

## REVIEW

## Impacts and management of feral cats *Felis catus* in Australia

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### ABSTRACT

1. Feral cats are among the most damaging invasive species worldwide, and are implicated in many extinctions, especially in Australia, New Zealand and other islands. Understanding and reducing their impacts is a global conservation priority.
2. We review knowledge about the impacts and management of feral cats in Australia, and identify priorities for research and management.
3. In Australia, the most well understood and significant impact of feral cats is predation on threatened mammals. Other impacts include predation on other vertebrates, resource competition, and disease transmission, but knowledge of these impacts remains limited.
4. Lethal control is the most common form of management, particularly via specifically designed poison baits. Non-lethal techniques include the management of fire, grazing, food, and trophic cascades. Managing interactions between these processes is key to success.
5. Given limitations on the efficacy of feral cat management, conservation of threatened mammals has required the establishment of insurance populations on predator-free islands and in fenced mainland enclosures.
6. Research and management priorities are to: prevent feral cats from driving threatened species to extinction; assess the efficacy of new management tools; trial options for control via ecosystem management; and increase the potential for native fauna to coexist with feral cats.

### INTRODUCTION

As a consequence of human introductions, domestic cats *Felis catus* have a near-global distribution, occurring on all continents except Antarctica and on hundreds of

islands (Long 2003). Cats are successful invaders because they have versatile diets (Bonnaud et al. 2011) and habitat use (Doherty et al. 2014), high fecundity and wide thermal tolerance, and do not require free drinking water (Bradshaw et al. 2013). Domestic cats become feral (hereafter 'feral

cats') when they live independently of humans in the wild; they are termed stray cats when they depend on humans for incidental provision of food or shelter (Denny & Dickman 2010). Feral cats are implicated in 26% of bird, mammal and reptile species extinctions worldwide (Doherty et al. 2016). They affect native species mostly through predation (Medina et al. 2011), but also through competition (Medina et al. 2014), disease transmission (Dubey 2008), and hybridisation (i.e. with the wildcat *Felis silvestris*; Beaumont et al. 2001). Feral cats also have socio-economic impacts, mostly as disease vectors affecting agricultural production and human health (Dubey 2008).

Reducing the impacts of feral cats is a global conservation priority (Courchamp et al. 2003, Nogales et al. 2013), and their impacts are greatest in Australia, New Zealand, and many smaller islands (see Campbell et al. 2011, Nogales et al. 2013 and references therein). Accordingly, our review focuses on Australia, where feral cats are a primary driver of mammal declines and extinctions (Woinarski et al. 2015). To some extent, assessment of feral cat impacts in Australia has been complicated by the widespread occurrence of another introduced predator, the red fox *Vulpes vulpes*. This review complements an earlier review of foxes in Australia (Saunders et al. 2010). While there is much interplay in the impacts and management of these two predators, key differences are that foxes have a more restricted distribution than feral cats (being largely absent from the far northern tropics), there has been a longer and more successful history of fox management, and although there is substantial overlap in diet, smaller mammals are less commonly affected by foxes (Fisher et al. 2014). The conservation of many native species depends upon the successful management of both predators.

Controlling feral cats is challenging, and eradication from mainland Australia is currently impossible (Denny & Dickman 2010). Detailed knowledge of feral cat ecology and impacts is essential for developing effective management tools, and many advances have been made since earlier reviews (Dickman 1996, 2014, Denny & Dickman 2010). There is also increasing policy development focused on feral cats. Predation by feral cats is listed as a key threatening process under Australian legislation, and management is coordinated broadly through a *Threat Abatement Plan* developed by the Department of the Environment (Anonymous 2015b). Further, feral cats are recognised as a priority for conservation management in Australia's first *Threatened Species Strategy* (Anonymous 2015c). It is therefore timely to integrate current knowledge of feral cat impacts and management options, and identify research and management priorities.

## HISTORY AND DISTRIBUTION

The earliest record of domestic cats in Australia dates from the time of European colonisation in 1788, when

cats were brought by settlers as companion animals and pest control agents (Abbott 2008). Feral populations became established around settlements and spread rapidly; historical records and genetic analyses demonstrate continent-wide colonisation (7.7 million km<sup>2</sup>) within 70 years (Abbott 2008, Koch et al. 2015, Spencer et al. 2015). Rapid expansion and population increase was facilitated by the release and spread of European rabbits *Oryctolagus cuniculus* from the mid-1800s onwards, which provided abundant prey across much of the continent (Abbott 2008). Cats were also transported to many locations in attempts to control rabbits, mice *Mus musculus*, or native species (Abbott 2008). Feral cats are now distributed throughout mainland Australia, occur on nearly 100 offshore islands, and occupy most habitats (Denny & Dickman 2010, Doherty et al. 2014).

## IMPACTS ON BIODIVERSITY

Feral cats directly affect native species through predation, disease transmission, and resource competition (Denny & Dickman 2010). They also interact with and compound the impacts from other threats such as changed fire regimes and pastoralism (Doherty et al. 2015b). In some circumstances, feral cats reduce impacts from other threats, for instance, by controlling introduced rodents and rabbits (Dickman 2009).

### Predation

Most evidence of feral cat impacts relates to predation on mammals. Although the causes of some historic extinctions are difficult to elucidate, feral cats are considered to have been a major cause of the extinction of 22 Australian endemic mammals, including the lesser bilby *Macrotis leucura* and at least five species of hopping mouse *Notomys* species (Woinarski et al. 2015). Feral cats also threaten a further 75 threatened or near-threatened mammals (Woinarski et al. 2015). Many of Australia's threatened mammals now occur only on small islands that have never been invaded by cats or foxes, or as reintroduced populations in small fenced mainland sites free from introduced predators.

Feral cats were also the principal cause of extinction of at least one Australian bird subspecies (Macquarie Island red-fronted parakeet *Cyanoramphus novaehollandiae erythrotis*; Taylor 1979), and potentially threaten 40 bird, 21 reptile and four frog species at risk of extinction, including the western ground parrot *Pezoporus flaviventris* and the great desert skink *Liopholis kintorei* (Anonymous 2015b), although less is known about cat impacts on these groups. Four lines of evidence point to predation impacts: dietary and predation studies, comparative

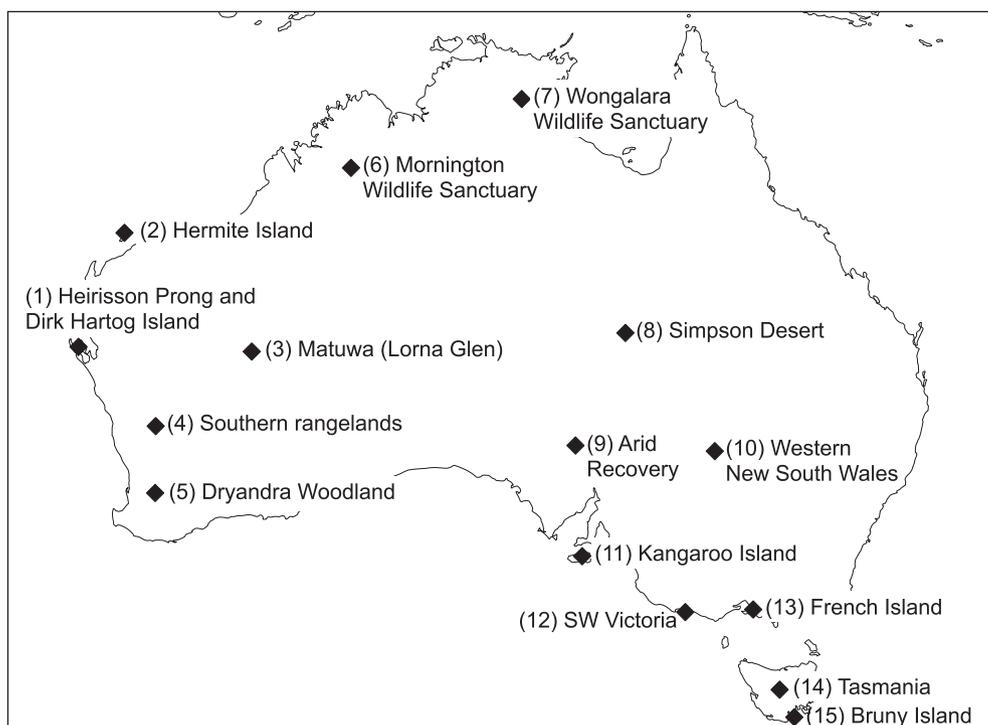


Fig. 1. Locations in Australia mentioned in the text.

analyses of correlates of declines, spatial and temporal analyses of declines, and predator manipulation experiments.

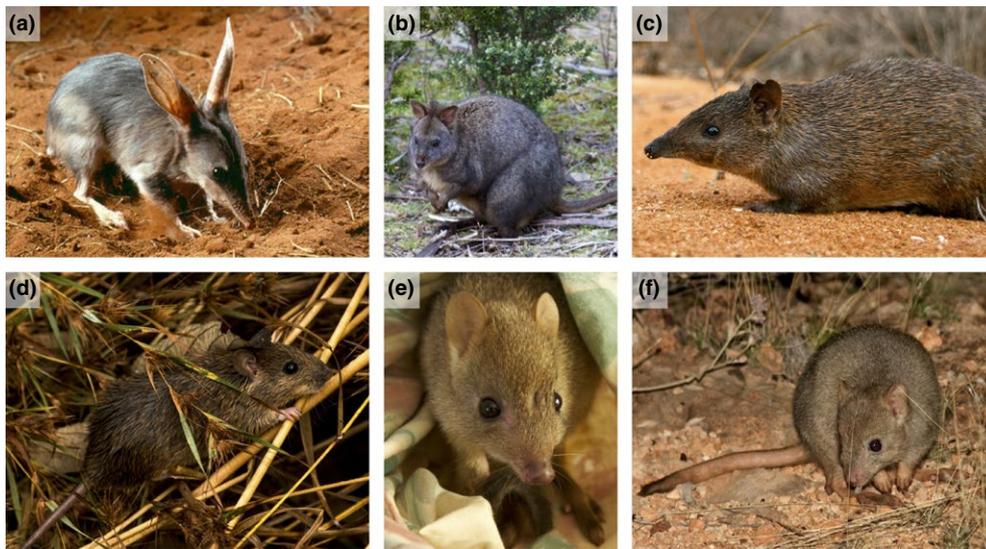
#### DIETARY AND PREDATION STUDIES

Feral cats consume at least 400 vertebrate species and many invertebrates in Australia (Doherty et al. 2015a). However, dietary studies provide little insight into predation-effects on prey populations. Stronger inferences can be drawn if information is available on both prey availability and diet. Because cats may specialise on particular prey species and subject them to intense *per capita* predation when populations are already low or declining, population-level impacts may be significant (Dickman & Newsome 2015). For example, Spencer et al. (2014) showed that long-haired rats *Rattus villosissimus* and central short-tailed mice *Leggadina forresti* were selectively preyed upon by feral cats. Central short-tailed mouse occurred in over 20% of cat scats even when they were virtually undetectable in surveys. In such situations, prey populations may be driven into a 'predator pit' and remain at such low numbers that stochastic events lead to local extinction. At Dryandra Woodland (Fig. 1, site 5), feral cats were responsible for 65% of predator kills in two rapidly declining populations of the threatened woylie *Bettongia penicillata* (Fig. 2e; Marlow et al. 2015).

Focussed and catastrophic predation by feral cats has also been recorded for many other free-ranging mammal populations, including greater bilbies *Macrotis lagotis* (Fig. 2a) and rufous hare-wallabies *Lagorchestes hirsutus* (reviewed by Moseby et al. 2015).

#### COMPARATIVE ANALYSES OF CORRELATES OF DECLINE

Comparative analyses have established consistent associations between extent of decline of species and traits likely to predispose them to predation by feral cats. Most Australian mammal species that have declined severely or become extinct, such as the lesser bilby and broad-faced potoroo *Potorous platyops*, lie within a 'critical weight range' (35 g–5.5 kg), that is the preferred prey-size range of feral cats and foxes (Burbidge & McKenzie 1989). In northern Australia, where foxes are mostly absent, declining mammal species are mostly within the preferred prey-size range of feral cats (Fisher et al. 2014). Terrestrial and semi-arboreal species are more likely to decline than arboreal or rock-dwelling species, which are less accessible to cats and foxes (Smith & Quin 1996). Finally, native species in open habitats are more susceptible to decline than those in structurally complex habitats (Burbidge & McKenzie 1989), where the hunting success of feral cats is reduced (McGregor et al. 2015).



**Fig. 2.** Some mammal species threatened by feral cats in Australia and mentioned in the text: (a) greater bilby *Macrotis lagotis*; (b) Tasmanian pademelon *Thylogale billardieri*; (c) golden bandicoot *Isoodon auratus*; (d) pale field rat *Rattus tunneyi*; (e) juvenile woylie *Bettongia penicillata*; (f) burrowing bettong *Bettongia lesueur*. Photo credits: (a) Kevin503 (Wikimedia commons, CC BY-SA 3.0); (b–c, e–f) Judy Dunlop; (d) Henry Cook.

#### SPATIAL AND TEMPORAL ANALYSES OF DECLINE

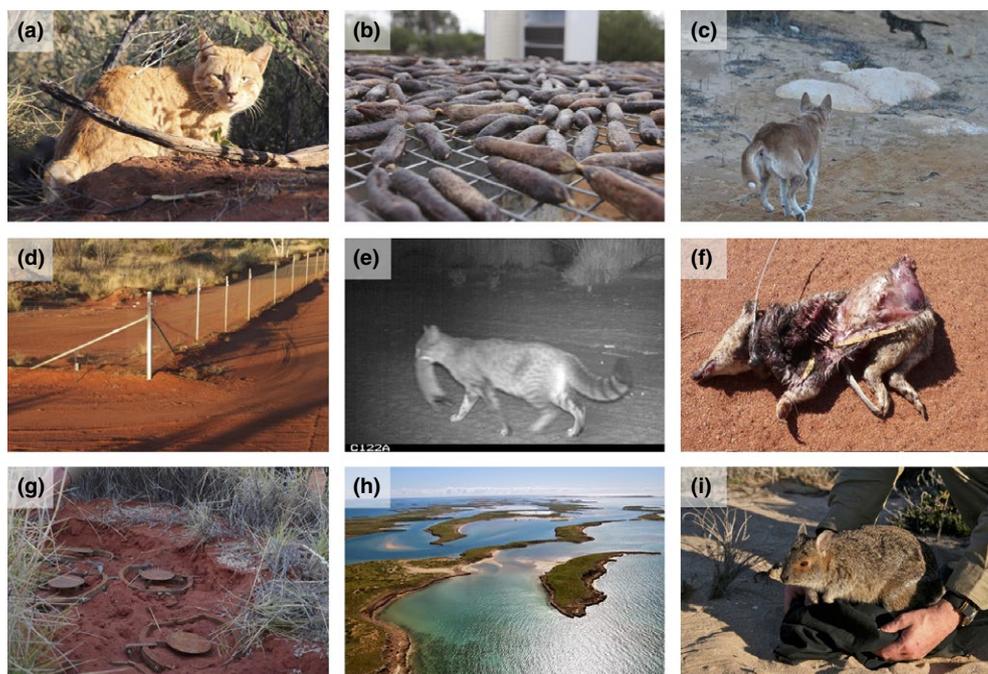
Historical data and field observations show many cases where mammals (e.g. Burbidge & McKenzie 1989, Smith & Quin 1996) and, in some cases, birds (Whitlock 1923) have declined rapidly following feral cat arrival or increases in local abundance. Dickman et al. (1993) concluded that feral cats were the sole or primary cause of extinction of 10 species of small (<220 g) mammals in western New South Wales (Fig. 1, site 10) in the first half of the 19th century. Smith and Quin (1996) also identified feral cats as the primary driver of range decline for conilurine rodents in areas where rabbits and foxes are scarce or absent. Burbidge and Manly (2002) found that feral cat and fox presence was associated with mammalian extinctions on islands and that the effect of cats was strongest on arid islands. Conversely, several mammal species that are extinct on the mainland survive only on islands that are free of cats and foxes (Abbott & Burbidge 1995).

#### PREDATOR MANIPULATION EXPERIMENTS

A few experimental studies have been used to assess the impacts of feral cats by manipulating cat density and measuring changes in prey populations. In the Simpson Desert (Fig. 1, site 8), trap capture rates of the sandy inland mouse *Pseudomys hermannsburgensis* increased by 42% following the removal of feral cats and foxes, whereas capture rates declined by 63% on experimental control plots where the predators remained (Mahon 1999). At

Heirisson Prong (Fig. 1, site 1), trap capture rates of small mammals declined by 80% in a low fox and high cat density treatment, doubled in a low fox and low cat treatment, and were intermediate in a control area with moderate densities of cats and foxes (Risbey et al. 2000). At Arid Recovery (Fig. 1, site 9), the abundance of native rodents in a fenced reserve with no feral cats, foxes, or rabbits was 15 times higher than outside the reserve (Moseby et al. 2009).

Further compelling evidence of the impacts of feral cats comes from comparing the fates of reintroduced mammals inside and outside predator-free reserves and islands. In the northern monsoonal savannas (Fig. 1, site 7), feral cats quickly extirpated two populations each of long-haired rats and pale field rats *Rattus tunneyi* (Fig. 2d) reintroduced to predator-accessible areas, while two populations of each species in cat-proof enclosures persisted (Frank et al. 2014, Tuft et al. 2014). Predation by feral cats has caused or contributed to failures of reintroduction attempts for the golden bandicoot *Isoodon auratus* (Figs 2c and 3e–f), western barred bandicoot *Perameles bougainville* (Short 2016), greater bilby (Moseby et al. 2011), rufous hare-wallaby and banded hare-wallaby *Lagostrophus fasciatus* (Hardman et al. 2016), and burrowing bettong *Bettongia lesueur* (Fig. 2f) and woylie (reviewed by Clayton et al. 2014). In contrast, removal and exclusion of feral cats and foxes from fenced areas and islands allows stable or increasing populations of these and many other species to exist (Fig. 3i; e.g. Langford & Burbidge 2001, Moseby et al. 2011). The single biggest influence on translocation



**Fig. 3.** (a) A feral cat *Felis catus*; (b) *Eradicat*<sup>®</sup> 1080 poison baits; (c) dingo *Canis dingo* chasing a cat; (d) cat exclusion fence at Matuwa (Lorna Glen; Fig. 1, site 3); (e) cat with a golden bandicoot *Isoodon auratus* in its mouth; (f) radiocollared golden bandicoot preyed on by a cat outside the fence at Matuwa; (g) padded foot-hold traps used to catch cats; (h) Hermite Island (Fig. 1, site 2) where feral cats and black rats *Rattus rattus* were eradicated and native mammals translocated to; (i) spectacled hare-wallaby *Lagorchestes conspicillatus* being released on Hermite Island. Photo credits: (a–b) Tim Doherty; (c) Jen Parker; (d, f, g–i) Judy Dunlop; (e) Mike Wyson.

success of native mammals in Australia is the presence or absence of cats and foxes at release sites (Clayton et al. 2014).

### Interacting factors

Feral cat impacts are context-dependent and vary with temporal dynamism in ecological drivers, such as rainfall and the extent of other threats (e.g. frequent fire or intense pastoralism; Doherty et al. 2015b). Comparative evidence suggests that impacts are greatest in habitats with less vegetative ground cover (Burbidge & McKenzie 1989, Burbidge & Manly 2002, Fisher et al. 2014, Lawes et al. 2015). This is supported by studies demonstrating that feral cats in Australian tropical savannas (Fig. 1, site 6) preferentially hunt in recently burnt and heavily grazed areas (McGregor et al. 2014), that their hunting success is higher in these relatively open areas (McGregor et al. 2015), and that predation rates on rodents are greater in burnt areas than in unburnt areas (Leahy et al. 2016). The impacts of feral cats on native species may also be especially pronounced in the transition from wet to dry periods in arid areas, when large populations of cats impose intense predation on declining populations of native prey (Letnic & Dickman 2010).

Feral cat density and impacts are strongly influenced by interactions with other invasive species. Feral cats may suppress introduced prey populations that are themselves damaging (e.g. rabbits on Macquarie Island; Bergstrom et al. 2009). Conversely, high abundance of introduced rodents and rabbits can sustain high feral cat densities (Pedler et al. 2016). Reductions in these prey may cause feral cats to switch hunting to native species (Marlow & Croft 2016).

As larger predators, dingoes *Canis dingo* and foxes can suppress the abundance of, or influence the behaviour of feral cats (Fig. 3c; Risbey et al. 2000, Brawata & Neeman 2011, Kennedy et al. 2011, Brook et al. 2012, Wang & Fisher 2013, Marlow et al. 2015). The numbers and impacts of feral cats can increase when fox density is reduced (Risbey et al. 2000, Marlow et al. 2015) because foxes compete with cats for resources, sometimes resulting in lethal encounters (Glen & Dickman 2005). Similarly, the impacts of feral cats may be reduced by the presence of dingoes, so dingo persecution may lead to increased impacts of cats (Brook et al. 2012; see ‘Managing trophic cascades’ below).

### Disease transmission

Thirty-six pathogens or diseases have been recorded from Australian feral cats (Henderson 2009). The protozoan

parasite *Toxoplasma gondii* is the most significant and well-studied, due to its potentially harmful effects on humans, wildlife and livestock (Henderson 2009). In Australia, cats are the sole definitive host of *Toxoplasma gondii*, which is spread through oocysts in cat faeces. Seroprevalence of stray and feral cats in Australia ranges from 0 to 96% (mean = 45%,  $n = 13$ ; reviewed by Fancourt & Jackson 2014). Infection with *Toxoplasma gondii* can cause death in some marsupials (e.g. Bettiol et al. 2000), but the prevalence and clinical effects of *Toxoplasma gondii* infection in native species are poorly understood (Hillman et al. 2016).

*Toxoplasma gondii* infection may increase predation risk in infected mammals, either by altering their behaviour or decreasing their fitness. Hollings et al. (2013) found that road-killed Tasmanian pademelons *Thylogale billardierii* (Fig. 2b) had higher *Toxoplasma gondii* seroprevalence (31%,  $n = 16$ ) than culled individuals assumed to represent background population levels (11%,  $n = 212$ ). Fancourt et al. (2014) found that seroprevalence was higher in declining populations (seroprevalence 77–100%) than in non-declining populations (9–29%) of eastern quolls *Dasyurus viverrinus* in Tasmania (Fig. 1, site 14). However, there was no effect of infection on quoll reproduction or survival, suggesting that seroprevalence reflects exposure to cats and that cats may be suppressing quolls through predation, competition or exclusion, rather than disease (Fancourt et al. 2014). *Toxoplasma gondii* infection has been detected in many free-ranging animal populations without obvious clinical symptoms (e.g. Parameswaran et al. 2009). Thus, we need a better understanding of the biological and ecological contexts in which native species are susceptible to, and adversely affected by, infection (Hillman et al. 2016).

### Competition with native carnivores

Resource competition with feral cats may threaten quolls *Dasyurus* species, Tasmanian devils *Sarcophilus harrisii*, raptors, and varanids *Varanus* species. Glen and Dickson (2008) and Glen et al. (2011) recorded dietary and spatial overlap between feral cats and spotted-tail quolls *Dasyurus maculatus* in eastern Australia, suggesting the potential for resource competition. During a rodent population irruption in central Australia, Pavey et al. (2008) recorded extensive dietary overlap between letter-winged kites *Elanus scriptus*, feral cats, and foxes. They suggested that kites could suffer from competition during rodent population declines, because kites have narrower dietary niches than the introduced predators. Few other researchers have compared the resource use of feral cats and native carnivores (e.g. Sutherland et al. 2011, Moseby et al. 2012), and

none has experimentally investigated the extent, or the potential impacts, of resource competition.

### Indirect impacts

By causing or contributing to the extinction of many native mammal species, feral cats have indirectly affected multiple ecological processes. Many extinct mammal species in Australia dug prolifically to forage or construct burrows (Fleming et al. 2014). Reduced disturbance to litter and topsoil following the loss of digging mammals has led to landscapes with reduced organic matter accumulation, water retention, fungal diversity, seed germination and seedling establishment (reviewed by Fleming et al. 2014). Other extinct native mammals were herbivorous, and their consumption of seedlings and young plants probably affected plant recruitment patterns and community composition (Verdon et al. 2016). The suite of mammalian extinctions may also have resulted in the co-extinction of their parasites (Strona 2015).

The widespread loss of many mammals from Australia must also have resulted in major rearrangements of food webs. For example, some now-extinct mammals preyed upon invertebrates, including large predatory invertebrates. Comparisons of invertebrate faunas inside and outside mammal reintroduction sites have recorded trophic cascades associated with changes to large scorpion and spider abundances following mammal reintroductions (Silvey et al. 2015).

Continent-wide losses of fossorial and digging mammals may also have influenced fire regimes. The volume of flammable surface litter is greater at sites without reintroduced mammals than at matched control sites with them (Hayward et al. 2016). Abundant surface litter may increase the frequency and/or intensity of fires (Hayward et al. 2016), thus affecting plant and animal communities.

### IMPACTS ON AGRICULTURE

The impacts of feral cats on agriculture are understudied, probably because of a perception that cats are economic assets to farmers because they control rodents and rabbits on farms. Feral cats, along with foxes, can suppress rabbit populations when environmental conditions are poor, but this effect is weakened when rabbits benefit from improved environmental productivity (reviewed by Norbury & Jones 2015). Feral cats may damage agricultural production as vectors of disease, because toxoplasmosis is a major cause of infective ovine abortion (Dubey 2008), although little information is available on the economic costs of this (Masters 2015). *Sarcocystis gigantea* is another protozoan parasite spread by cats that infects sheep, causing cysts

in muscle that can render the meat unsuitable for human consumption (Masters 2015).

## MANAGEMENT

Until recently, broad-scale control of feral cats has been attempted far less frequently than fox control. This is because the severity and extent of detrimental impacts of feral cats was not widely recognised, management actions were considered too expensive relative to their potential benefits, and there was little expectation of success in eradication attempts, or of feasibility of long-term control.

Options for managing feral cats range from eradication on islands and complete exclusion from small fenced areas, to population reduction over areas of varying size. Some options involve killing feral cats, while others focus on reducing impacts by modifying features of their environment. The best choice of control option is likely to be context-specific. Here, we discuss the use of exclusion techniques (eradication and fencing), lethal control in unfenced areas (e.g. poison baiting), and non-lethal control in unfenced areas (e.g. habitat management).

### Exclusion

Native mammal species vary markedly in their susceptibility to feral cat predation; some are unable to tolerate even very low densities of feral cats. Their conservation requires sustained elimination of feral cats, or translocations to cat-free sites. The establishment or maintenance of predator-free havens on offshore islands (Fig. 3h) and within fenced mainland enclosures (Fig. 3d) is a core conservation action for many threatened mammals. The simplest and most cost-effective action is to ensure that the many islands currently supporting threatened species but no introduced predators have biosecurity protection that prevents establishment of introduced predators. Another frequently used approach is to translocate threatened species to islands without introduced predators (Burbidge 1999). Safe havens have also been created by eradicating introduced predators from islands, and then reintroducing threatened species. Island predator eradications can also allow native species to recolonise naturally (Dunlop et al. 2015), or for *in situ* populations to recover from feral cat predation (Jones et al. 2016).

In the case of mainland 'islands', the above steps are preceded by construction of a predator-proof fence (reviewed by Long & Robley 2004). There are 16 such sites with reintroduced, but now self-sustaining, populations of predator-susceptible native mammal species in Australia, covering a total area of 273.1 km<sup>2</sup>, and ranging in size from 0.5 km<sup>2</sup> to 78 km<sup>2</sup> (Woinarski et al. 2014, S. Legge,

unpublished data). There are at least 117 predator-free islands (3690 km<sup>2</sup>) supporting populations of terrestrial, cat-susceptible mammal species listed as near-threatened or threatened in the Action Plan for Australian Mammals (Woinarski et al. 2014). Collectively, islands and fenced enclosures hold populations of at least 44 predator-susceptible terrestrial taxa listed as near threatened or threatened in the mammal Action Plan (Woinarski et al. 2014).

Fences require large upfront capital costs, ongoing maintenance, and vigilance against incursions. These costs, and the difficulties of complete eradication and ongoing exclusion of introduced species, may limit the size of areas that can be protected. Fenced areas can be more susceptible to incursions than offshore islands, and some have failed due to inadequate security or maintenance. Both fences and islands can have unwanted consequences by creating the potential for local overabundance, inbreeding, and restricted evolutionary potential (Hayward & Kerley 2009). Additionally, fences can block animal movements and cause mortality from fence-strikes (Hayward & Kerley 2009). Fences eventually deteriorate and require replacement; cost-efficiency modelling (e.g. Helmstedt et al. 2014) may assist in planning for maintenance and replacement costs that are currently unknown. Advantages fences have over islands include the ability to target particular ecosystems and the potential for passive two-way exchange of some animals through fences. Although managing offshore islands as safe havens entails lower initial capital costs and much lower ongoing maintenance costs, relatively remote and uninhabited islands may pose logistic problems for ongoing surveillance for incursions and monitoring of translocated populations. Eradicating feral cats from islands, or preventing their colonisation of islands where they are absent, can also protect endemic taxa and significant seabird rookeries, which feral cats can readily deplete (e.g. Dunlop et al. 2015).

### Lethal control in unfenced areas

#### POISON BAITING

Aerial poison baiting can provide landscape-scale control (e.g. over an area of 2350 km<sup>2</sup>; Algar et al. 2013). However, until recently, such programs have targeted foxes and dogs rather than feral cats, because cats prefer live prey and high bait-take usually only occurs when live prey are scarce (Algar & Burrows 2004). Two recently developed baits, *Curiosity*<sup>®</sup> and *Eradicat*<sup>®</sup> (Fig. 3b), have enhanced uptake. *Eradicat*<sup>®</sup> contains 4.5 mg of 1080 poison (sodium monofluoroacetate) per 15-g bait and was registered in December 2014 for use in Western Australia. Native fauna there, particularly in the south-west, have naturally high

tolerances to 1080 because they co-evolved with endemic plants containing similar compounds (Twigg & King 1991). *Eradicat*<sup>®</sup> baits are generally distributed from an aircraft at 50 baits km<sup>-2</sup> (Algar et al. 2013), although they have also been dispersed by hand in the southern rangelands (Fig. 1, site 4; Doherty & Algar 2015) and suspended above ground to limit interference from non-target species at Christmas Island (Algar & Brazell 2008).

*Curiosity*<sup>®</sup> baits contain 78 mg of PAPP poison (para-aminopropiophenone) encapsulated in a 'hard shelled delivery vehicle'. *Curiosity*<sup>®</sup> is not yet registered, but has been developed for use where native fauna are less tolerant of 1080. Encapsulating the poison reduces non-target risk because native species are more likely than cats to reject the capsule (Marks et al. 2006, Hetherington et al. 2007). *Curiosity*<sup>®</sup> has been trialled at temperate, arid, and semi-arid mainland and island sites (see Johnston et al. 2014 and references therein). However, its suitability in warm northern climates is limited, because susceptible non-target species, such as varanids, are active all year. Its use in Tasmania is precluded by risks to non-target species, such as Tasmanian devils. A third bait, *Hisstory*, that contains encapsulated 1080, is being tested in northern Australia where native species susceptible to PAPP are active at the time of baiting (Algar et al. 2015).

In arid and semi-arid Australia, the efficacy of feral cat baiting is highest when prey availability is lowest (Christensen et al. 2013). Baiting operations therefore generally take place in autumn and early winter when rabbit abundance and reptile activity is lowest (Algar et al. 2013). Nonetheless, baiting operations may fail if high antecedent rainfall elevates prey populations (e.g. Johnston et al. 2012).

Poison baits pose risks to many native species, but also kill foxes and dingoes, which often consume baits more readily than feral cats (Algar & Burrows 2004). Removal of dingoes and foxes could have the unwanted effect of releasing feral cats from top-down control (Risbey et al. 2000, Brook et al. 2012, Wang & Fisher 2013, Marlow et al. 2015), highlighting the need to use integrated, multi-species approaches (discussed below). Further, baiting will be effective only if implemented strategically to accomplish consistent and large reductions in feral cat density, otherwise rapid immigration will replace the killed individuals (Lazenby et al. 2014, Lieury et al. 2015). Over the medium- to long term, the efficacy of recurrent baiting may diminish because of acquired toxin resistance (e.g. Twigg et al. 2002).

#### SHOOTING AND TRAPPING

Shooting and trapping are labour-intensive methods that may be suitable when control areas are relatively small

and accessible. Feral cats have high reinvasion potential (Lazenby et al. 2014), so shooting and trapping are unlikely to be effective broad-scale control tools in isolation. These two techniques are most useful for removing 'problem' individual cats preying on threatened species (e.g. Moseby et al. 2015) and in the later stages of eradication programs (e.g. Algar et al. 2002). Conventional trapping (Fig. 3g) typically presents ethical and logistical challenges; non-target species may be caught, and traps must be checked daily. Automated cat-specific grooming traps that spray a toxin onto passing individuals circumvent many of these issues (Read et al. 2014). Until they become economically viable for broad-scale deployment, such tools are most appropriate for small-scale operations.

#### Non-lethal control in unfenced areas

Given that, other than in fenced or island systems, lethal control is a temporary solution or requires recurrent inputs, it is important to consider alternative methods for reducing the impacts of feral cats. Such methods include the management of habitat, food and trophic cascades, and the use of guardian dogs.

#### MANAGING HABITAT

Habitat structure modifies species' vulnerability to predation (Burbidge & McKenzie 1989, Fisher et al. 2014, Lawes et al. 2015). Reduction in ground or understorey vegetation cover by fire and grazing can make prey species more vulnerable to predators (McGregor et al. 2014, 2015, Hradsky 2016, Leahy et al. 2016). Accordingly, appropriately managing grazing and fire should increase the ability of at least some species to coexist with predators (Doherty et al. 2015b). Experiments with landscape-scale fire and grazing in northern Australia show that management of these two habitat modifiers can boost native mammal populations even without feral cat control (Kutt & Woinarski 2007, Legge et al. 2011), probably by reducing the impacts of cats (McGregor et al. 2014, 2015, Leahy et al. 2016) and by increasing resource availability.

#### MANAGING FOOD SUPPLIES

Anthropogenic resource subsidies, such as carcass dumps and municipal refuse facilities, can sustain exceptionally high densities of predators (Newsome et al. 2015b). Accordingly, removing resource subsidies such as food (Bino et al. 2010) or shelter (Denny 2005) can reduce local densities of predators. Appropriate fencing should also help exclude feral cats from waste facilities. The potential benefits to native fauna through decreased hyperpredation are yet to be demonstrated in Australia.

Large populations of introduced rabbits can support high densities of feral cats and potentially lead to hyperpredation of native species (Smith & Quin 1996, Courchamp et al. 2000), especially during transitions from wet periods to droughts (Letnic & Dickman 2010). Disease-induced declines in rabbit abundance can cause declines in feral cat numbers and recovery of mammal populations (Pedler et al. 2016). However, there is a risk that once rabbit numbers fall below a critical threshold, feral cats will prey-switch (Marlow & Croft 2016), so management of introduced prey populations needs to be carried out carefully.

#### MANAGING TROPHIC CASCADES

As apex predators, dingoes can suppress feral cat activity or abundance by killing cats (Moseby et al. 2012), or by causing them to alter their activity patterns, either spatially or temporally, to avoid encounters with dingoes (Brawata & Neeman 2011, Brook et al. 2012, Wang & Fisher 2013). Such observations have led to calls for positive management of dingo populations as a conservation technique (Dickman et al. 2009), but this remains contentious. In much of Australia, dingoes are persecuted due to their attacks on livestock, although lethal control can have perverse impacts including increased calf losses (Allen 2013) and lower productivity due to increased grazing by kangaroos (*Macropus* species) released from predation (Prowse et al. 2014). Studies using similar methodologies have produced divergent conclusions on the ecological impacts of dingoes in Australia. Additional experimental studies are therefore required to help resolve scientific conjecture that currently hinders advances in predator management (Newsome et al. 2015a). Dingoes also prey on some threatened species, and could increase risks to those with restricted distributions and small populations (e.g. Banks et al. 2003).

Consideration of trophic interactions should also encompass the possibility that reduced numbers of feral cats may allow increases to occur in populations of other introduced pests (notably black rats *Rattus rattus*, house mice and rabbits), potentially leading to net detriments to some threatened species (e.g. Courchamp et al. 1999), with particular risks for threatened birds in some island situations (e.g. Bergstrom et al. 2009).

#### GUARDIAN DOGS

Guardian dogs are bred and trained to accompany livestock and protect them from predators. In Australia, guardian dogs effectively prevent predation on livestock by wild canids (van Bommel 2010). Applications of guardian dogs to wildlife conservation have not been explored in Australia,

except for two cases in which Maremma sheepdogs eliminated predation by foxes on breeding colonies of little penguins *Eudyptula minor* and gannets *Morus serrator* in south-west Victoria (Fig. 1, site 12; van Bommel 2010). It is not known whether guardian dogs may likewise reduce the impacts of feral cats, nor whether the model can be extended from colonial seabird species to wider ranging, solitary, and nocturnal mammal species.

### PRIORITIES FOR FUTURE MANAGEMENT AND RESEARCH

Our understanding of the impacts and management of feral cats in Australia is advancing, yet uncertainty remains about the efficacy of different management approaches in different contexts. Given the urgency of the problem, we need a layered management and research strategy that includes emergency intervention for the native species that are most at risk, and research that provides richer understanding for longer term management of feral cat impacts in larger areas. It is essential that management interventions are well-supported by evidence, so they meet their intended objectives, provide return on investment, and are implemented within an adaptive management framework (Doherty & Ritchie 2016). We emphasise that management actions and measures of their success should focus on reducing the impacts of feral cats rather than on reductions in their numbers alone. Embracing experimental design principles in management trials is likely to produce the most reliable information regarding the efficacy of different approaches (Doherty & Ritchie 2016).

Here, we consider four priorities for future research and management: 1) prevent feral cats from driving the most vulnerable species to extinction, 2) assess the efficacy of new management tools, 3) trial options for control via ecosystem management, and 4) increase potential for native fauna to coexist with feral cats.

#### Preventing further extinctions

The most urgent priority is to prevent the imminent extinction of species most imperilled by feral cat predation. Examples include the Critically Endangered woylie, mountain pygmy possum *Burramys parvus*, Kangaroo Island dunnart *Sminthopsis aitkeni*, central rock rat *Zyzomys pedunculatus*, and western ground parrot (Woinarski et al. 2014, Anonymous 2015b). Captive breeding programs or intense lethal control of feral cats may be necessary interventions for some species. Conservation of threatened mammals will probably require strategic establishment of insurance populations on predator-free islands and/or in fenced enclosures, either within or beyond their former ranges. Although more challenging, eradicating cats from

large islands (e.g. >50 km<sup>2</sup>) would yield greater conservation benefits than eradicating them from small islands. Larger islands typically support more habitat types, more species and larger animal populations, all of which are important for species reintroduction success. Feral cat eradication is now being attempted on Dirk Hartog (620 km<sup>2</sup>) and Christmas Islands (135 km<sup>2</sup>); future eradications are proposed on Kangaroo (4405 km<sup>2</sup>), French (174 km<sup>2</sup>) and Bruny Islands (362 km<sup>2</sup>; Fig. 1). The logistical challenges and economic cost of eradications increase with island or fenced reserve size and are complicated further when humans or other invasive mammals (e.g. rats) inhabit the island. Ownership of pet cats means that community support is essential for cat eradications on human-inhabited islands (Algar et al. 2011).

The effectiveness of these approaches can be improved by modelling approaches, such as prioritisation of eradication efforts (Helmstedt et al. 2016), optimisation of the order in which multiple invasive species are removed (Bode et al. 2015), and determination of optimal fence locations (Bode et al. 2012) and arrangements (Helmstedt et al. 2014). The longer term aim of re-establishing populations in unfenced mainland areas relies on new management approaches to reduce predation risk from feral cats and foxes sufficiently.

## New management tools

The limited success of conventional management tools, such as trapping and baiting, means that developing new tools (e.g. guardian animals, van Bommel 2010, grooming traps, Read et al. 2014) should be a priority. The usefulness of these tools is likely to be greatest where intensive control is needed on a small scale, such as at translocation sites and drought refuges, and to protect remnant populations of threatened species.

In some situations, landscape-scale baiting programs will be necessary to achieve the recovery of native species susceptible to predation by feral cats. However, such programs should be undertaken in a precautionary manner to avoid undesirable consequences (Doherty & Ritchie 2016). For example, since baiting can reduce dingo populations (Algar & Burrows 2004, Johnston et al. 2014), baiting protocols will need to target feral cats as tightly as possible such that the benefits of baiting outweigh any associated reductions in dingo numbers. This issue will benefit from the development of decision support tools that help predict the likely outcomes of different control options in varying environmental contexts. There is also substantial scope for increasing the spatial prioritisation of feral cat control efforts. Refuges such as riparian areas and drainage lines can promote fauna population persistence during drought (Pavey et al. 2016). As drought length

and severity are projected to increase in the future (Anonymous 2015a), strategic control of feral cats at refuge sites may be needed to secure fauna persistence during these times.

An effective biological control agent has not yet been developed for feral cats (but see Beeton et al. 2015). Immunocontraceptive viruses that interfere with animals' fertility are currently being tested for cats (Munks 2012). Although in its infancy, gene drive technology also may be able to induce sex bias or toxin sensitivity in target species through genetic modification (Strive & Sheppard 2015). A major challenge in developing new biocontrols is the need to reduce risks of infection for pet cats and felids in other parts of the world. Investment in biocontrol research may facilitate the development of an effective, long-term control tool.

## Ecosystem management

Studies from northern Australia indicate that sympathetic grazing and fire regimes can reduce feral cat impacts (McGregor et al. 2014, 2015, Leahy et al. 2016). Further studies are now needed to test this result in different habitats, including in the mesic parts of southern Australia where prescribed burning, and foxes, are common (but see Hradsky 2016). Current evidence does not yet confirm that environmental management can reduce feral cat impacts sufficiently to recover critical weight range species, such as bandicoots (Peramelidae), bettongs and potoroos (Potoroidae).

## Increased potential for native fauna to coexist with cats

Feral cats are unlikely to be eradicated from mainland Australia in the foreseeable future. Therefore, it is important to explore the potential for enhancing the capability of native fauna to persist with feral cats. The naivety of native species to cats is a major impediment to their coexistence (Banks & Dickman 2007). One proposed solution is to use *in situ* encounters between wild predator and prey populations to promote natural selection of appropriate prey defensive traits (Moseby et al. 2016). Early results at Arid Recovery in South Australia show that 350 burrowing bettongs are coexisting with three feral cats inside a 24 km<sup>2</sup> enclosure and are exhibiting increased vigilance behaviour (K. Moseby, personal communication).

## CONCLUSIONS

Feral cats continue to be an exceptionally severe threat to Australian biodiversity. A major conservation benefit

can be obtained by increasing the effectiveness of their management. Managing the impacts of feral cats will be best achieved by using islands and fenced mainland enclosures to protect vulnerable native species, as well as by implementing actions that reduce impacts sufficiently that populations of other native species can persist. Success will depend on managing factors that may compound the impacts of feral cats, such as fire and overgrazing.

Management of feral cats should adhere to an explicit decision-making process that considers social, economic and environmental contexts, the full range of control methods available, relevant time-scales, how feral cats will be monitored pre- and post-control, and importantly, measures the responses of species that control is designed to benefit. Such a robust and multi-dimensional framework will help to ensure the most cost-effective and ecologically sound outcomes are achieved from feral cat management.

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