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# 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*)

*James Q. Radford*[A,U,*], *John C. Z. Woinarski*[B], *Sarah Legge*[C,D], *Marcus Baseler*[E], *Joss Bentley*[F], *Andrew A. Burbidge*[G], *Michael Bode*[H], *Peter Copley*[I], *Nicholas Dexter*[J], *Chris R. Dickman*[K], *Graeme Gillespie*[L], *Brydie Hill*[L], *Chris N. Johnson*[M], *John Kanowski*[N], *Peter Latch*[O], *Mike Letnic*[P], *Adrian Manning*[D], *Peter Menkhorst*[Q], *Nicola Mitchell*[R], *Keith Morris*[S], *Katherine Moseby*[T], *Manda Page*[S] and *Jeremy Ringma*[R]

[A]Bush Heritage Australia, PO Box 329, Flinders Lane, Melbourne, Vic. 8009, Australia.
[B]Research Institute for the Environment and Livelihoods, Charles Darwin University, Casuarina, NT 0909, Australia.
[C]Centre for Biodiversity and Conservation Science, University of Queensland, St Lucia, Qld 4072, Australia.
[D]Fenner School of Environment and Society, The Australian National University, Canberra, ACT 2601, Australia.
[E]Environmental Resources Information Network, Department of the Environment and Energy, GPO Box 787, Canberra, ACT 2601, Australia.
[F]Ecosystems and Threatened Species, Office of Environment and Heritage, 11 Farrer Place, Queanbeyan, NSW 2620, Australia.
[G]Independent Researcher, WA 6014, Australia.
[H]School of Mathematical Sciences, Queensland University of Technology, 2 George St, Gardens Point, Brisbane, Qld. 4000, Australia.
[I]Conservation and Land Management Branch, Department of Environment, Water and Natural Resources, GPO Box 1047, Adelaide, SA 5001, Australia.
[J]Booderee National Park, Parks Australia, Village Road, Jervis Bay, NSW 2540, Australia.
[K]Desert Ecology Research Group, School of Life and Environmental Sciences, University of Sydney, Sydney, NSW 2006, Australia.
[L]Flora and Fauna Division, Department of Environment and Natural Resources, 564 Vanderlin Drive, NT 0828, Australia.
[M]School of Biological Sciences & Australian Research Council Centre of Excellence for Australian Biodiversity and Heritage, University of Tasmania, Hobart, Tas. 7005, Australia.
[N]Australian Wildlife Conservancy, Subiaco East, WA 6008, Australia.
[O]Terrestrial Species Conservation, Department of the Environment and Energy, GPO Box 787, Canberra, ACT 2601, Australia.
[P]Centre for Ecosystem Science, University of New South Wales, Sydney, NSW 2052, Australia.
[Q]Arthur Rylah Institute for Environmental Research, Department of Environment, Land, Water and Planning, PO Box 137, Heidelberg, Vic. 3084, Australia.
[R]School of Biological Sciences, The University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia.
[S]Department of Biodiversity, Conservation and Attractions, Locked Bag 104, Bentley Delivery Centre, WA 6983, Australia.
[T]Arid Recovery, PO Box 147, Roxby Downs 5725; and University of NSW, Sydney, NSW 2052, Australia.
[U]Corresponding author. Email: J.Radford@latrobe.edu.au

[*]James Q. Radford is now affiliated with Department of Ecology, Environment and Evolution and Research Centre for Future Landscapes, La Trobe University, Bundoora, Vic. 3086, Australia.

**Abstract**

***Context.*** Over the last 230 years, the Australian terrestrial mammal fauna has suffered a very high rate of decline and extinction relative to other continents. Predation by the introduced red fox (*Vulpes vulpes*) and feral cat (*Felis catus*) is implicated in many of these extinctions, and in the ongoing decline of many extant species.

***Aims.*** To assess the degree to which Australian terrestrial non-volant mammal species are susceptible at the population level to predation by the red fox and feral cat, and to allocate each species to a category of predator susceptibility.

***Methods.*** We collated the available evidence and complemented this with expert opinion to categorise each Australian terrestrial non-volant mammal species (extinct and extant) into one of four classes of population-level susceptibility to introduced predators (i.e. 'extreme', 'high', 'low' or 'not susceptible'). We then compared predator susceptibility with conservation status, body size and extent of arboreality; and assessed changes in the occurrence of species in different predator-susceptibility categories between 1788 and 2017.

***Key results.*** Of 246 Australian terrestrial non-volant mammal species (including extinct species), we conclude that 37 species are (or were) extremely predator-susceptible; 52 species are highly predator-susceptible; 112 species are of low susceptibility; and 42 species are not susceptible to predators. Confidence in assigning species to predator-susceptibility categories was strongest for extant threatened mammal species and for extremely predator-susceptible species. Extinct and threatened mammal species are more likely to be predator-susceptible than Least Concern species; arboreal species are less predator-susceptible than ground-dwelling species; and medium-sized species (35 g–3.5 kg) are more predator-susceptible than smaller or larger species.

***Conclusions.*** The effective control of foxes and cats over large areas is likely to assist the population-level recovery of ~63 species – the number of extant species with extreme or high predator susceptibility – which represents ~29% of the extant Australian terrestrial non-volant mammal fauna.

***Implications.*** Categorisation of predator susceptibility is an important tool for conservation management, because the persistence of species with extreme susceptibility will require intensive management (e.g. predator-proof exclosures or predator-free islands), whereas species of lower predator susceptibility can be managed through effective landscape-level suppression of introduced predators.

**Additional keywords:** invasive species, conservation management, introduced predator-proof exclosures, introduced predator-free islands, wildlife management.

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## Introduction

The Australian terrestrial mammal fauna has suffered severe rates of loss over the last ~200 years, with the extinction of at least 30 species (~10% of the modern fauna) at a rate of 1–2 extinctions per decade since the 1850s (Woinarski *et al*. 2015). Many surviving species have declined extensively, and many that persist do so tenuously and only because of ongoing intensive conservation management. The likelihood of the recovery of this fauna (or of the prevention of further extinctions) hinges on accurate identification of key causal factors, and effective control of those threats. Many factors are implicated in the declines (McKenzie 1981; Burbidge and McKenzie 1989; Morton 1990), but predation by the introduced red fox (*Vulpes vulpes*) and/or feral cat (*Felis catus*) is implicated – with varying levels of certainty – in a majority of the declines and extinctions (Burbidge and McKenzie 1989; Short and Smith 1994; Smith and Quin 1996; Kinnear *et al*. 2002; Johnson 2006; Woinarski *et al*. 2014; Woinarski *et al*. 2015; Ziembicki *et al*. 2015).

Increasingly over recent decades, Australian conservation managers have used a range of actions to reduce predation pressure to recover threatened mammal species (Woinarski *et al*. 2014; Legge *et al*. 2018). Much of this conservation effort is highly interventionist, so it is imperative that resources are effectively targeted to the species most in need, and to the management actions that are most likely to result in long-term conservation benefit. For native Australian species susceptible at a population level to introduced predators, these management responses include: establishing fenced areas (exclosures) from which introduced predators can be removed (Dickman 2012; Hayward *et al*. 2014); managing naturally occurring populations on, or translocating susceptible species to, islands without introduced predators or from which introduced predators have been eradicated (Burbidge *et al*. 2018); poison-baiting, trapping or shooting to reduce introduced predator density at landscape or local scales (Algar *et al*. 2013); and managing other factors (e.g. fire, dingoes (*Canis familiaris*), livestock and alternative prey sources) that may influence the abundance, hunting proficiency or diet of introduced predators (Doherty *et al*. 2017). In this paper, predator susceptibility refers specifically to susceptibility to the red fox and feral cat, and does not include susceptibility to native predators.

These management options vary appreciably in their cost, spatial extent and duration of effectiveness, in their ability to reduce predator density, in the logistical and geographic constraints on implementation, and consequently, in their efficacy in recovering threatened mammal species. Furthermore, for a range of life history, anatomical, physiological, behavioural and ecological reasons, native mammal species will vary in the degree to which they are susceptible to introduced predators.

If managers are to apply the most appropriate and effective management options for controlling introduced predators for a particular threatened species, it is important to determine the extent to which the population viability of the threatened species varies in response to the occurrence of these two introduced predators.

The predator susceptibility of native mammal species can be assessed from various sources of evidence. Strong inference can be gained from rigorous experimental studies (e.g. comparisons of population sizes in matched areas with and without introduced predators), although such experimental studies are uncommon in Australia and have generally been undertaken over relatively short time frames (Kinnear *et al*. 1988; Kinnear *et al*. 1998; Hone 1999; Kinnear *et al*. 2010; Frank *et al*. 2014). Reasonably strong inference is also provided by studies that compare the fate of native mammals on islands or mainland areas with or without introduced predators, or before and after predator introduction or removal (Woinarski *et al*. 2011; Jones *et al*. 2016). Translocations of mammals to fox- and cat-free offshore islands is a well established conservation management tool in Australia (Burbidge 1999; Morris *et al*. 2015; Burbidge *et al*. 2018), and has contributed greatly to our knowledge about predator susceptibility. More recently, translocations into fox- and cat-free fenced exclosures in different regions and environments (Moseby *et al*. 2011; Dickman 2012; Hayward *et al*. 2014) have augmented this evidence base for predator susceptibility, although knowledge gaps remain for northern Australia where there have been relatively few translocations to islands and fenced areas (Legge *et al*. 2018).

Strong inference can also be provided by studies that document rates of mortality due to introduced predators, contextualised within population viability models; however, there are few such examples for Australian mammal species (Lindenmayer *et al*. 1993). Weaker inference is available from correlative studies that chart the temporal and spatial pattern of decline in native mammal species in relation to the spread of foxes and cats (Burbidge *et al*. 1988; Dickman *et al*. 1993; Smith and Quin 1996; Short 1998; Johnson *et al*. 2007; McKenzie *et al*. 2007; Abbott 2008*a*; Abbott 2008*b*; Menkhorst 2009; Abbott *et al*. 2014; Pedler *et al*. 2016). Limited historical information makes it difficult to describe the pattern of decline for some species (Burbidge *et al*. 1988; Bilney *et al*. 2010; Bilney 2014; Ziembicki *et al*. 2013), but such correlative insights may be the only evidence available to infer the factors involved in the decline of some species. Even correlative evidence may be unavailable for poorly known species where the extent of decline and factors contributing to that decline are largely unresolved, the timing of their extinction is difficult to pinpoint or there may have been spatial and temporal coincidence in the arrival of other novel factors that contributed to their decline (McDowell *et al*. 2015).

Native mammal species may be ordered along a predator-susceptibility gradient, from those that are highly unlikely to persist with any incidence of foxes or cats, through those that can persist – albeit at reduced densities – with some level of fox or cat presence, to those that are relatively unaffected by foxes or cats. For those species most sensitive to introduced predators, conservation management needs to ensure that the control of introduced predators is absolute (or in some cases, virtually so), mindful that simply reducing but not eliminating introduced predators may be a waste of resources. In contrast, such intensive interventions may not be required to retain or recover species with lower susceptibility. Instead, sustained management that perpetually reduces introduced predator abundance below a given threshold (at which the native mammal species can retain population viability) may be adequate and more cost efficient.

Detrimental impacts of introduced predators on native mammal species may not be due to predation alone. Introduced predators may exert competitive interference by reducing the abundance of prey species used by native carnivores and insectivores (Glen and Dickman 2008; Pavey *et al*. 2008). They may also transmit novel diseases to native mammals. Most notably, cats are the sole primary host in Australia for toxoplasmosis, although the population-level impacts of this disease on Australian mammals remain poorly resolved (Fancourt *et al*. 2014). In this paper, we do not seek to differentiate the mechanism (predation, competition or disease) that drives the responses of native mammal species to introduced predators, but rather to characterise the population-level susceptibility of native species to these introduced predators.

Our objective here is to assess the population-level susceptibility of all Australian terrestrial non-volant mammal species to introduced foxes and cats (as per Table 1). Bats were excluded from this assessment because they are not currently a primary focus for translocations and introduced predator management, but it should be noted that this does not imply that introduced predators have no impacts on bats. Previous approaches have ranked the susceptibility of some threatened species to introduced predators on the basis of bodyweight, habitat use, mobility, behaviour and life-history traits (Dickman 1996; Newsome *et al*. 1997). Our assessments were informed by this approach but we undertake a more comprehensive review, informed by a much larger evidence base comprised of the population-level response of species to the occurrence of introduced predators.

We then consider predator susceptibility in relation to a species' conservation status, weight and arboreal habit, and compare the historic (before the widespread introduction of cats and foxes) and contemporary occurrence of species by predator-susceptibility categories. This assessment is essential for characterising a continental-scale response of a large group of species to a single threatening process (introduced predators) and for shaping conservation management interventions: predator susceptibility will be a major determinant of the intensity, type and cost of introduced predator management required for a particular native mammal species.

## Materials and methods

For all 246 Australian terrestrial non-volant mammal species (*sensu* Jackson and Groves 2015; and subsequent taxonomic updates; e.g. Travouillon and Phillips (2018)), we collated relevant information relating to predator susceptibility. The 124 species considered Extinct, threatened (Critically Endangered, Endangered or Vulnerable), Near Threatened, or Data Deficient under IUCN Red List Version 2017-3 (IUCN 2017) classification were also subject to an expert elicitation process (see below). For a small number of species not considered by the IUCN classification, we used a recent comprehensive review of the conservation status of Australian mammals (Woinarski *et al*. 2014; and subsequent updates published online – http://members.iinet.net.au/~amburbidge@westnet.com.au/). The predator response information was derived from a wide range of published and unpublished (e.g. expert opinion, local knowledge and government, non-government and community groups associated with translocation and predator control programs) sources, including: information on responses of native mammal species to introduced predator exclusion and other forms of predator control; the fate of island populations with and without introduced predators; spatial and temporal patterning of decline with respect to spread of introduced predators; and mortality patterns and incidence of the focal species in the diet of introduced predators. This information is summarised for each species in Table S1a, available as Supplementary Material to this paper. Based on this information, we categorised each species into one of the mutually exclusive predator-susceptibility classes described in Table 1, wherever possible seeking to discriminate the impacts of foxes from those attributable to cats. We used a series of guiding questions, or indicative characteristics (Table 2), to 'cross-check' the allocation of species to predator-susceptibility categories. We also assigned a degree of confidence in this categorisation ('strong', 'medium' or 'weak'), based on the consistency of the evidence and the strength of inference associated with the type of evidence.

Categorisation of predator susceptibility is challenging in many cases, particularly for those species where the evidence base is limited or apparently ambiguous. We provide a few examples here that illustrate the logic of our categorisation. The eastern bettong (*Bettongia gaimardi*) was extirpated from its mainland range, with predation by foxes being the primary cause (Short 1998), but has persisted in Tasmania, where foxes are absent but feral cats are present. It has recently been reintroduced successfully to an introduced predator-free exclosure in its former mainland range (Batson *et al*. 2016). Eastern quolls (*Dasyurus viverrinus*) exhibit similar characteristics (TSSC 2015). In both cases, we categorised the species as extremely predator-susceptible, but with this categorisation explicitly in relation to fox predation.

Many species (e.g. southern brown bandicoot (*Isoodon obesulus*), long-footed potoroo (*Potorous longipes*), long-nosed bandicoot (*Perameles nasuta*)) are now restricted to habitats with dense understorey vegetation (e.g. heathlands), which provide some degree of protection from predators, and their abundance may be relatively stable (Robley *et al*. 2014). Some of these species may have had more extensive distributions

**Table 1. Definition of categories of predator susceptibility used in this assessment and their implications for conservation management**

| Category | Population-level response | Implications for management |
|---|---|---|
| 0 | *Extreme predator susceptibility*: unable to persist where at least one of the introduced predators occur (may persist in areas where less impactful predator occurs at very low density). | Entirely dependent on introduced predator-free islands or fenced sanctuaries for persistence in the short term; translocations to open landscapes are likely to fail unless there is permanent and very stringent predator control. |
| 1 | *High level of predator susceptibility*: likely to persist over at least the short-term (e.g. 20 years) with introduced predators, but with severe reduction in population size or viability, *or* likely to persist with introduced predators where the predator abundance has been much reduced through predator control. The combined impacts of predation and other factors may render populations non-viable, but predation alone will not. | Will benefit from but not be absolutely dependent upon translocations to introduced predator-free islands or fenced sanctuaries *or* will need effective and sustained introduced predator control in open landscapes. |
| 2 | *Low level of predator susceptibility*: likely to persist with introduced predators with some reduction in population size or viability; will have higher viability where predators are more effectively controlled. | Population viability will benefit from, but persistence is not dependent on, effective and sustained introduced predator control in open landscapes, and are not dependent on islands or fenced sanctuaries. |
| 3 | *Not predator-susceptible*: viability is unaffected by introduced predators. | No requirements for introduced predator management (will not benefit from islands or fenced sanctuaries). |

**Table 2. Factors taken into account during predator susceptibility assessment**

| | Extreme | High | Low | Not |
|---|---|---|---|---|
| Is the species extirpated (due to introduced predators) from its former range on the mainland? | Yes | No | No | No |
| Is the species persisting only in introduced predator-free fenced sanctuaries or islands? | Yes | No | No | No |
| Is the species extant in the wild only in natural predator-free refuges or outside the range of primary introduced predator? | Yes | Yes | No | No |
| Has the species range contracted in areas without introduced predator control? | Yes | Yes | No | No |
| Has the species density decreased in areas without introduced predator control? | Yes | Yes | Yes | No |
| If the species has been reintroduced into the wild with introduced predators controlled but present, was the release successful? | No | Yes | Yes | Yes |
| If the species has been released into the wild with no introduced predator control has it been successful? | No | No | Yes | Yes |

and/or habitat breadth before the spread of introduced predators, but have contracted to those habitats or sites providing the most protection from predators. However, when these densely vegetated habitats are burnt or otherwise degraded, the resulting more-open vegetation may allow for episodes of substantially increased predation pressure, leading to population decline (Leahy *et al*. 2016; Hradsky *et al*. 2017). Conversely, where broad-scale predator control has been implemented effectively, local-scale population increases have been observed. We categorised these species as being highly predator-susceptible.

In contrast, some Australian mammal species are restricted to rainforests, where cats occur at low densities and foxes are usually absent (Johnson 2006; Legge *et al*. 2017). These habitats are generally not exposed to episodic disturbances that would allow for periods of more intense predation, so these species were mostly categorised as not predator-susceptible. Many Australian mammals (such as yellow-footed rock-wallaby, *Petrogale xanthopus*) live in rocky areas, which provide some natural refuge from predators. However, dispersal of these mammals between rocky sites, or foraging in surrounding areas, may be severely constrained by introduced predators, and introduced predators may have population-level impacts on the species even in rocky refuges (e.g. Sharp *et al*. 2015). In these cases, we concluded that predation pressure was constraining population growth, and such species were generally scored as highly predator-susceptible unless there was robust evidence indicating population stability, in which case they were scored as having low predator susceptibility. In a few cases (e.g. Maclear's rat (*Rattus macleari*) and the Bramble Cay melomys (*Melomys rubicola*)), extinction occurred primarily for reasons other than predation or before the introduction of foxes or cats. In these cases, we provided a 'not assessed' predator-susceptibility rating.

We recognise that there is some subjectivity in our judgement of predator susceptibility. To avoid any particular biases of individuals in this assessment, we convened a workshop attended by 26 experts with relevant and extensive research and management experience. For this exercise, experts were randomly assigned to one of four groups that each independently came to a consensus decision on a species' predator susceptibility. Each group assessed all threatened and Near Threatened taxa for which they felt qualified. We then calibrated the assessments of the four groups through facilitated group discussion. Note that this process was not undertaken in a rigorous expert-elicitation manner (McBride *et al*. 2012), but through consensus among group members; however, the use of four separate groups of experts provides some degree of cross-validation. The workshop focused on extant threatened and Near Threatened taxa only, and provided assessments at subspecies level (where subspecies were listed as threatened) – in the present paper, we combine those subspecies' categorisations into those for the species as a whole. Assessment of Extinct and Least Concern species occurred after the workshop, via email exchange among workshop participants, until consensus was reached.

We used chi-square tests to compare variation in the frequency distribution of species in predator-susceptibility categories in relation to IUCN conservation status and the extent to which species occupy arboreal habitats (i.e. fully arboreal, partly arboreal or terrestrial); we used ordinal logistic regression to examine the effect of female bodyweight ($\log_{10}$ transformed) on predator susceptibility. We used chi-square tests to compare confidence in allocation among predator-susceptibility categories, and in relation to IUCN conservation status.

We compared the historic and contemporary occurrence of species to examine differences in the geographic distribution of species' declines by predator-susceptibility category. To do this, for each predator-susceptibility category we first summed the total number of terrestrial non-volant native mammal species recorded from each of the Interim Biogeographic Regionalisation for Australia (IBRA) regions (Commonwealth of Australia 2017) in 1788. This is the 1788 'species score', which represents the number of species in each predator-susceptibility category per IBRA region in 1788. Each species was then assigned a score in each IBRA region that reflects their current (2017) status, whereby extinct = 0; severe decline of >90% of 1788 range or abundance = 0.1; decline of 50–90% of 1788 range or abundance = 0.5; persists in >50% of former range or abundance = 1, and increases of >50% of 1788 range or abundance = 1. We then calculated the 2017 'species score' by summing the individual species' scores. A 2017 species score that is comparable to the 1788 species score reflects minimal change in abundance or range of species within a given predator-susceptibility category for that IBRA region. A 2017 species score that is lower than the 1788 species score reflects a decline (or loss) of species within a given predator-susceptibility category within that region – the greater the discrepancy, the more severe the decline and loss of species. The 1788 and 2017 species scores were then mapped to graphically display the change in occurrence within each of the predator-susceptibility categories (low and not susceptible were combined). Data on mammal status by IBRA region were derived from McKenzie *et al*. (2007) and Burbidge *et al*. (2008), with ongoing updates. We note some level of circularity in this depiction, given that distributional contraction or stability was included as evidence in our assessment of a species' predator susceptibility.

## Results

Of the 246 Australian terrestrial non-volant mammal species, we categorised 37 as extremely predator-susceptible, 52 as highly predator-susceptible, 112 as of low predator susceptibility and 42 as not predator-susceptible; three species were not assessed (Table 3; Table S1a). Confidence in allocation to categories was weak for 152 species, and strong for only 24 of the 246 species. Confidence was highest for extremely predator-susceptible species and lowest for species of low predator susceptibility ($\chi^2 = 91.9$; d.f. = 6, $P < 0.001$; Fig. 1*a*). Confidence was also highest for Extinct and threatened species, and lowest for species categorised as Least Concern ($\chi^2 = 60.3$; d.f. = 6, $P < 0.001$; Fig. 1*b*).

There was reasonable agreement among the four independent groups of experts in predator-susceptibility categorisation for the set of threatened, Near Threatened and Data Deficient species they considered (Table S2). However, there was

**Table 3. Cross-tabulation of predator-susceptibility categories with IUCN conservation status for all Australian terrestrial non-volant mammal species**

Values in body of table are numbers of species. Values in parenthesis relate to species not assessed by IUCN (mostly because of recent taxonomic recognition) where conservation status is based on the Action Plan for Australian Mammals (Woinarski *et al*. 2014)

| Conservation status | Predator-susceptibility category | | | | | |
|---|---|---|---|---|---|---|
| | Extreme | High | Low | Not | Not assessed | Total |
| Extinct | 21 (+4) | 1 | 0 | 1 | 3 | 26 (+4) |
| Critically Endangered | 2 | 4 | 3 (+1) | 2 | 0 | 10 (+1) |
| Endangered | 1 | 7 | 1 (+2) | 2 | 0 | 11 (+2) |
| Vulnerable | 5 | 17 | 6 (+2) | 2 (+2) | 0 | 30 (+4) |
| Near Threatened | 3 | 7 (+1) | 13 (+2) | 10 | 0 | 33 (+3) |
| Least Concern | 1 | 15 | 80 (+3) | 23 | 0 | 119 (+3) |
| Total | 33 (+4) | 51 (+1) | 102 (+10) | 40 (+2) | 3 | 229 (+17) |

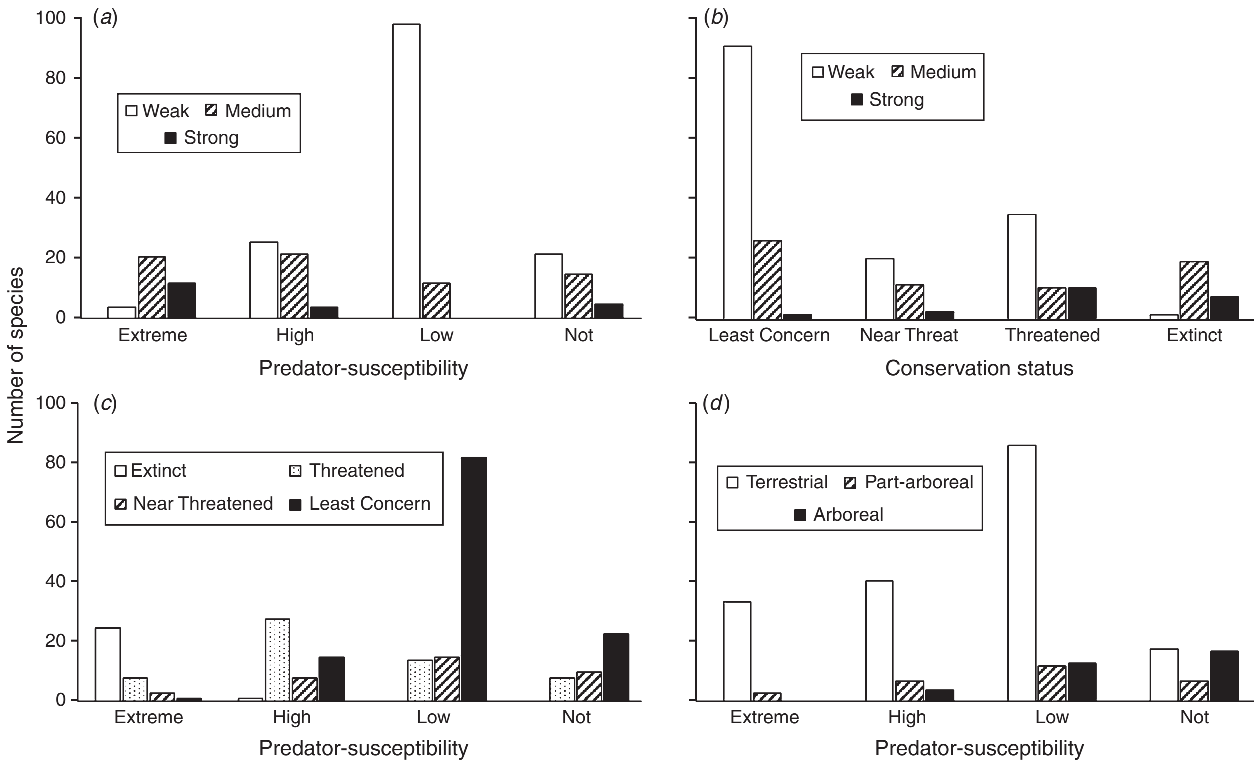


**Fig. 1.** Confidence in allocation of Australian native terrestrial non-volant mammal species to predator-susceptibility categories in relation to (*a*) predator susceptibility and (*b*) conservation status; and predator susceptibility of Australian native terrestrial non-volant mammal species in relation to (*c*) conservation status and (*d*) extent of arboreal habit.

divergent opinion for some species, mostly those with a particularly sparse information base, or where predator susceptibility appears to vary geographically or differ between the two introduced predator species.

Predator susceptibility was significantly associated with conservation status (note: Critically Endangered, Endangered and Vulnerable species were combined into 'threatened': $\chi^2 = 189$; d.f. = 9, $P < 0.001$; Fig. 1*c*). Of the 37 species categorised as of extreme predator susceptibility, 25 are Extinct, eight are threatened, three are Near Threatened and only one is of Least Concern. Most notably, 25 of the 30 Extinct species were categorised as extremely susceptible to predation, and threatened species (especially Endangered and Vulnerable species) were disproportionately more likely to be categorised as highly predator-susceptible (Table 3). Conversely, Least Concern species were more likely to be considered of low predator susceptibility (Table 3; Fig. 1*c*).

Terrestrial species were more predator-susceptible than partly or fully arboreal species ($\chi^2 = 37.1$; d.f. = 6, $P < 0.001$; Fig. 1*d*). Predator susceptibility was also related to body size, with species weighing between 35 g and 3.5 kg being more susceptible to predators than either smaller or larger species (Fig. 2). This was reflected in the ordinal logistic regression ($\chi^2 = 55.7$; d.f. = 2, $P < 0.001$), which supported a negative

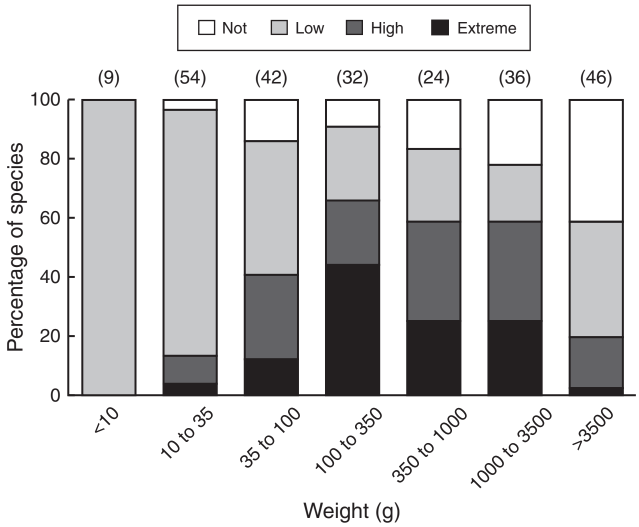


**Fig. 2.** Percentage of Australian native terrestrial non-volant mammal species in each predator-susceptibility category as a function of female bodyweight. Number of species in each weight division are in parentheses above each column.

quadratic relationship between predator susceptibility and female bodyweight: predator susceptibility ~intercept – 5.1 ($\log_{10}$weight) + 1.1($\log_{10}$weight)$^2$, where the intercept for extreme predator susceptibility = –7.0 ± 0.9, for high predator susceptibility = –5.7 ± 0.9, and for low predator susceptibility = –3.2 ± 0.8 (relative to not predator susceptible).

The spatio-temporal comparison indicates that before 1788, the occurrence of extremely predator-susceptible species was concentrated in the arid inland, parts of Western Australia and the sheep and wheat belt of south-eastern Australia (Fig. 3*a*). There has been a catastrophic collapse of these species across their continental range, except for some species in Tasmania (for species that can withstand some cat predation) and on offshore islands (Fig. 3*a*). Highly predator-susceptible species were more evenly distributed across the country and have also suffered broad-scale range reduction (Fig. 3*b*). The majority of highly predator-susceptible species now persist in northern Australia and Tasmania (outside the range of foxes), and some parts of south-western Australia where poison-baiting for foxes and cats is widespread, and in habitats of greater vegetation height and/or complexity along the eastern seaboard (Fig. 3*b*). The occurrence of low or not susceptible species has not exhibited such stark spatio-temporal changes (Fig. 3*c*). Decline of these species has occurred mainly in those bioregions subject to most environmental modification, such as the Murray–Darling Basin and Brigalow Belt of inland south-eastern Queensland (Fig. 3*c*).

## Discussion

More than half (73 of 124) of Australia's Extinct, threatened and Near Threatened terrestrial non-volant mammal species are here considered to exhibit (or have exhibited) an extreme or high degree of population-level susceptibility to foxes and/or cats. Most (25 species) of the 30 Extinct species considered here were assessed to have shown extreme susceptibility, and predation by foxes and/or cats was likely to have been a primary cause of these extinctions. This provides further support for the contention that introduced predators can exert sustained population-level impacts resulting in substantial to catastrophic declines in abundance and range, local extirpation and global extinction of native prey species, even at a continental scale (Bellard *et al*. 2016; Loss and Marra 2017; Russell and Blackburn 2017).

The recognition here that over half of Australia's Extinct and threatened or Near Threatened terrestrial non-volant mammal species are extremely or highly susceptible to introduced predators is consistent with claims that Australia's native fauna is particularly susceptible to introduced predators relative to native fauna on other continents (Salo *et al*. 2007). Most likely, this is attributable to Australia's geographic isolation and long evolutionary history without large placental mammalian predators, which has rendered most native mammal species without behavioural or morphological defences to avoid detection, or reduce probability of capture once detected, by introduced predators. The relatively recent arrival ~4000 years ago of the dingo (Corbett 2008) is the notable exception. However, their preference is for larger mammalian prey and carrion where available (Newsome *et al*. 1983; Thomson 1992; Brook and Kutt 2011) – most of which have relatively low predator susceptibility to foxes and cats (Fig. 2) – and dingoes may not have applied sufficient predation pressure to counter the inherent predator naiveté in most small to medium-sized mammals. Further, the rapidity with which foxes and cats spread to occupy virtually every habitat in Australia (often preceded and aided by the spread of rabbits *Oryctolagus cuniculus*) may have been too fast to allow adaptive responses by native species. The relatively slow reproductive rates of many Australian marsupials and rodents (Yom-Tov 1985) – a legacy of phylogeny and the low productivity of Australian environments – further decreases population viability under high predation rates. Changes to habitat structure caused by introduced mammalian herbivores and changes to fire regimes have also been concomitant with the expansion of introduced predators across much of Australia, further exposing native mammals (especially ground-dwelling species) to predation from introduced predators. Finally, the absence of any top-down predation pressure has allowed for the establishment of high densities of foxes and cats (especially in areas without dingoes), limited only by prey abundance (whether native species, introduced rabbits and rodents, or domestic stock).

Our results have profound implications for the conservation management of Australia's mammal fauna. Only 12 of the 216 extant terrestrial non-volant mammal species are categorised here to be of extreme predator susceptibility, and hence requiring the most stringent predator control management (typically translocations to islands and/or fenced exclosures). Ten of these species are already afforded some conservation security through recent management efforts that include them in predator-free exclosures, or through translocations to (or natural occurrence on) predator-free islands (Legge *et al*. 2018).

Our analyses suggest that a further 51 extant species would benefit from predator exclusion (i.e. those considered to be of high predator susceptibility), but should also persist (at lower densities) under management regimes that significantly reduce predator numbers in perpetuity, without necessarily eradicating

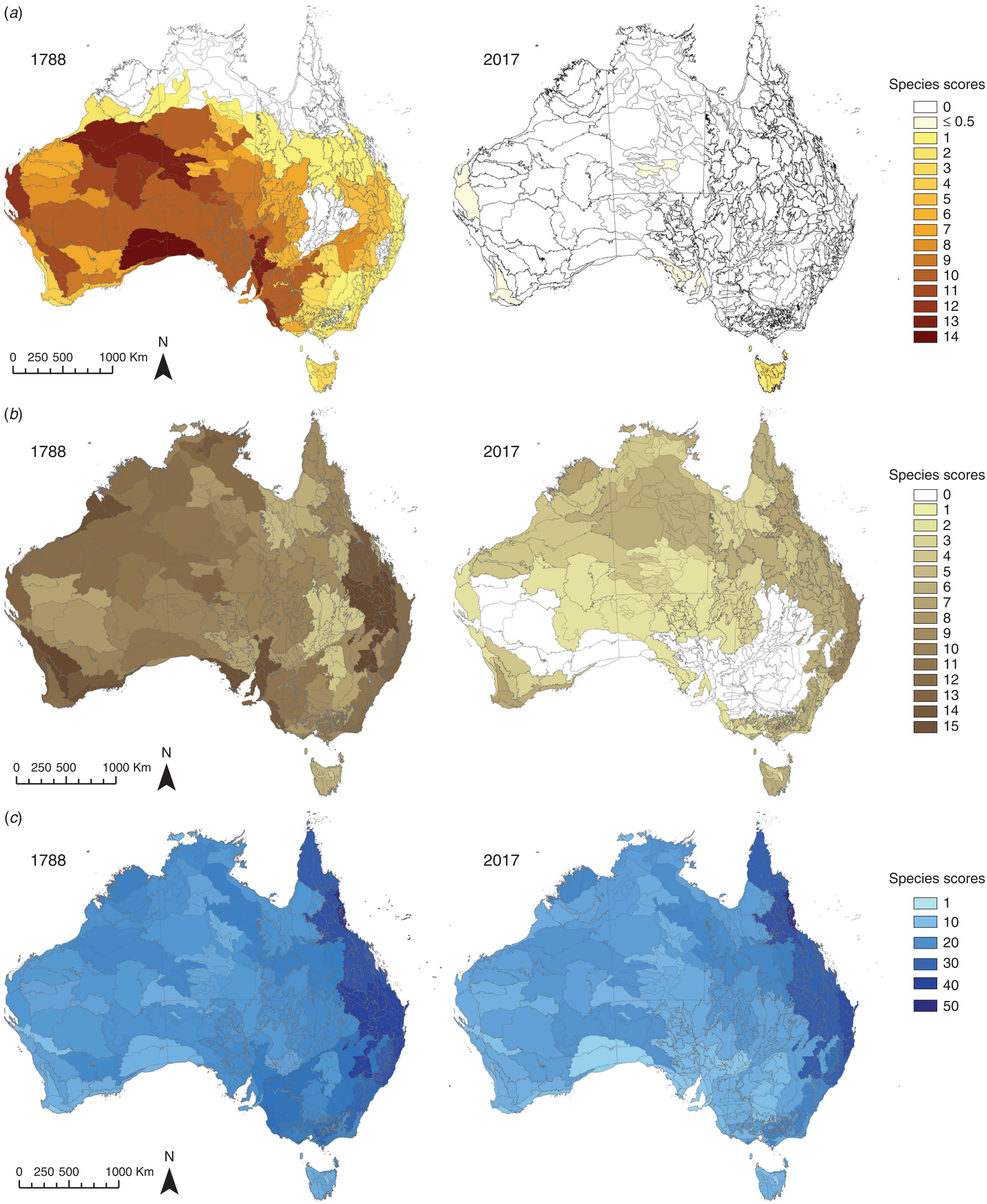


**Fig. 3.** Change from 1788 to 2017 in the bioregional occurrence of species by predator-susceptibility category (*a*) extreme, (*b*) high and (*c*) low and not susceptible combined. 'Species scores' in 1788 represent the number of species per Interim Biogeographic Regionalisation for Australia (IBRA) region in 1788. 'Species scores' in 2017 reflect the current number of species in each IBRA region, with species that have declined in a bioregion down-weighted accordingly (see Methods for details). Note that changes (or lack of changes) on most islands are not visible at this scale.

them. However, in most cases, there is insufficient information available to circumscribe thresholds for either predator density or the spatial extent of control that would allow for species persistence in different contexts, or of the degree of management intervention required to achieve that threshold. Notably, 23 of these 51 species are not yet considered threatened, but are likely to become so if effective predator management is not implemented (including in some cases, more effective biosecurity to prevent predator incursions to islands).

A further 112 species (i.e. those rated to be of low predator susceptibility), 14 of which are threatened and 15 Near Threatened, would also benefit from some level of predator control, but are unlikely to require intensive predator management in order to persist. It is unlikely that introduced predators are the main constraint on population growth or the primary reason for range contraction of these species. For these species, management of predators may be of secondary priority, and if implemented should be designed to complement other conservation interventions.

It is also worth noting that, excluding bats, nearly one-fifth of Australia's extant threatened (8 of 58 species) and Near Threatened (10 of 36 species) mammal species were considered to be not susceptible to cats and foxes. Other factors, most notably habitat loss, changed fire regimes and climate change, are primary threats for these species, and species recovery will depend upon the enhanced control of such factors, where possible.

Body size and arboreal habit influenced predator susceptibility in predictable ways. Those species within the preferred prey weight range of foxes and cats (35 g–3.5 kg) were more likely to be extremely or highly predator-susceptible, consistent with the critical weight range theory of mammal declines (Burbidge and McKenzie 1989; Johnson and Isaac 2009). Smaller species (especially rodents) also typically have higher fecundity and shorter generation times, which allows them to absorb predation pressure and reduces population-level impacts of introduced predators (Burbidge and McKenzie 1989). For larger species, introduced predators may prey selectively on juvenile individuals, conferring some population-level resilience. Both introduced predators take their prey mostly on the ground, reducing risk for arboreal species, although individuals of such species may become susceptible when they come to ground.

The categorisation of predator susceptibility is nuanced and spatio-temporally variable. For example, a species may persist with introduced predators in some environments (e.g. those that provide a dense cover of vegetation, offer abundant food resources, or refuge from predators) but not others; it may persist with introduced predators if no other threats are present, but not if predation combines interactively or additively with other threats; it may persist in most years, but predation pressure may be unsustainable in years of low rainfall and little recruitment. This illustrates the dependence of predator susceptibility on habitat structure for many species, and hence the interacting and compounding effects of other land management practices, particularly fire management and grazing pressure (McGregor *et al*. 2014; Doherty *et al*. 2015).

The abundance, behaviour and diet (and hence impacts) of introduced predators may also vary with the occurrence and abundance of dingoes, the apex native predator in Australia (Glen and Dickman 2005; Johnson *et al*. 2007). Foxes and cats may also vary their selectivity of native mammals as prey depending upon the abundance of other prey sources, particularly rabbits (Marlow and Croft 2016; Pedler *et al*. 2016; Read and Bowen 2001). Furthermore, predator abundance (and hence possibly also impact) shows marked temporal variability in many Australian environments, particularly in arid and semi-arid regions in association with variation in rainfall (Letnic *et al*. 2005; Letnic and Dickman 2006; Legge *et al*. 2017).

Some native mammal species have different susceptibility to foxes than to cats. For example, several species that have been extirpated (or nearly so) on the mainland in the presence of cats and foxes persist in Tasmania in the presence of cats only (e.g. eastern bettong (*Bettongia gaimardi*), eastern barred bandicoot (*Perameles gunnii*)). In other cases, it may be challenging (and sometimes pointless) to tease apart the separate impacts of the two introduced predators. For instance, most predator exclosures typically exclude cats and foxes alike, many islands on which native species have persisted have neither introduced predator species, and management actions taken to reduce the abundance of one introduced predator species may produce complex responses from the other introduced predator species. As an example of this complex response, sustained and effective fox control may deliver short-term respite and recovery for predator-susceptible native mammal species, but this recovery may be reversed if the cat population then increases because of reduced fox abundance (Marlow *et al*. 2015; Wayne *et al*. 2017).

In some cases, predator susceptibility may also vary notably among individuals within a species (related to age, sex or size) and between populations of a species (with island populations potentially more predator naïve and hence more susceptible). Variation in susceptibility among individuals may also be related to exposure to predators. Accordingly, using predators as agents of natural selection under controlled conditions in which the density of predators can be closely managed (i.e. *in situ* predation) may reduce the predator susceptibility of predator-exposed populations by making individuals more alert and appropriately responsive to predators (West *et al*. 2018). However, it is not yet known whether predator-susceptible native mammals are able to evolve effective defences against foxes and cats, sufficient and sufficiently quickly to allow persistence in the wild. Although *in situ* predation may benefit predator-exposed populations and increase the probability of reintroduction success, exposure of prey to predators under controlled conditions is unlikely to confer population-level or species-level benefits for broadly distributed species. However, in the case of broadly distributed and genetically diverse species, the same benefits of predator-imposed natural selection should apply provided that the rate of encounters between predators and prey can be kept sufficiently low (through management of introduced predators) such that the rate of increase of the prey population exceeds the rate of predation (Anson and Dickman 2013).

There is a varied and rapidly increasing evidence base for assessments of predator susceptibility, but for many species (especially those classified as low susceptibility), the strength of inference remains weak. Given this limited information base and the likelihood that many poorly known species may be detrimentally affected by introduced predators, there is a substantial need to undertake more targeted research and management of such impacts. Such assessment should not be restricted to those species currently considered threatened or Near Threatened because the evidence base was particularly weak for many currently non-threatened species (especially many small dasyurids and rodents), largely because they have not been the subject of the intensive research and management that has elucidated the predator-susceptibility status for many threatened species.

The present study focused solely on the Australian mammal fauna. However, the approach and framework developed here could strengthen conservation management and prioritisation in other countries and ecosystems. The insights gained by explicitly focusing on species susceptibility to a priority threat (in this case introduced predators) should help direct conservation management responses most effectively and complement assessments of conservation status. This approach could also be applied to other components of the fauna (notably birds and reptiles, e.g. Dickman 1996), which also benefit from management actions that reduce the abundance, distribution or impacts of cats and foxes. Collectively, this is a large and important component of Australia's vertebrate diversity, and such high susceptibility in the native fauna to two introduced species is unparalleled on any other continent, but is typical of smaller island systems elsewhere (Alcover *et al*. 1998; Loehle and Eschenbach 2012). The categorisation of predator susceptibility presented here, complemented with the assessment of Australia's network of 'havens' (Legge *et al*. 2018), provides a robust foundation for further prioritisation of investment in predator-management interventions to ensure the most effective actions are directed towards the species most in need of protection from introduced predators.

## Conflicts of Interest

The authors declare no conflicts of interest.

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