number of extant, terrestrial, native Australian mammal species reported as consumed or killed by feral and/or pet cats *Felis catus*. The number of records is also given as a percentage of total Australian extant, terrestrial, native species (in parentheses), i.e. 210, 78, and 288 for non-volant, volant, and total mammal species, respectively

Record type	Non-volant (210)	Volant (78)	Total (288)
Consumed by cats (records from all cat sources, i.e. feral and pet cats; and also including large-bodied mammal species weighing > 2 kg and assumed to be consumed as carrion)	146 (70%)	24 (31%)	170 (59%)
Killed (preyed upon) by cats (records from all cat sources, i.e. feral and pet cats)	127 (60%)	24 (31%)	151 (52%)
Killed by feral cats (records only from feral cat diet studies, autecological studies)	118 (56%)	9 (12%)	127 (44%)
Killed by pet cats (records only from pet cat diet studies, autecological studies, museums, veterinary records)	61 (29%)	20 (26%)	81 (28%)

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 traits of non-volant species to the presence/absence of cat-predation records derived from all cat (feral and pet cat) sources, 18 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 (rock-dwelling) and body mass, respectively, i.e. most of the variation in each of these variables was explained by its 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 cats, and the optimal model containing these variables showed that the relative probability of a non-volant mammal species being preyed upon by 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, six 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 cat prey (Table 3). Body mass, rainfall and saxicoline were highly influential predictors, but the slope of the body mass trend was less steep and confidence intervals broadened, particularly for smaller body mass (Fig. 3). These relationships were similar when records were reduced to those obtained from feral cat sources only (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 diet studies in a species' range was the only important predictor of cat predation from all data sources, as well as when reduced to feral cat sources only ($w+ = 1.00$); 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 only, 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 non-volant mammal species with the greatest risk of predation by feral cats included mulgaras *Dasycercus* spp., kowari *Dasyuroides*

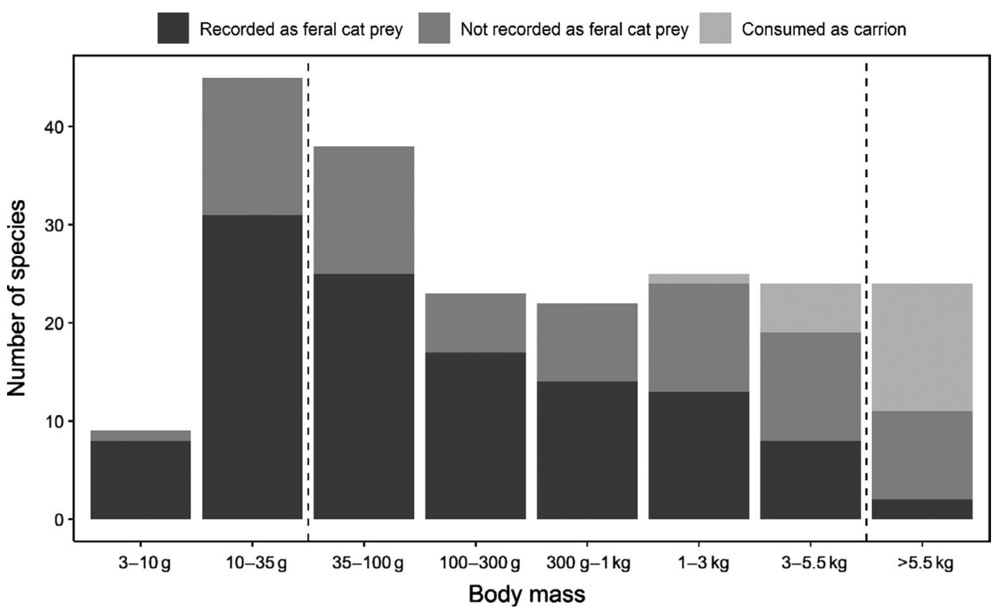

Fig. 2. Number of non-volant, extant, terrestrial, native mammal species in each body mass category recorded as, or not recorded as, feral cat prey in Australia. Also shown are records of the number of species consumed as carrion, or assumed to be consumed as carrion, for large-bodied species > 2 kg. Only records of predation by feral cats are included, i.e. museum-sourced records of predation, veterinary records and pet cat diet or autecological studies are excluded (see Appendix S1). Dashed lines represent the body mass extent of the 'critical weight range' (CWR) for mammals, i.e. 35–5500 g (Burbidge & McKenzie 1989).

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 predation by all cats (feral cats and pet cats), or by feral cats alone (i.e. museum-sourced records of predation, veterinary records and pet cat diet studies are excluded) on non-volant native mammals, with inclusion and exclusion of offsets to account for abundance and sampling bias. Highly influential variables ($w+ \geq 0.73$) are indicated in bold. See Table 1 for variable definitions

		Offsets included		Offsets excluded	
Records	Variable	$w+$	N	$w+$	N
All cats (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
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

byrnei, marsupial moles *Notoryctes* spp., greater stick-nest rat *Leporillus conditor*, many smaller dasyurids and medium-sized to large rodents, among others (Table 4, Appendix S3): 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; 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 researchers previously reporting these patterns have largely speculated that predation by the introduced domestic cat and the European red fox *Vulpes vulpes* may be responsible for this patterning of decline. Here, we show from analysis of records of predation by cats that this inference is reasonable, because the 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 of most species of Australia's diverse native mammal fauna, and traits analysis associates this predation directly with the extremely high rates of mammal decline and extinction seen throughout the continent over the last 200 years (Woinarski et al. 2015). Fifty threatened Australian mammal species are known to be killed by cats, and we

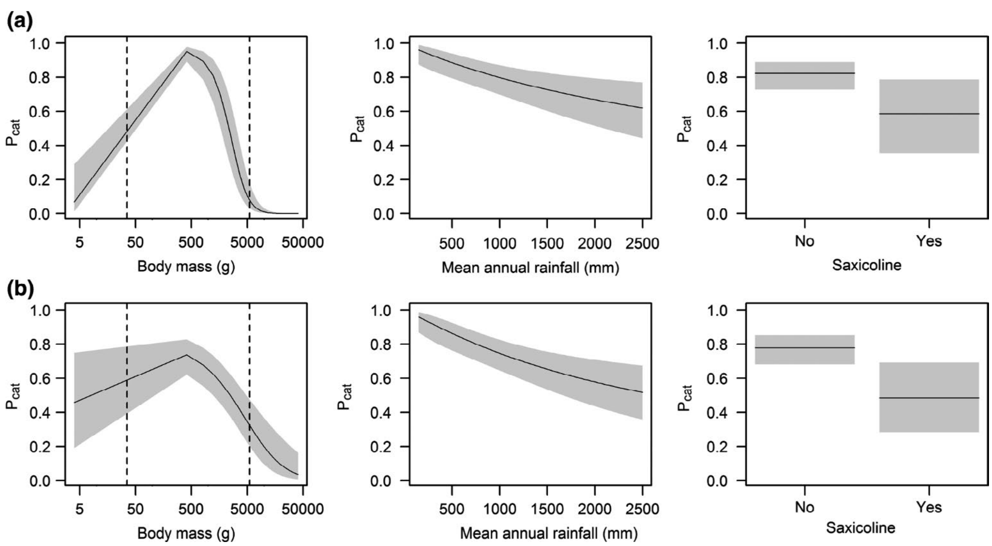

Fig. 3. Relationship between the relative likelihood of a non-volant mammal species being preyed upon by cats (including feral and pet cats; P_{cat}) and predictor variables derived from logistic regression (a) including and (b) excluding offsets for abundance and sampling bias. All variable relationships 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). Prey animals classed as saxicoline mostly inhabit rocky substrates. See Appendix S5 for relationships derived only from feral cat sources.

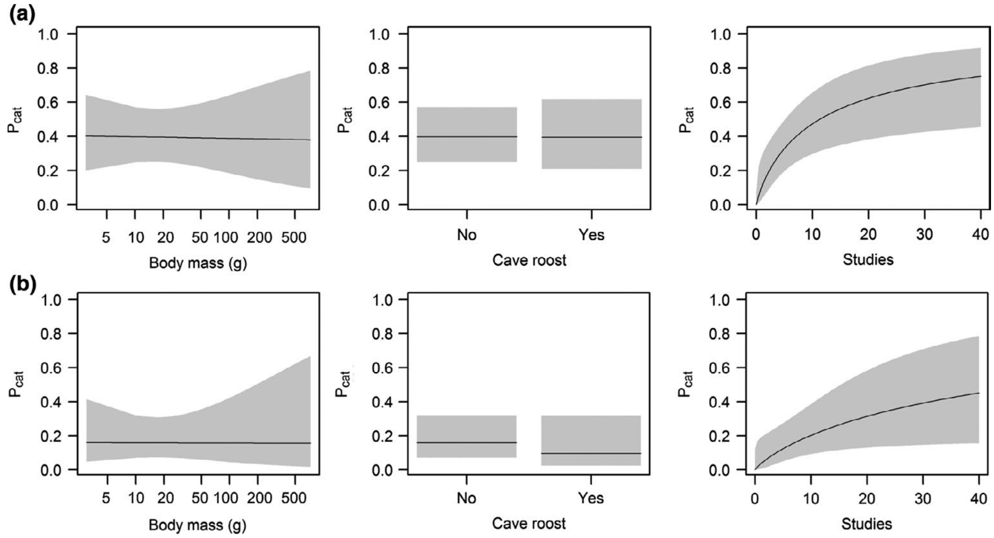

Fig. 4. Relationship between predictor variables and the relative likelihood of a bat species being preyed upon by (a) all cats, or (b) feral cats (P_{cat}), derived for each variable from the optimal logistic regression model while holding other variables at their mean value (continuous variables) or most common category (categorical variable). Continuous black lines represent model fit and grey bands represent the 95% confidence intervals. The variable 'Cave roost' indicates whether bats roost in caves or elsewhere; 'Studies' is the total number of cat diet studies conducted within a species' extant range.

show that many of these species have traits associated with the greatest risk 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 diet studies, additional unpublished diet studies, autecological studies, museum records, and veterinary reports. Most of the 64 non-volant species for which we could locate no records of predation or consumption by cats are rare or poorly studied or occupy restricted ranges (< 10000 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 predation by cats for all but the larger species is a sampling artefact and that almost all species are in fact preyed upon by cats. We also note that cats may fatally injure or kill mammals that they do not consume (McGregor et al. 2015), so that diet studies alone may result in an underestimate of the 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 percentage 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 predation of bats by cats, and the impacts of such predation, may be greater than previously recognised (Ancillotto et al. 2013, Welch & Leppanen 2017). The clear relationship we found between records of predation by cats and the number of cat diet 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 that the many recent taxonomic changes to Australian bats (e.g. Reardon et al. 2014) render past records from cat diet 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; such records are typically of intact animals that are 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

Table 4. The non-volant, extant, terrestrial, native mammal species with greatest relative likelihood 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 a complete listing of the relative likelihood (ranging from 0 to 1) of feral cat predation on all mammal species

Scientific name	Common name	Likelihood	95% CI	
			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

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

such a magnitude of cat diet 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 smaller 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. For example, 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 that 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 predation by cats 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 predation by cats 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 they are 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 predation by cats.

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, so they exhibited the traits we found to be highly associated with greatest likelihood of predation by cats. Although predation by cats is likely to have played a role in many of these extinctions, there are no or few records of predation by cats 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 they are active. Furthermore, our analysis linking traits with the likelihood of predation by cats of 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 than in other habitats (Hohnen et al. 2016), and in years of heavy 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 similar 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 poison baiting to reduce numbers of cats and foxes (Algar et al. 2013, Legge et al. 2018); in many cases, these measures result in at least local-scale recovery of some of the threatened 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 ranging from pet to feral cats, and community education and communication should be an important part of any management programme (Denny & Dickman 2010, Loss et al. 2018, Crowley et al. 2019).

ACKNOWLEDGEMENTS

The collation and analysis of data and the preparation of this paper were supported by the Australian Government's National Environmental Science Program through the Threatened Species Recovery Hub. We thank the Australian Research Council for grant funding (project DP 140104621) to CRD. We thank the Museum and Art Gallery of the Northern Territory (and curator Gavin Dally), Museum of Victoria (Laura Cook), Tasmanian Museum and Art Gallery (Belinda Bauer), Western Australian Museum (Rebecca Bray), Australian National Wildlife Collection (CSIRO: Leo Joseph), Queensland Museum (Heather Janetzki, Andrew Amey), South Australian Museum (David Stemmer, Philippa Horton) and Australian Museum (Cameron Slatyer, Mark Eldridge) for records of mammals in their collection reported as killed by cats. We also thank Tony Buckmaster for provision of raw data and Joanne Antrobus (Parks Victoria) for providing assistance to DKPH. Thank you to Emiliano Mori and two anonymous reviewers who provided valuable comments on the manuscript. This paper rests on data arising from the labours of many people who have searched for and through cat faeces and the internal organs of dead cats; that effort is much appreciated.

REFERENCES

Abbott I, Peacock D, Short J (2014) The new guard: the arrival and impacts of cats and foxes. In: Glen AS, Dickman CR (eds) *Carnivores of Australia: Past, Present and Future*, 69–104. CSIRO Publishing, Collingwood, Australia.

Algar D, Onus M, Hamilton N (2013) Feral cat control as part of Rangelands Restoration at Lorna Glen (Matuwa), Western Australia: the first seven years. *Conservation Science Western Australia* 8: 367–381.

Ancillotto L, Serangeli MT, Russo D (2013) Curiosity killed the bat: domestic cats as bat predators. *Mammalian Biology* 78: 369–373.

Anson JR (2017) Predator proofing for conservation: an AWC perspective. *Australian Zoologist* 39: 352–358.

Banks PB, Dickman CR (2007) Alien predation and the effects of multiple levels of prey naiveté. *Trends in Ecology & Evolution* 22: 229–230.

Barton K (2018) *MuMIn: Multi-Model Inference*. R package version 1.40.4. https://CRAN.R-project.org/package=MuMIn. Accessed 17 December 2017.

Bradshaw JWS, Goodwin D, Legrand-Defrétin V, Nott HMR (1996) Food selection by the domestic cat, an obligate carnivore. *Comparative Biochemistry and Physiology* 114: 205–209.

Brunner H, Coman BJ (1974) *The Identification of Mammalian Hair*. Inkata Press, Melbourne, Australia.

Brunner H, Moro D, Wallis R, Andrasek A (1991) Comparison of the diets of foxes, dogs and cats in an urban park. *Victorian Naturalist* 108: 34–37.

Burbidge AA, Manly BFJ (2002) Mammal extinctions on Australian islands: causes and conservation implications. *Journal of Biogeography* 29: 465–473.

Burbidge AA, McKenzie NL (1989) Patterns in the modern decline of western Australia's vertebrate fauna: causes and conservation implications. *Biological Conservation* 50: 143–198.

Burbidge AA, Woinarski JCZ (2016) *Notoryctes typhlops*. *The IUCN Red List of Threatened Species* e.T14879A21965004.

Burbidge AA, McKenzie NL, Brennan KEC, Woinarski JCZ, Dickman CR, Baynes A, Gordon G, Menkhorst PW, Robinson AC (2009) Conservation status and biogeography of Australia's terrestrial mammals. *Australian Journal of Zoology* 56: 411–422.

Burnham KP, Anderson DR (2003) *Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach*. Springer, New York, USA.

Canfield PJ, Hartley WJ, Dubey JP (1990) Lesions of toxoplasmosis in Australian marsupials. *Journal of Comparative Pathology* 103: 159–167.

Childs JE (1986) Size-dependent predation on rats (*Rattus norvegicus*) by house cats (*Felis catus*) in an urban setting. *Journal of Mammalogy* 67: 196–199.

Coman BJ, Brunner H (1972) Food habits of the feral house cat in Victoria. *The Journal of Wildlife Management* 36: 848–853.
Crowley SL, Cecchetti M, McDonald RA (2019) Hunting behaviour in domestic cats: an exploratory study of risk and responsibility among cat owners. *People and Nature* 1: 18–30.
Denny EA, Dickman CR (2010) *Review of Cat Ecology and Management Strategies in Australia*. Invasive Animal Cooperative Research Centre, Canberra, Australia.
Dickman CR (1996) *Overview of the Impacts of Feral Cats on Australian Native Fauna*. Australian Nature Conservation Agency, Canberra, Australia.
Dickman CR, Newsome TM (2015) Individual hunting behaviour and prey specialisation in the house cat *Felis catus*: implications for conservation and management. *Applied Animal Behaviour Science* 173: 76–87.
Doherty TS (2015) Dietary overlap between sympatric dingoes and feral cats at a semiarid rangeland site in Western Australia. *Australian Mammalogy* 37: 219.
Doherty TS, Davis RA, van Etten EJB, Algar D, Collier N, Dickman CR et al. (2015) A continental-scale analysis of feral cat diet in Australia. *Journal of Biogeography* 42: 964–975.
Doherty TS, Glen AS, Nimmo DG, Ritchie EG, Dickman CR (2016) Invasive predators and global biodiversity loss. *Proceedings of the National Academy of Sciences of the United States of America* 113: 11261–11265.
Fancourt BA (2014) Rapid decline in detections of the Tasmanian bettong (*Bettongia gaimardi*) following local incursion of feral cats (*Felis catus*). *Australian Mammalogy* 36: 247–253.
Fancourt BA (2015) Making a killing: photographic evidence of predation of a Tasmanian pademelon (*Thylogale billardierii*) by a feral cat (*Felis catus*). *Australian Mammalogy* 37: 120–124.
Fancourt BA, Jackson RB (2014) Regional seroprevalence of *Toxoplasma gondii* antibodies in feral and stray cats (*Felis catus*) from Tasmania. *Australian Journal of Zoology* 62: 272–283.
Fisher DO, Johnson CN, Lawes MJ, Fritz SA, McCallum H, Blomberg SP et al. (2014) The current decline of tropical marsupials in Australia: is history repeating? *Global Ecology and Biogeography* 23: 181–190.
Fitzgerald BM (1988) Diet of domestic cats and their impact on prey populations. In: Turner DC, Bateson P (eds) *The Domestic Cat: its Biology and Behaviour*, 123–144. Cambridge University Press, Cambridge, UK.
Fleming PA, Anderson H, Prendergast AS, Bretz MR, Valentine LE, Hardy GES (2014) Is the loss of Australian digging mammals contributing to a deterioration in ecosystem function? *Mammal Review* 44: 94–108.
Gibson DF, Lundie-Jenkins G, Langford DG, Cole JR, Clarke DE, Johnson KA (1994) Predation by feral cats, *Felis catus*, on the rufous hare-wallaby, *Lagorchestes hirsutus*, in the Tanami Desert. *Australian Mammalogy* 17: 103–107.
Glen AS, Berry O, Sutherland DR, Garretson S, Robinson T, de Tores PJ (2010) Forensic DNA confirms intraguild killing of a chuditch (*Dasyurus geoffroii*) by a feral cat (*Felis catus*). *Conservation Genetics* 11: 1099–1101.
Groenewegen R, Harley D, Hill R, Coulson G (2017) Assisted colonisation trial of the eastern barred bandicoot (*Perameles gunnii*) to a fox-free island. *Wildlife Research* 44: 484–496.
Gurevitch J, Padilla DK (2004) Are invasive species a major cause of extinctions? *Trends in Ecology & Evolution* 19: 470–474.
Hayward MW, Poh ASL, Cathcart J, Churcher C, Bentley J, Herman K et al. (2015) Numbat nirvana: conservation ecology of the endangered numbat (*Myrmecobius fasciatus*) (Marsupialia : Myrmecobiidae) reintroduced to Scotia and Yookamurra Sanctuaries, Australia. *Australian Journal of Zoology* 63: 258–269.
Hohnen R, Tuft K, McGregor HW, Legge SM, Radford IJ, Johnson CN (2016) Occupancy of the invasive feral cat varies with habitat complexity. *PLoS ONE* 11: e0152520.
Hollings T, Jones M, Mooney N, McCallum H (2013) Wildlife disease ecology in changing landscapes: mesopredator release and toxoplasmosis. *International Journal for Parasitology: Parasites and Wildlife* 2: 110–118.
Jackson S, Groves C (2015) *Taxonomy of Australian Mammals*. CSIRO Publishing, Melbourne, Australia.
Johnson CN (2006) *Australia's Mammal Extinctions: a 50,000 Year History*. Cambridge University Press, Port Melbourne, Australia.
Johnson CN, Isaac JL (2009) Body mass and extinction risk in Australian marsupials: the 'Critical Weight Range' revisited. *Austral Ecology* 34: 35–40.
Jones E (1977) Ecology of the feral cat, *Felis catus* (L.), (Carnivora: Felidae) on Macquarie Island. *Australian Wildlife Research* 4: 249–262.
Kutt AS (2012) Feral cat (*Felis catus*) prey size and selectivity in north-eastern Australia: implications for mammal conservation. *Journal of Zoology* 287: 292–300.
Leahy L, Legge SM, Tuft K, McGregor HW, Barmuta LA, Jones ME, Johnson CN (2016) Amplified predation after fire suppresses rodent populations in Australia's tropical savannas. *Wildlife Research* 42: 705–716.
Legge S, Murphy BP, McGregor H, Woinarski JCZ, Augusteyn J, Ballard G et al. (2017) Enumerating a continental-scale threat: how many feral cats are in Australia? *Biological Conservation* 206: 293–303.
Legge S, Woinarski J, Burbidge A, Palmer R, Ringma J, Radford J et al. (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: 627–644.

Loss SR, Marra PP (2017) Population impacts of free-ranging domestic cats on mainland vertebrates. *Frontiers in Ecology and the Environment* 15: 502–509.

Loss SR, Will T, Marra PP (2013) The impact of free-ranging domestic cats on wildlife of the United States. *Nature Communications* 4: 1396.

Loss SR, Will T, Longcore T, Marra PP (2018) Responding to misinformation and criticisms regarding United States cat predation estimates. *Biological Invasions* 20: 3385–3396.

McComb LB, Lentini PE, Harley DKP, Lumsden LF, Antrobus JS, Eyre AC, Briscoe NJ (2018) Feral cat predation on Leadbeater's possum (*Gymnobelideus leadbeateri*) and observations of arboreal hunting at nest boxes. *Australian Mammalogy* 41: 262–265.

McDonald PJ, Brim-Box J, Nano CEM, Macdonald DW, Dickman CR (2018) Diet of dingoes and cats in central Australia: does trophic competition underpin a rare mammal refuge? *Journal of Mammalogy* 99: 1120–1127.

McEvoy J, Sinn DL, Wapstra E (2008) Know thy enemy: behavioural response of a native mammal (*Rattus lutreolus velutinus*) to predators of different coexistence histories. *Austral Ecology* 33: 922–931.

McGregor H, Legge S, Jones ME, Johnson CN (2015) Feral cats are better killers in open habitats, revealed by animal-borne video. *PLoS ONE* 10: e0133915.

McKenzie NL, Burbidge AA, Baynes A, Brereton RN, Dickman CR, Gordon G et al. (2007) Analysis of factors implicated in the recent decline of Australia's mammal fauna. *Journal of Biogeography* 34: 597–611.

Medina FM, Bonnaud E, Vidal E, Tershy BR, Zavaleta ES, Donlan JC et al. (2011) A global review of the impacts of invasive cats on island endangered vertebrates. *Global Change Biology* 17: 3503–3510.

Mifsud G, Woolley PA (2012) Predation of the Julia Creek dunnart (*Sminthopsis douglasi*) and other native fauna by cats and foxes on Mitchell grass downs in Queensland. *Australian Mammalogy* 34: 188–195.

Molsher R, Newsome AE, Dickman CR (1999) Feeding ecology and population dynamics of the feral cat (*Felis catus*) in relation to the availability of prey in central-eastern New South Wales. *Wildlife Research* 26: 593–607.

Moseby KE, Read JL, Paton DC, Copley P, Hill BM, Crisp HA (2011) Predation determines the outcome of 10 reintroduction attempts in arid South Australia. *Biological Conservation* 144: 2863–2872.

Murphy BP, Woolley L-A, Geyle HM, Legge SM, Palmer R, Dickman CR et al. (2019) Introduced cats (*Felis catus*) eating a continental fauna: the number of mammals killed in Australia. *Biological Conservation* 237: 28–40.

Paltridge R (1998) Occurrence of marsupial mole (*Notoryctes typhlops*) remains in the faecal pellets of cats, foxes and dingoes in the Tanami Desert, N.T. *Australian Mammalogy* 20: 427–429.

Paltridge R, Gibson D, Edwards G (1997) Diet of the feral cat (*Felis catus*) in Central Australia. *Wildlife Research* 24: 67–76.

Peacock D, Abbott I (2014) When the 'native cat' would 'plague': historical hyperabundance in the quoll (Marsupialia : Dasyuridae) and an assessment of the role of disease, cats and foxes in its curtailment. *Australian Journal of Zoology* 62: 294–344.

Pedler RD, Brandle R, Read JL, Southgate R, Bird P, Moseby KE (2016) Rabbit biocontrol and landscape-scale recovery of threatened desert mammals. *Conservation Biology* 30: 774–782.

Phillips S, Coburn D, James R (2001) An observation of cat predation upon an eastern blossom bat *Syconycteris Australis*. *Australian Mammalogy* 23: 57–58.

Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* 52: 273–288.

R Core Team (2018) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Radford IJ, Gibson LA, Corey B, Carnes K, Fairman R (2015) Influence of fire mosaics, habitat characteristics and cattle disturbance on mammals in fire-prone savanna landscapes of the Northern Kimberley. *PLoS ONE* 10: e0130721.

Radford J, Woinarski J, Legge S, Baseler M, Bentley J, Burbidge AA et al. (2018) Degrees of population-level susceptibility of Australian terrestrial non-volant mammal species to predation by the introduced red fox (*Vulpes vulpes*) and feral cat (*Felis catus*). *Wildlife Research* 45: 645–657.

Read J, Bowen Z (2001) Population dynamics, diet and aspects of the biology of feral cats and foxes in arid South Australia. *Wildlife Research* 28: 195–203.

Read JL, Dagg E, Moseby KE (2018) Prey selectivity by feral cats at central Australian rock-wallaby colonies. *Australian Mammalogy* 41: 132–141.

Reardon TB, McKenzie NL, Cooper SJB, Appleton B, Carthew S, Adams M (2014) A molecular and morphological investigation of species boundaries and phylogenetic relationships in Australian free-tailed bats Mormopterus (Chiroptera: Molossidae). *Australian Journal of Zoology* 62: 109–136.

Richards SA (2005) Testing ecological theory using the information-theoretic approach: examples and cautionary results. *Ecology* 86: 2805–2814.

Simberloff D, Martin J-L, Genovesi P, Maris V, Wardle DA, Aronson J et al. (2013) Impacts of biological invasions: what's what and the way forward. *Trends in Ecology & Evolution* 28: 58–66.

Spencer EE, Crowther MS, Dickman CR (2014) Diet and prey selectivity of three species of sympatric mammalian predators in central Australia. *Journal of Mammalogy* 95: 1278–1288.

Stokeld D, Fisher A, Gentles T, Hill B, Triggs B, Woinarski JCZ, Gillespie GR (2018) What do predator diets tell us about mammal declines in Kakadu National Park? *Wildlife Research* 45: 92–101.

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

Welch JN, Leppanen C (2017) The threat of invasive species to bats: a review. *Mammal Review* 47: 277–290.

Woinarski JCZ, Burbidge AA, Harrison PL, Milne DJ (2014) *The Action Plan for Australian Mammals 2012*. CSIRO Publishing, Collingwood, Victoria, Australia.

Woinarski JCZ, Burbidge AA, Harrison PL (2015) Ongoing unraveling of a continental fauna: decline and extinction of Australian mammals since European settlement. *Proceedings of the National Academy of Sciences of the United States of America* 112: 4531–4540.

Woinarski JCZ, Murphy BP, Legge SM, Garnett ST, Lawes MJ, Comer S et al. (2017a) How many birds are killed by cats in Australia? *Biological Conservation* 214: 76–87.

Woinarski JCZ, Woolley LA, Garnett ST, Legge SM, Murphy BP, Lawes MJ et al. (2017b) Compilation and traits of Australian bird species killed by cats. *Biological Conservation* 216: 1–9.

Woinarski JCZ, Murphy BP, Palmer R, Legge SM, Dickman CR, Doherty TS et al. (2018) How many reptiles are killed by cats in Australia? *Wildlife Research* 45: 247–266.

Yip SJS, Rich M-A, Dickman CR (2014) Diet of the feral cat, *Felis catus*, in central Australian grassland habitats during population cycles of its principal prey. *Mammal Research* 60: 39–50.

Ziembicki MR, Woinarski JCZ, Mackey B (2013) Evaluating the status of species using indigenous knowledge: novel evidence for major native mammal declines in northern Australia. *Biological Conservation* 157: 78–92.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1. List of extant Australian mammal species and records of predation by cats.

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

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

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

Appendix S5. Feral cat predation records. Regression relationships between highly influential predictor variables and the likelihood of a non-volant mammal species being killed by feral cats.

Appendix S6. 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 feral and pet cat sources), as well as including records for all larger species (>2 kg) assumed to be attributed to carrion consumption by cats.