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Ongoing unraveling of a continental fauna: Decline and extinction of Australian mammals since European settlement

John C. Z. Woinarski[a,b,1], Andrew A. Burbidge[c], and Peter L. Harrison[d]

[a]Northern Australian Hub of National Environmental Research Program and [b]Threatened Species Recovery Hub of National Environmental Science Program, Charles Darwin University, Darwin, NT 0909, Australia; [c]Research Fellow, Department of Parks and Wildlife, Wanneroo, WA 6069, Australia; and [d]Marine Ecology Research Centre, School of Environment, Science and Engineering, Southern Cross University, Lismore, NSW 2480, Australia

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The highly distinctive and mostly endemic Australian land mammal fauna has suffered an extraordinary rate of extinction (>10% of the 273 endemic terrestrial species) over the last ~200 y: in comparison, only one native land mammal from continental North America became extinct since European settlement. A further 21% of Australian endemic land mammal species are now assessed to be threatened, indicating that the rate of loss (of one to two extinctions per decade) is likely to continue. Australia's marine mammals have fared better overall, but status assessment for them is seriously impeded by lack of information. Much of the loss of Australian land mammal fauna (particularly in the vast deserts and tropical savannas) has been in areas that are remote from human population centers and recognized as relatively unmodified at global scale. In contrast to general patterns of extinction on other continents where the main cause is habitat loss, hunting, and impacts of human development, particularly in areas of high and increasing human population pressures, the loss of Australian land mammals is most likely due primarily to predation by introduced species, particularly the feral cat, *Felis catus*, and European red fox, *Vulpes vulpes*, and changed fire regimes.

conservation | biodiversity | marsupial | predation | feral animal

The world's biodiversity is in decline as humans increasingly use our planet's natural resources and modify its environments (1). Much of the current biodiversity decline is occurring in areas subject to the most rapid human population growth and highest rate of habitat loss and transformation, and in countries whose limited economies constrain the allocation of resources to biodiversity conservation (2). On these criteria, Australia should have relatively few conservation concerns: its population density is extremely low (~3 km^{-2}) by global standards (~50 km^{-2}), most of the continent remains very sparsely settled and little modified, and the Australian nation is relatively affluent: indeed, most of the continent comprises one of the world's few remaining large areas of largely natural environments (3).

Mammals are one of the biodiversity groups showing the most rapid global decline, mostly due to habitat loss and hunting (4). Australia's terrestrial mammal fauna is the most distinctive in the world (5), including ancient lineages of monotremes, very diverse marsupials, and a wide range of eutherians: 87% of Australia's 316 terrestrial mammal species are endemic. The Australian marine mammal fauna is also diverse (58 species) but has a lower rate of endemism: one pinniped species and two near-endemic cetacean species (6–8).

We comprehensively reviewed the fate and conservation status of all Australian land and marine mammal species and subspecies, and charted that status over the course of the 225 y since European settlement of Australia (7). This paper summarizes that review and describes the extent of loss and why that loss has occurred. We conclude that the rate of extinction is appreciably greater than previously recognized and that many surviving Australian native mammal species are in rapid decline, notwithstanding the generally low level in Australia of most of the threats that are typically driving biodiversity decline elsewhere in the world.

Earlier Losses

European settlement at 1788 marks a particularly profound historical landmark for the Australian environment, the opening up of the continent to a diverse array of new factors, and an appropriate baseline for measuring biodiversity change (9). However, the continent was not then paradisiacal: its mammal fauna had undergone profound changes before that date. The fossil record attests to appreciable change in the Australian mammal fauna over the previous hundred thousand years, most notably the loss of the continent's megafauna (10). The principal cause of these losses remains sharply contested but most likely involved a combination of rapid climate changes, environmental changes associated with the establishment of Aboriginal fire management, and hunting by Aboriginal people (who arrived on the continent about 50,000 y ago) (10–12). The arrival of the dingo, *Canis lupus dingo*, about 3,500 y ago (13) most likely caused further decline and change in the abundance of many species, although its role in broadscale extirpations at and since that time remains debated (14–16).

Taking Stock: The Current Conservation Status of and Outlook for the Australian Land Mammal Fauna

Our comprehensive review (7) concluded that 28 Australian endemic land mammal species have become extinct since 1788, with a further extinction (of the Bramble Cay melomys, *Melomys rubicola*) reported since June 2014 (Table 1). Another endemic species (the Christmas Island shrew, *Crocidura trichura*) is probably extinct, with no record for nearly 30 y (7). One nonendemic species, the western long-beaked echidna, *Zaglossus bruijnii*, is

Significance

The island continent of Australia harbors much of the world's most distinctive biodiversity, but this review describes an extent of recent and ongoing loss of its mammal fauna that is exceptionally high and appreciably greater than previously recognized. The causes of loss are dissimilar to those responsible for most biodiversity decline elsewhere in the world.

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[1]To whom correspondence should be addressed. Email: john.woinarski@cdu.edu.au.

Table 1. List of the 30 Australian mammal species that became extinct in Australia subsequent to 1788

Common name	Scientific name
Western long-beaked echidna	*Zaglossus bruijnii* (Peters and Doria, 1876)
Thylacine	*Thylacinus cynocephalus* (Harris, 1808)
Pig-footed bandicoot	*Chaeropus ecaudatus* (Ogilby, 1838)
Desert bandicoot	*Perameles eremiana*, Spencer, 1897
Yallara (lesser bilby)	*Macrotis leucura* (Thomas, 1887)
Desert bettong	*Bettongia anhydra*, Finlayson, 1957
Nullarbor dwarf bettong	*Bettongia pusilla*, McNamara, 1997
Desert rat-kangaroo	*Caloprymnus campestris* (Gould, 1843)
Broad-faced potoroo	*Potorous platyops* (Gould, 1844)
Kuluwarri (central hare-wallaby)	*Lagorchestes asomatus*, Finlayson, 1943
Eastern hare-wallaby	*Lagorchestes leporides* (Gould, 1841)
Toolache wallaby	*Macropus greyi*, Waterhouse, 1846
Crescent nailtail wallaby	*Onychogalea lunata* (Gould, 1840)
Dusky flying-fox	*Pteropus brunneus*, Dobson, 1878
Lord Howe long-eared bat	*Nyctophilus howensis*, McKean, 1975
Christmas Island pipistrelle	*Pipistrellus murrayi*, Andrews, 1900
White-footed rabbit-rat	*Conilurus albipes* (Lichtenstein, 1829)
Capricorn rabbit-rat	*Conilurus capricornensis*, Cramb and Hocknull, 2010
Lesser stick-nest rat	*Leporillus apicalis* (Gould, 1853)
Short-tailed hopping-mouse	*Notomys amplus*, Brazenor, 1936
Long-tailed hopping-mouse	*Notomys longicaudatus* (Gould, 1844)
Large-eared hopping-mouse	*Notomys macrotis*, Thomas, 1921
Darling Downs hopping-mouse	*Notomys mordax*, Thomas, 1922
Broad-cheeked hopping-mouse	*Notomys robustus*, Mahoney, Smith, and Medlin, 2008
Long-eared mouse	*Pseudomys auritus*, Thomas, 1910
Blue-gray mouse	*Pseudomys glaucus*, Thomas, 1910
Gould's mouse	*Pseudomys gouldii* (Waterhouse, 1839)
Bramble Cay melomys	*Melomys rubicola*, Thomas, 1924
Maclear's rat	*Rattus macleari* (Thomas, 1887)
Bulldog rat	*Rattus nativitatis* (Thomas, 1889)

All are endemic to Australia except for the western long-beaked echidna.

extirpated in Australia (17) but survives, albeit in Critically Endangered status, in New Guinea. Twenty-two of these extinct species were restricted to mainland Australia, and seven were island endemics. In comparison, the larger land mass of continental North America has had only one extinction of a terrestrial mammal species since its (earlier) European settlement: the localized sea mink, *Neovison macrodon*, exterminated through intensive hunting pressure (18).

Extinctions in the Australian land mammal fauna have occurred at a rate of about one to two mammal species per decade since the first post-1788 Australian mammal extinction, probably in the 1840s (Fig. 1). The losses are continuing: consistent with that rate, one Australian endemic mammal species, the Christmas Island pipistrelle, *Pipistrellus murrayi*, became extinct in 2009 (19), and another, the Bramble Cay melomys, became extinct some time in the period of 2006–2014.

An additional 56 Australian land mammal species meet International Union for Conservation of Nature (IUCN) Red List criteria (20) for listing as threatened and a further 52 species as Near Threatened. Of the 273 Australian endemic land mammal species, 11% are extinct, 21% are extant but threatened, and a further 15% are Near Threatened. The proportions are significantly ($\chi^2 = 8.2$, $P = 0.004$) lower for native but nonendemic land mammal species (2.1% for extinct in Australia, 8.3% for threatened).

Although the information base is constrained by the very limited amount of monitoring, most threatened and Near Threatened Australian land mammal species are continuing to decline (7), with some monitoring programs indicating population reductions of >90% in multiple species over the last two decades, even in large conservation reserves (21–23). With retrospective assessment of conservation status, the review concluded that 55 terrestrial mammal taxa now have a worsened conservation status than they had in 1992 and only a small minority of species is doing better than 20 y ago (Fig. 2).

The extent of decline and extinction of mammals is greater than has been documented for any other taxonomic group in Australia (Fig. 3). To a limited extent, this may reflect biases in the

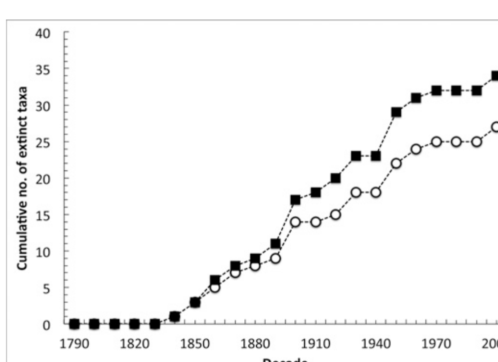

Fig. 1. The cumulative number of extinct mammal taxa in Australia. Open circles denote species; filled squares also include subspecies. Note that dates could not be estimated for some extinct taxa, so the tally given here is less than the total number of extinct taxa. Note also that the decade value refers to the 10 y following the date given (i.e., 2000 is the period 2000–2009 inclusive). Reproduced with permission from ref. 7.

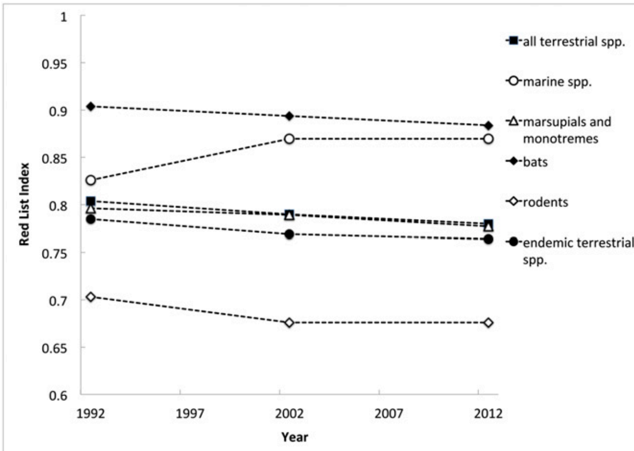

Fig. 2. Change in the Red List Index for Australia's endemic terrestrial mammal fauna over the period 1992–2012. Note that this index varies from 0 (if all taxa are Extinct) to 1 (if all taxa are Least Concern). Reproduced with permission from ref. 7.

legislated threatened species listing process against more poorly known groups (24); however, the main reason is more likely to be that the Australian mammal fauna has proven particularly susceptible to novel threats. The most precise comparison available is with the well-known Australian bird fauna (25). Only one Australian endemic bird species has become extinct from mainland Australia since European settlement (i.e., about 0.3% of Australian land birds), a far smaller number and proportion than for mammals. However, as with the Australian mammal fauna, birds restricted to Australian islands have a high rate of extinction, with eight extinct species (25).

This loss of Australian mammals has also been far more than that reported over this period for the terrestrial mammal fauna in any other continent. The IUCN Red List (www.iucnredlist.org/about/summary-statistics) reports that 77 of the world's mammal species have become extinct since 1500; with the inclusion of seven Australian endemic extinct mammals not currently shown in the Red List, that figure should be 84. The 29 Australian endemic mammal extinctions comprise 35% of the world's modern mammal extinctions. Some 1.5% of the world's 5,500 mammal species are extinct, a proportion substantially less than for Australia. Our assessment of 30 Australian mammal extinctions is also appreciably greater than that recognized under Australian environmental legislation, which lists 20 Australian mammal species as extinct, a tally also reported in previous assessments of the extent of loss of Australian biodiversity (26).

As noted in previous studies (27–30), the losses of Australian mammal species have been taxonomically uneven, with relatively higher rates of loss in rodent and marsupial species, and relatively less loss in bat species (Fig. 2). Much of the loss of Australian mammals has been of phylogenetically distinctive species and species groups, removing a disproportionately large component of the genetic complement of the earth's biodiversity. For example, the sole species in the family Thylacinidae (the thylacine *Thylacinus cynocephalus*) is now extinct; the sole extant species in the family Ornithorhynchidae (the platypus *Ornithorhynchus anatinus*) is now Near Threatened; the sole extant species in the family Myrmecobiidae (the numbat) is Endangered; the sole species in the family Chaeropodidae (the pig-footed bandicoot, *Chaeropus ecaudatus*) is now extinct; of the two species in the family Thylacomyidae, one (lesser bilby, *Macrotis leucura*) is extinct and the other (bilby, *Macrotis lagotis*) is Vulnerable; the sole species in the family Phascolarctidae (the koala) is now Vulnerable; the sole remaining species in the relictual subfamily Lagostrophinae (the banded hare-wallaby, *Lagostrophus fasciatus*) is now Vulnerable. However, even in groups that are also well represented outside Australia, such as the Muridae (rats and mice), there has been much loss of distinctive Australian groups: for example, two of the three species in the genus *Conilurus* are now extinct and the third is Vulnerable; one of the two species in the genus *Leporillus* is now extinct and the other is Near Threatened (Conservation Dependent); the sole species in the genus *Mastacomys* is Near Threatened; one of the two species in the genus *Mesembriomys* is Vulnerable and one is Near Threatened; 5 of the 10 species in the genus *Notomys* are now extinct, and two of the remaining species are Vulnerable; of the five species in the genus *Zyzomys*, two are Critically Endangered and one is Vulnerable; and the single species of *Xeromys* is Vulnerable.

Many of the now extinct or highly threatened mammals had important ecological roles, for example in ecological engineering including biopedturbation (reworking of soils) (31) and in increasing the dispersal and germination of seeds (32). Many were pivotal in the culture of Aboriginal Australians, as food sources, as totemic beings (33), and as part of their understanding of their "country" and its creation.

Other than the iconic thylacine, Australians, and the global community generally, have been relatively oblivious of this extinction calamity. In part, this is because many of the now lost species were obscure, small, nocturnal, and shy, and lived remote from most human settlement. Indeed, to some extent, the apparent naturalness and extent of the Australian Outback has beguiled the public into thinking that Australia's unique biodiversity was and is secure. This complacency may change as the decline of high profile mammal species, such as the koala and platypus, becomes increasingly apparent.

This review is sobering in its assessment of the current extent of loss of Australia's mammal fauna, but some perceptive observers long ago foresaw this catastrophic outcome. A notable such Cassandra was the naturalist Hedley Finlayson who wrote the following in 1945:

> It is not so much, however, that species are exterminated by the introduction of stock, though this has happened often enough, but the complex equilibrium which governs long established floras and faunas is drastically disturbed or even demolished altogether. Some forms are favoured at the expense of others; habits are altered; distribution is modified, and much evidence of the past history of life of the country slips suddenly into obscurity.... The old Australia is passing. The environment which moulded the most remarkable fauna in the world is beset on all sides by influences which are reducing it to a medley of semi-artificial environments, in which the original plan is lost and the final outcome of which no man may predict (34).

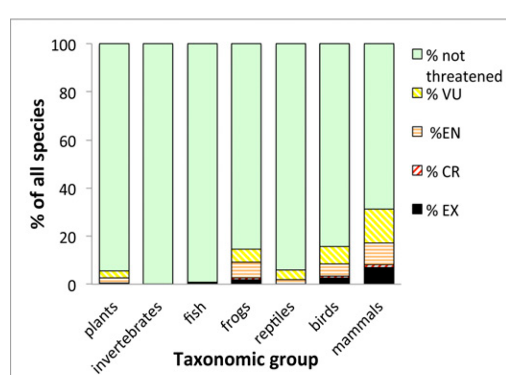

Fig. 3. Comparison of the extent of extinction and threatened status across different taxonomic groups in Australia. Data relate to numbers on the formal Australian list of threatened species (24). Abbreviations: EX, Extinct; CR, Critically Endangered; EN, Endangered; VU, Vulnerable.

The Pattern and Drivers of Terrestrial Mammal Decline Since European Settlement of Australia

Some of the causes of the post-1788 Australian mammal losses remain unresolved, baffling, and contested. This is so for even the most recent of the mammal extinctions. For example, notwithstanding ecological studies occurring at the time of decline and extinction, the primary driver of the 2009 extinction of the Christmas Island pipistrelle was not identified (19). However, determining the cause of extinction is now more self-evidently difficult for mammal species whose decline happened more than 50 y ago and in areas remote from settlement. Many of these species left almost no trace: for example, the now-extinct desert bettong, *Bettongia anhydra*, is known from only a single specimen collected in 1933 (35), and the only tangible record of the kuluwarri (central hare-wallaby), *Lagorchestes asomatus*, is of a single specimen (now only a skull) collected in 1932. Other "modern" Australian endemic species have been discovered recently only from subfossil material that postdates European settlement: although surviving on the continent subsequent to 1788, at least four species were not detected before their extinction and there is no scientific record of them as living animals (36, 37). It is highly likely that some other Australian mammal species that became extinct after 1788 have left no (discovered) record, and their existence and loss has been unnoticed.

Three contrasting and complementary approaches have provided much forensic insight into the former distribution of these now lost species, of their ecology, and of the timing of their decline. Such knowledge can then be related to the timing of establishment of different threat factors (38–40) and hence provides some inference on causality of decline.

The subfossil record, mostly of scattered bones in caves and in caches of regurgitated owl pellets, has revealed—in pinpricks in the landscape—a rich trove of mammal evidence, typically characterized by the former abundance of now rare or extinct species and the formerly broad geographical and habitat distribution of species that are now highly localized or restricted to a narrow habitat range (41–43). A notable recent example, of analysis of owl pellets in forests in southeastern Australia, demonstrated that the loss since European settlement of native mammals in that region had been "under-estimated and severe" (42, 43). However, it is not only bones that now lost mammals have left behind. The large and distinctive, but now abandoned, mounds and burrow complexes of the boodie *Bettongia lesueur* (a 1.2-kg rat-kangaroo, now restricted to a few small islands and reintroduced populations in mainland fenced areas) occur extensively and abundantly across the Australian Outback, and their crumbling remnants are readily visible from ground and aerial surveys or satellite images (44). The similarly now abandoned large (to 6 m^3) constructions of the two species (one now extinct, the other threatened and with a current range of <1% of its former distribution) of stick-nest rats (*Leporillus apicalis* and *Leporillus conditor*) have remained across much of the Outback decades after the loss of their builders (45). These constructions have revealed not only the former abundance and distribution of these native rodents, but the nest components and detritus have also provided novel insight into historic vegetation change (46).

The records of early explorers, naturalists, and settlers provide some remarkably vivid and detailed, but geographically threadbare, documentation of the Australian environment and its mammal species before and during the spread of novel factors introduced following European settlement (47–49). As noted in one recent review that compared these accounts with the environments and species present today, these historic records offer "clues to a lost world" (49).

With greater geographic coverage and reflecting on more recent changes, the third investigative approach to understanding the past pattern of distributions in Australian mammals has been the use of ethnozoology, the documentation of knowledge held by Aboriginal Australians. Many older Aboriginal men and women have lived across the cusp of the Australian mammal decline and have retained intricate recollections of these now lost species, and such knowledge has done much to pinpoint the timing of decline in different regions and offered some inference on the factors that contributed to that decline (33, 50). Some current such studies are indicating that the decline is continuing in some regions (51).

At the time of European settlement, many of the now lost or threatened mammal species were extremely abundant, had extraordinarily large (continental-scale) ranges, and occurred across a very wide range of habitats (Fig. 4) (43, 52): by most measures, these were remarkably successful and ecologically flexible species. Examples among the now extinct and threatened species include the brush-tailed rock-wallaby, *Petrogale penicillata*, for which almost 100,000 skins were marketed by a single company in 1 y (1908) (53); the koala, *Phascolarctos cinereus*, for which more than 500,000 skins were collected in just 31 d in the last open season, in Queensland in 1927 (54); the now extinct subspecies of brush-tailed bettong, *Bettongia penicillata penicillata*, for which in about 1900 "the dealers in Adelaide did a great trade in selling them by the dozen at about ninepence a head for coursing on Sunday afternoons" (55). This disparity between the abundance of mammals at the time of European settlement and the present day was not a feature of closely settled areas alone. In central Australia, early observers reported "countless swarms" of the now-threatened black-footed rock-wallaby (56), whose population is now less than 10,000 individuals. In remote northern Australia, collectors in the late 19th century noted of the now rapidly declining pale field-rat, *Rattus tunneyi*, "I have traveled through square miles of country where the ground was literally undermined by these rodents to such an extent that the hoofs of my horses at nearly every step would break through and sink deep down in the burrows" (57).

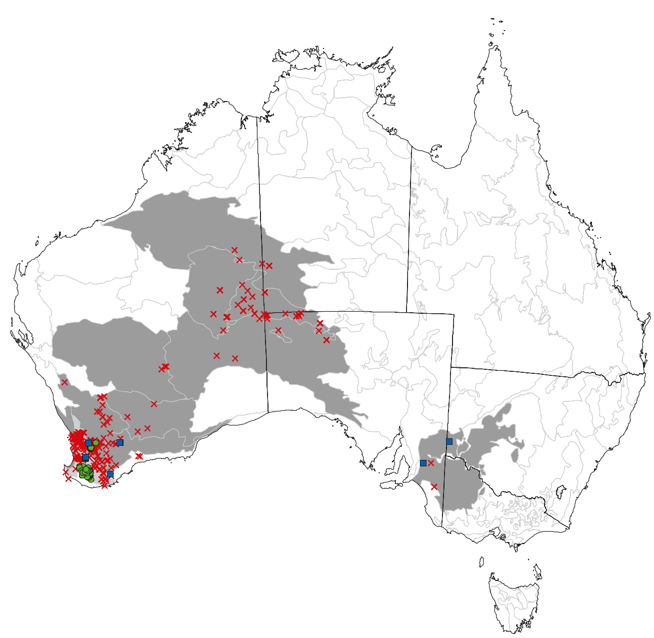

Fig. 4. Example of the distributional retreat of the Australian terrestrial mammal fauna—in this case, the numbat, *Myrmecobius fasciatus*. Green circles represent current (post-1992) range, red crosses represent records between 1788 and 1992, gray shading indicates presumed range at the time of European settlement, and blue squares represent recent attempts to reintroduce the species to its former range. Reproduced with permission from ref. 7.

Although the detail of the patterning is imprecise, the available evidence indicates a broad sequential wave of mammal losses, beginning from the first settled areas in southeastern Australia (coincident with the first arrivals of some associated threats) from the 1840s, reaching central Australia in the 1890s with rapid declines there particularly over the period of 1930–1960, and marked losses continuing from about the 1960s to the present day in much of northern Australia (10, 23, 33, 50). Much of this timing was coincident with the continent-wide spread of the introduced cat *Felis catus* and the slightly later and only marginally less extensive spread of the introduced red fox *Vulpes vulpes* (40). The timing of decline is also partly associated with the geographically variable timing of loss of indigenous land management, particularly of fire. The loss of indigenous land management has occurred to a lesser extent and far more recently in many parts of northern Australia (58).

The spatial pattern of loss provides some important clues to causality. Many of these mammal species have disappeared from their formerly extensive mainland ranges, but some fortunately also occurred on islands fringing the continent, and many of these island populations have persisted (59). Seven species once widespread on the Australian mainland now remain naturally only on islands. In general, the most marked difference in threat regimes between continental areas and islands was that feral cats and foxes had not colonized the islands (59–62). Analysis of historical records has also demonstrated that when either of these two predator species (and, in some cases, the nonnative black rat, *Rattus rattus*) have established on islands, many of the native mammal populations have rapidly followed the mainland trajectory of decline and loss (61, 63). A recent assessment of the fate of mammals in one Australian island group has recognized these ostensibly antithetical conservation values of islands, labeling them a "refuge and death-trap" (64). The few Australian land mammals that were restricted to oceanic islands at the time of European settlement have shown a very marked propensity for extinction: four of the six such species have become extinct, some very rapidly following the first influence of European discovery (65), and both the remaining species are now considered threatened.

These retrospective assessments provide variably strong or weak inference for causality based on the coincidence or correlation of decline of native mammals with the advent, incidence, or intensity of threats. A range of more sophisticated modeling approaches has also been used to link traits of Australia's mammal species and their environments with their conservation fate. With some dispute about the details, most of these modeling approaches have shown that Australian native mammals that dwell or forage largely on the ground and that are broadly in the "critical weight range" of 35 g to 5.5 kg have been far more likely to have become extinct or declined than mammals that do not have these traits (27, 28, 66, 67). This size pattern for extinction risk in Australian mammals is notably different to the global trend, whereby larger mammals have been and are most likely to become extinct (68). The characteristics of increased extinction risk for Australian terrestrial mammals are consistent with an explanation for decline based on predation by feral cats and foxes: the lost species are meal-sized for, and accessible to, these introduced predators (43, 66, 67, 69).

More compelling evidence derives from manipulative experimental studies, some conducted as part of conservation management activities and some as explicit hypothesis-testing research. Removal of the red fox from around declining black-footed rock-wallaby *Petrogale lateralis* colonies provided compelling evidence of predation impact, with subsequent recovery of a prey species (70). Later similar studies involving other native mammal species, such as the numbat, *Myrmecobius fasciatus*, provided comparable evidence (71). A different approach to the same predator manipulation issue has been to establish predator-proof fencing and then to monitor the responses of native mammals already present within the exclosure or of native mammal species introduced to those exclosures. Many of these exclosure studies have been spectacularly successful, leading to rapid and sustained population growth of native mammals in the predator-proof areas (72). Another approach has been to translocate threatened mammals to cat- and fox-free continental islands; again with marked success (73). Conversely, reintroduction attempts that have not adequately controlled foxes and/or cats have typically failed (74). One recent controlled experiment in northern Australia (beyond the range of the fox), found that a reintroduced native rodent, *Rattus villosissimus*, persisted in study sites at which cats were excluded but was rapidly eliminated from paired sites to which cats had access (75). In complementary studies examining the diet of feral cats and red foxes in many parts of Australia, a high rate of predation on native mammal species has been demonstrated, often with particular selectivity to the species groups of native mammals exhibiting decline (76, 77).

There is now compelling evidence for a principal role for predation by cats and foxes in driving the decline of the Australian terrestrial mammal fauna. However, Australian environments have been affected by many other factors, mostly imposed since European settlement. Some of these factors have individually had significant detrimental impacts on particular mammal species, and many of the factors operate in a synergistic manner. Such multiple and interactive drivers of decline may be typical of extinction events globally (68, 78). However, in the Australian case, these interacting factors may be unusually well meshed, because they largely result from the rapid continental-scale replacement of a purposeful and long-established indigenous land management regime by a substantially more exploitative and transformative set of land management practices and a medley of introduced species (23, 58, 79), many of which are themselves environmental transformer species (80).

Among the Australian mammal fauna, there are many diverse examples of impacts of different threats. Unsurprisingly, different species may also vary substantially in their susceptibility to different threats (23, 40), and even individual species may vary in their responses to individual threat factors at different sites or in different times, because the magnitude of any threat factor may vary substantially in space and time, or with the variable constellation of co-occurring threats.

In an unusual case of the influence of a prey species on a predator, the northern quoll, *Dasyurus hallucatus* (a ∼0.5-kg carnivorous marsupial), has declined rapidly, extensively, and catastrophically (and continues to do so) because a central American toad species, *Rhinella marina*—introduced in a benighted biological control exercise—mortally poisons the quoll during predation attempts (81). Consequently, over the last few decades, the northern quoll has been extirpated from large proportions of its range. An even more rapid population crash (of about 80% over the last 20 y) is currently affecting the largest remaining marsupial carnivore, the Tasmanian devil, *Sarcophilus harrisii*, because of a novel and extremely unusual transmissible cancer, the devil facial tumor disease, without known cure (82). In the tall forests of montane southeastern Australia, Leadbeater's possum, *Gymnobelideus leadbeateri*, suffered a ∼45% population loss (of its already small population, of about 2,200 individuals) in the course of a single week because of an intensive wildfire in 2009, and its burnt habitat is unlikely to return to suitability for many decades (83). However, the impacts of single fires are simply an acute manifestation of a pervasive change in fire regimes since the loss of indigenous land management practices. With variation across different regions, land uses, and environments in Australia, the current fire regime is now marked by fires that are too frequent and extensive (21, 84) or, in some places, of fires that are now too infrequent (85) for the retention of some components of biodiversity. Modeling has indicated that at least some mammal species are likely to be extirpated by current fire regimes (86), and that finescale mosaic burning may be required in some environments (87). In some cases, this is because changed fire regimes have affected resource availability: for example, archaeological evidence (of seeds at midden sites) has demonstrated that key native fruits eaten by some mammals have become substantially rarer since European settlement because of the discontinuation of the previously long-established indigenous fire regime (88).

Pastoralism based on introduced sheep and cattle is now the dominant land use across much of Australia, and many other introduced herbivores (notably including the rabbit, goat, donkey, camel, horse, and buffalo) collectively occur abundantly beyond the pastoral estate across the entire Australian land mass, including in many conservation reserves (89). Competition with, and habitat degradation caused by, introduced herbivores has also been detrimental to many Australian mammals, as demonstrated by livestock removal experiments (90) and correlative studies that compare mammal assemblages in comparable areas with and without introduced herbivores (91–93).

Direct exploitation or persecution substantially reduced the abundance of some mammal species, including koalas and macropods (and seals and whales in marine habitats), but such exploitation was probably not the primary cause of extinction for any Australian mammal species, and there is no substantial ongoing hunting of any threatened Australian mammal species.

Many of these diverse threatening factors directly or indirectly increase the intensity and impact of predation by feral cats and foxes. In many areas, shelter sites for native mammals (including hollow logs and dense ground vegetation) are reduced by the current fire regime and/or by grazing pressure of livestock and feral herbivores, allowing more effective hunting by feral predators (94). Across extensive areas of mainland Australia, dingo *Canis lupus dingo* populations have been reduced substantially by the pastoral industry, using exclosure fencing, concerted trapping, and poison-baiting programs, and such reduction in a top-order predator typically results in increases in the abundance of foxes and feral cats with consequently greater predation pressure on native mammals (95).

Many individual Australian mammal species are now affected by a wide range of factors that may differ in impacts across different regions, environments, or times. For example, the iconic koala has been shown to be detrimentally affected by several diseases (including *Chlamydia* and a retrovirus), habitat loss and fragmentation, predation by feral dogs, wildfire, timber harvesting, road traffic, habitat degradation caused by its own short-term population cycling, habitat degradation due to complex interactive impacts of a despotic native bird species, drought, and days of extreme heat (7). Comparably, the platypus—the most phylogenetically distinctive mammal in the world (96)—is now in significant decline due to the combined and interactive impacts of water extraction and pollution, river modification, drought, predation by cats, dogs, and foxes, catchment-scale environmental change, bycatch in some fishing traps, and a disease (mucormycosis) probably introduced through the pet frog trade (7).

This medley of threats is likely to be exacerbated by, and there will be additional influences directly due to, climate change. For the Australian land mammal fauna, some climate change impacts are probably already being realized, but impacts will be magnified substantially in the next few decades, with modeling predicting severe to catastrophic losses due to climate change in the diverse and highly distinctive mammal faunas of the already limited area of high-altitude tropical rainforests (97) and alpine environments (98), for the koala (99), for the mammal fauna of the extensive tropical savannas of northern Australia (100), for mammals of coastal areas (101), and island species (102). The mechanisms for this impact include marked habitat loss or change, likely increased fire intensity and frequency, increased incidence of severe drought and days of extreme heat, and changes in foliage nutrient composition.

With due regard to the limited evidence base for ascribing decline or extinction to particular threat factors for many species, and to the recognition that many declines are most likely due to interactions among threats, we tallied assessments of the impacts of individual threat factors across all Extinct, threatened, and Near Threatened terrestrial mammal species (*Methods*). Table 2 indicates that the main factors that have contributed to extinction and are currently causing decline among the largest number of Australian terrestrial mammal fauna are predation by the introduced cat and red fox, and changed fire regimes.

A Different World: The Fate of Australia's Marine Mammals

Australia's 10,000,000-km^2 marine estate, ranging from tropical to Antarctic polar waters, supports at least 58 marine mammal species. However, almost all of these species also occur elsewhere, and individuals of many of these mammal species disperse beyond

Table 2. Major threat factors considered responsible for the extinction or decline of Australian mammal species

	Conservation status					
Threat factor	Extinct (30 spp.)	Critically Endangered (10 spp.)	Endangered (10 spp.)	Vulnerable (36 spp.)	Near Threatened (52 spp.)	All Extinct, threatened, and Near Threatened (138 spp.)
Predation by feral cats	5.4 (22)	4.6 (8)	2.9 (9)	2.9 (29)	1.9 (29)	3.2 (97)
Predation by red fox	3.0 (13)	2.4 (4)	1.5 (5)	1.9 (19)	1.1 (17)	1.9 (58)
Inappropriate fire regimes	0.6 (6)	4.4 (7)	2.1 (6)	2.3 (22)	1.4 (22)	1.7 (63)
Habitat loss and fragmentation	1.8 (11)	1.0 (2)	1.3 (4)	0.9 (13)	0.8 (15)	1.2 (45)
Livestock and feral herbivores	2.1 (14)	0 (0)	0.2 (1)	0.5 (7)	0.5 (8)	0.8 (30)
Disease	1.4 (7)	1.2 (2)	1.0 (2)	0.4 (7)	0.2 (4)	0.7 (22)
Climate change; severe weather	0.2 (1)	0.8 (1)	0.5 (1)	0.9 (9)	0.8 (14)	0.6 (26)
Predation by dingoes and dogs	0.1 (2)	0 (0)	0.2 (1)	0.8 (9)	0.1 (2)	0.3 (15)
Hunting	0.6 (3)	0 (0)	0 (0)	0.1 (1)	0.1 (2)	0.2 (6)
Predation by black rats	0.4 (2)	0.4 (1)	0 (0)	0.1 (2)	0.0 (1)	0.2 (6)
Poisoning by cane toads	0 (0)	0 (0)	0.6 (1)	0.3 (3)	0.0 (1)	0.1 (5)
Timber harvesting	0 (0)	0.3 (2)	0.2 (1)	0.1 (1)	0.1 (3)	0.1 (8)
Other	0.5 (2)	1.4 (4)	2.0 (5)	1.2 (12)	0.3 (6)	0.8 (29)

Values in body of table are mean threat impact score across species (where 8 indicates that the threat poses an extreme extinction risk; 6, a very high risk; 4, a high risk; and 2, a moderate risk; *Methods*). The bracketed number indicates the number of species for which the threat factor was considered a risk. The category "other" includes a wide range of factors including disturbance at roost sites, pollution, habitat degradation due to weeds, and hybridization.

Australian waters. Unsurprisingly then, many of these species are affected by factors that operate almost ubiquitously across the world's marine areas; hence the conservation status of Australian populations are significantly influenced by factors operating beyond Australia. These global factors include exploitation, bycatch in fisheries, marine pollution, potential resource depletion due to fishing, anthropogenic noise disturbance, and the consequences of global climate change, altered oceanography, and ocean acidification.

Substantial declines of marine mammals in Australian waters occurred historically for some exploited species, particularly larger whales, seals, and sea lions. Very large breeding colonies of some seal species, particularly on Macquarie Island and in the islands of Bass Strait in southeastern Australia, were extirpated by sealers in the 19th century (103), and some of these colonies and some of these species (such as the endemic Australian sea lion, *Neophoca cinerea*, and the subantarctic fur seal, *Arctophoca tropicalis*) have not recovered (7). Similarly, unregulated commercial whaling led to massive declines in most great whale species in the Southern Hemisphere, including Australian populations. In Australian waters, blue whales (*Balaenoptera musculus*), fin whales (*Balaenoptera physalus*), sei whales (*Balaenoptera borealis*), and sperm whales (*Physeter macrocephalus*) have not yet recovered and remain threatened many decades after whaling ceased. In contrast, the Australian subpopulations of humpback whale, *Megaptera novaeangliae*, have increased rapidly in recent decades (7).

The Australian population of the dugong, *Dugong dugon*, is globally significant for the species' conservation. However, dramatic declines along the urban coast of Queensland are evident from catch per unit effort data in shark nets for bather protection along the Queensland coast from 1962 to 1999, and dugongs are impacted by multiple threats including incidental bycatch in fishing nets, loss of seagrass, vessel strike, illegal poaching, and legal indigenous hunting in northern Australian waters (104). Two inshore dolphins, the Australian snubfin dolphin, *Orcaella heinsohni*, and Australian humpback dolphin, *Sousa sahulensis*, also face a similar range of threats from fisheries bycatch, habitat degradation, vessel strike, pollution, and acoustic disturbances (6, 7).

For Australia's marine mammals, our review concluded that six species are threatened, with a further five species Near Threatened, but a much higher proportion (60%) are Data Deficient.

Conservation Management Responses: What Is Working and What Needs to Be Done?

Australia has an extensive, reasonably representative, and robust terrestrial conservation reserve system, an expanding marine conservation reserve system, and relatively good environmental legislation (105). However, these foundations for biodiversity conservation are clearly not sufficient for maintaining the Australian mammal fauna. Although the reserve system provides fundamental conservation security for at least some other biodiversity groups (106), many of Australia's conservation reserves—even some of the largest and highest profile reserves—have lost or are rapidly losing some of their mammal species (21, 22). Furthermore, although the environmental legislation is arguably effective against some acute factors (such as broadscale land clearing, and localized development that may affect threatened species) and has led to the cessation of exploitation of marine mammals, it has proven to be largely ineffective against the insidious and pervasive threats that are responsible for most of the decline in Australia's terrestrial mammals (notably introduced predators and changed fire regimes). Many of these threatening factors are now deeply entrenched across extensive areas and are unlikely to be moderated by the typically short-term and local-scale projects that have characterized much of the Australian environmental management: to be effective, programs will have to be large-scale and sustained long-term.

Nonetheless, some active management programs—based on the identification and amelioration of the principal threats—have delivered some successes. One such initiative has been the use of assisted colonization, the translocation of threatened mammal species from sites at which the primary threat is difficult to manage in situ (107) to sites where the primary threat is absent. In the Australian context, this has mainly involved the "marooning" of threatened mammals on islands, on which feral predators have never been introduced or have been eradicated. There are now many successful examples where such translocations have rescued mammal species that were otherwise likely to become extinct (40, 73). A more recent variant on this approach has been the use of "mainland islands" (108), sites at which the primary threat is excluded, typically by fencing. Successful examples include the protection through such exclosure fencing of sites at which a threatened mammal species has persisted or, more commonly, to which it has been reintroduced. In most cases, the threat involved has been predation by feral cats and foxes, but translocations have also been used in cases where the primary threat has been disease, poisoning by the introduced cane toads, intensive development, and other factors.

However, there are logistical limits on translocation. Some species cannot readily be moved to islands, or islands are too small, do not have suitable habitat, or have other values that would be detrimentally affected by such translocations. Furthermore, predator-exclosure fences are expensive, prohibiting their implementation at landscape scales. Some threats are now being managed in some areas by broadscale control programs. The most successful of these cases involve sustained and intensive baiting campaigns for reduction in fox populations, with the longest established of these programs being the "Western Shield" program in southwestern Australia. This has led to substantial and sustained population increase for many native mammal species (109). However, in at least one case, this success has since been reversed. Together with a program of translocations, the fox-baiting program resulted in the first removal because of conservation action of a listed threatened species from Australian national and state lists—the woylie, *Bettongia penicillata*. Unfortunately, within the last decade, the population size of this species has again plummeted, even in the fox-baited area, and the woylie is again listed as threatened (110), probably because fox baiting has perversely led to increased predation pressure by feral cats (40). Notwithstanding this case of reversal of success, fox-baiting programs have been extended to some large areas in southeastern Australia and at least some threatened native mammal species are now increasing in response (111).

Some other instances of recovery of Australian threatened mammals have involved the broadscale removal of livestock and feral herbivores, and increasingly more active management of fire. A notable initiative has involved the rapid expansion of the Indigenous Protected Area system, a network of voluntary agreements for conservation management on Aboriginal lands. Since its establishment in 1997, the extent of such areas has increased to more than 500,000 km^2, and the principal focus of their management activity is the restoration of fire regimes that provide benefit to biodiversity (112). In an important recognition of the links between society and environmental responsibilities and condition, these indigenous ranger programs are delivering not only important conservation outcomes but also enhanced social, health, and economic outcomes to otherwise substantially disadvantaged communities (113).

Similarly, there has been a marked expansion of the private conservation reserve system in Australia over the last two decades. For example, the Australian Wildlife Conservancy now owns or manages 23 properties around Australia covering >3,000,000 ha, and it prioritizes active management for the conservation of threatened mammal species.

However, a major factor driving the decline of Australia's land mammal fauna remains largely unmanaged. Despite the recent development of baits attractive to cats (114), no broadscale and enduring mechanism with acceptably small nontarget effects has yet been developed for the control of feral cats (77). These now occur abundantly across all Australian terrestrial environments. This review of the parlous conservation status of the Australian mammal fauna concludes that the development of such a broadscale control mechanism is likely to provide the greatest conservation benefit to the Australian mammal fauna. It is possible that this may be through specific disease, but a transmissible biological control agent would have substantial risks to pet cats, potentially to other Australian mammal species, and to native felid species elsewhere in the world. It is a formidable challenge.

Conclusion

This review has documented the historic and ongoing unraveling of a continental fauna, resulting in the decline and extinction of some of the most distinctive species in the world. Causality has often been opaque, many factors are implicated, and these may work in a complex interactive manner. However, the major drivers of this decline have been predation by two introduced species, the cat and the red fox, and changed fire regimes. The key role of introduced predators and changed fire regimes contrasts markedly with the major threats to biodiversity in most other continents but is similar to the pattern of rapid decline of island biotas in response to introduced species (115). In this respect, Australia has been considered to be operating as a very large island rather than a small continent (28, 116). Australia's isolation has resulted in its remarkable biodiversity distinctiveness but also the extraordinary vulnerability of its biota to novel threats. With the dwindling abundance, range, and diversity of so many species, we see now only a faint shadow of the richness and abundance of the Australian mammal fauna that existed at the time of European settlement (43).

This review has documented some clear practical management priorities and demonstrated that success and recovery is possible. The Australian mammal fauna may have a brighter future if these examples are followed and priorities implemented. However, even more pressing is a sense of societal affinity for biodiversity, a recognition of and responsibility for the quintessentially Australian wildlife by the broader community. Two of the authors of this review have, during ethnozoological research, shown older Aboriginal people stuffed museum specimens of mammal species that became extinct during their lifetimes, and been struck by the depth of emotional response by those Aboriginal elders—stroking these skins, singing the songs of these animals, crying at their loss, and the feeling that they had failed in their responsibility to maintain these species in their country. It is an affinity for nature and a lesson that the rest of society should learn. Else, the many extinctions expected in the future will be seen as inconsequential. Furthermore, if such high rates of extinction of mammals are condoned in Australia, there may be little hope for the world's biodiversity more generally.

Methods

The current conservation status of all Australian terrestrial and marine mammal species and subspecies (extant as at 1788) was assessed using IUCN Red List criteria (20). Distributional data for all species were compiled from a wide range of available sources and used to calculate extent of occurrence and area of occupancy, and the extent of decline in these parameters.

To some extent, the assessments were constrained by a limited information base. Until recently, there was no national distributional database for Australia's biodiversity. Unlike the situation in many other countries (117, 118), there is still no integrated monitoring program that charts trends in the population for Australia's mammals, or biodiversity more generally. This deficiency presents major challenges in discerning population size and trends, and hence the urgency of conservation management responses. The dearth of information is particularly marked for marine mammals, 60% of which we considered to be Data Deficient.

Furthermore, the Australian mammal fauna remains very incompletely cataloged. At least 50 Australian endemic land mammals have been described since 1970, including at least 6 species since 2012 (119, 120): for comparison, the similarly sized mammal fauna of the United States has had only 10 new species described since 1950.

We also retrospectively (using current information) assessed the conservation status of Australian mammal taxa 10 and 20 y previously, to chronicle recent trends in the conservation status of the fauna, using the Red List Index (a measure that varies from 0 if all taxa are Extinct to 1 if all taxa are Least Concern) (1, 121).

There has been no previous attempt to document, for every Australian mammal species, the relative effects of different threat factors. For every mammal taxon, we reviewed all available information (comprising >3,000 studies) to derive a draft table of estimated impacts (consequence and extent) of threat factors (7). The consequences of threat factors were categorized as catastrophic [likely to cause (or have caused) complete population loss, where operating], severe (estimated to cause 25–75% reduction in population size, where operating), moderate (estimated to cause 10–25% reduction in population size, where operating), or minor (estimated to cause <10% reduction in population size, where operating). The spatial extent of threats was rated as entire (the threat operates across the whole Australian range of the taxon), large (the threat operates over 50–99% of the taxon's range), moderate (the threat operates over 25–50% of the taxon's range), minor (the threat operates over 10–25% of the taxon's range), or localized (the threat operates over <10% of the taxon's range). The consequence and extent combinations were used to rate the overall threat impact as representing an "extreme" risk of extinction if the threat was considered to have catastrophic consequences and occurred across the entire range of a species; "very high" risk if it had catastrophic consequences and occurred across a large proportion of the range, or had severe consequences and occurred across the entire range; "high" risk if it had moderate consequence and occurred across the entire range, or severe consequence and occurred across a large extent of the range, or catastrophic consequence and occurred across a moderate extent of the range; and "moderate" risk for the combinations of minor consequence-entire range, moderate consequence-large extent, severe consequence-moderate extent, and catastrophic consequence-minor extent.

These draft threat assessments and conservation status determinations were included within accounts for every taxon, and these accounts were then circulated to those experts familiar with the taxon, with ratings revised accordingly in light of the set of expert responses to these drafts. A total of more than 200 experts provided such feedback. Although we note that the evidence base is highly variable (and very limited for many species), our assessments of threats reflected the knowledge and opinion of an overwhelming majority of Australian and relevant international mammalogists and were informed by all available evidence (7).

In this paper, we provide a summary tabulation of the final threat assessments, tallying for individual threats the number of species for which that threat was scored as either extreme, very high, high, or moderate risk, and calculating a mean threat impact score across species, where an extreme risk was scored as 8, very high risk as 6, high risk as 4, and moderate risk as 2.

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