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Enumerating a continental-scale threat: How many feral cats are in Australia?

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ABSTRACT

Feral cats (*Felis catus*) have devastated wildlife globally. In Australia, feral cats are implicated in most recent mammal extinctions and continue to threaten native species. Cat control is a high-profile priority for Australian policy, research and management. To develop the evidence-base to support this priority, we first review information on cat presence/absence on Australian islands and mainland cat-proof exclosures, finding that cats occur across >99.8% of Australia's land area. Next, we collate 91 site-based feral cat density estimates in Australia and examine the influence of environmental and geographic influences on density. We extrapolate from this analysis to estimate that the feral cat population in natural environments fluctuates between 1.4 million (95% confidence interval: 1.0–2.3 million) after continent-wide droughts, to 5.6 million (95% CI: 2.5–11 million) after extensive wet periods. We estimate another 0.7 million feral cats occur in Australia's highly modified environments (urban areas, rubbish dumps, intensive farms). Feral cat densities are higher on small islands than the mainland, but similar inside and outside conservation land. Mainland cats reach highest densities in arid/semi-arid areas after wet periods. Regional variation in cat densities corresponds closely with attrition rates for native mammal fauna. The overall population estimate for Australia's feral cats (in natural and highly modified environments), fluctuating between 2.1 and 6.3 million, is lower than previous estimates, and Australian feral cat densities are lower than reported for North America and Europe. Nevertheless, cats inflict severe impacts on Australian fauna, reflecting the sensitivity of Australia's native species to cats and reinforcing that policy, research and management to reduce their impacts is critical.

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1. Introduction

Feral domestic cats *Felis catus* are one of the world's most damaging invasive species. They have contributed to the extinction of at least 33 species of birds, mammals and reptiles on islands alone, representing 14% of modern extinctions in these vertebrate groups (Medina et al., 2011). Since their introduction to Australia at or soon after European settlement in 1788 (Abbott, 2002; Abbott, 2008), cats have spread across the continent and many of its islands (Abbott and Burbidge, 1995; Burbidge and Manly, 2002), inflicting severe impacts on Australia's biodiversity. Recent reviews indicate that they were a causal factor in the extinction of most of the 30 Australian native mammal species lost since European settlement (Woinarski et al., 2014; Woinarski et al., 2015a), and they continue to subvert many recovery efforts (Hardman et al., 2016; Short, 2016). There is no effective broad-scale control method for feral cats, so they remain a major cause of decline of many Australian mammal species (and probably of some bird, reptile and frog species) (Department of the Environment, 2015; Woinarski et al., 2011; Ziembicki et al., 2014).

The Australian Government has recently implemented high-profile public policy focused on the recovery of threatened species, including through enhanced control of feral cats (Commonwealth of Australia, 2015; Department of the Environment, 2015). Good policy should rest on a robust evidence base, especially if it is likely to involve contentious issues with significant public interest and concern. The priority accorded to the control of feral cats has attracted public attention related to perceived animal welfare issues associated with control mechanisms, concerns about the implications of the policy focus on rights of pet-owners, and disagreement about the magnitude of impacts of feral cats and hence the need to control them (Wallach and Ramp, 2015).

One factor that has attracted considerable public attention is the number of feral cats in Australia. The focus on this issue stems partly from estimates such as that presented in Department of the Environment Water Heritage and the Arts (2008) of 18 million feral cats in Australia. Based on this number, Anon (2012) estimated that feral cats killed 75 million native animals in Australia per day. These large estimates have galvanised public interest and have been influential in shaping government commitment, policy and investment. However, such scenarios have been based on estimates of the feral cat population size in Australia that have not been tested or qualified by peer review (Hone and Buckmaster, 2014). Simple estimates of total population size also ignore spatial and temporal variation in the density of cats according to environmental factors, which may be more relevant to management and impact of cats than a simple continental total.

One particular component of recent public policy involves a numerical target (two million) for the number of feral cats to be killed by managers over the period 2015–2020 (Commonwealth of Australia, 2015). This particular target may not provide a useful measure of conservation benefit, nor may it be readily measurable (Woinarski et al., 2015b), and it may become an example of Goodhart's Law - that once a target is set, management effort becomes focussed on achieving the target in the most efficient way rather than solving the problem to which the target relates (Newton, 2011). For the culling of two million cats to be a defendable target, it must be contextualised with reference to the total number of feral cats in Australia.

Precise population estimates exist for only a very small proportion of animal species in Australia, mostly large native (such as some kangaroos, *Macropus* spp.) and feral vertebrates that can be detected and accurately counted through aerial surveys, and for which reliable monitoring is mandated or prioritised because the species have commercial value, or are economic pests with substantial public investment in management control (Caughley and Grigg, 1981). At the other extreme, there are also reasonably precise population estimates for a few highly imperilled species reduced to extremely small populations in very localised areas – essentially where almost every individual can be marked and counted (e.g. northern hairy-nosed wombat *Lasiorhinus krefftii;* Banks et al., 2003).

In contrast, there are severe constraints on the estimation of the feral cat population. Feral cats are cryptic, mostly nocturnal, and trap-shy (hence not amenable to mark-recapture population estimates). They occur across the continent, in varying densities, and in almost all environments. This makes it challenging to extrapolate national population size estimates from a set of site density estimates. Furthermore, the number of feral cats in Australia is likely to vary depending upon climatic and other conditions. Studies have demonstrated marked (>10-fold) fluctuations in local or regional abundance of feral cats in response to changing seasonal conditions, to oscillations in the abundance of native prey species, and to varying levels of control of introduced prey species,

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notably rabbits *Oryctolagus cuniculus* (Dickman, 2014; Jones and Coman, 1982; Read and Bowen, 2001).

Further complicating the problem is that some localised sites providing artificial food subsidies (such as rubbish dumps, grain silos, intensive farm operations, abandoned infrastructure in urban areas) may support extremely high densities of feral cats (e.g. >500 individuals km^{-2}: Denny et al., 2002; Denny, 2005; Short et al., 2013). Collectively, these relatively small areas may contribute disproportionately to the total national feral cat population. Similarly, in some situations, islands support densities of feral cats that are appreciably higher than mainland areas of similar habitat (e.g. Copley, 1991; Domm and Messersmith, 1990; Hayde, 1992), although the extent of their leverage on a national population estimate will depend on the proportion of Australian islands on which cats are present.

In a recent review, Hone and Buckmaster (2014) cautioned against the acceptance of popularly-used estimates of the population size of feral cats in Australia, because these estimates were poorly substantiated. In this paper, we aim to derive fundamental statistics on cat presence, density and population size across the Australian continent. We calculate the area of Australia in which feral cats are known, or presumed, to be absent. We assemble an extensive evidence base (including much previously unpublished data) of site-based cat density estimates, and characterise relationships between feral cat density and environmental and geographic variables. We use these relationships to develop a plausible estimate of the total number of feral cats in Australia. We relate our modelled spatial variation in feral cat densities to previously published accounts of regional variation in the extinction and decline in the Australian mammal fauna (Burbidge et al., 2008; McKenzie et al., 2007). Finally, we use our population estimate to provide a context for the recent national target to cull feral cats and we highlight priorities for further research.

2. Methods

2.1. Data collation

2.1.1. Areas from which feral cats are known, or presumed, to be absent

Cats are known to be absent from a small set of sites in Australia at which they have been removed and deliberately excluded by fencing in order to protect populations of threatened mammals. We compiled a list of such sites and tallied their total extent. In addition, cats are also known, or presumed, to be absent from many Australian islands. Using a number of data sources, we estimated the number and cumulative area of cat-free islands (methods and compilation provided in Appendix A).

Cats may also be absent or at extremely low densities in some habitats on the Australian mainland, including some wetlands and mangroves, areas with very dense ground vegetation (e.g. some rainforests and dense heathlands), and possibly some very rugged areas. These habitats are of limited extent in Australia, and reports indicate that feral cats do occur in closed forests and rugged areas (e.g. Gordon, 1991; Hohnen et al., 2016). We could not locate any site-based estimates of cat density in wetlands, mangroves, rainforests and dense heaths (data on cat density from these habitats in other countries are similarly rare: Doherty et al., 2015a) but our collation of site-based estimates includes at least three areas with extremely rugged topography.

2.1.2. Feral cats in natural environments

We collated all available estimates of densities of feral cats in relatively natural habitats (i.e. those still largely dominated by native vegetation) in Australia (Appendix B). This collation included sites spaced reasonably comprehensively across the country. It builds on, but extends by more than three-fold, previous collations (Denny and Dickman, 2010; Dickman, 1996). Partly because of the increasing interest in the impacts of feral cats on Australian wildlife, and in their management, there is an increasing body of contemporary field research on feral cat ecology. Although some recent publications report this research (e.g. Bengsen et al., 2012; Kutt, 2012; McGregor et al., 2014; McGregor et al., 2015a; McGregor et al., 2016; Yip et al., 2014), many density estimates used here have not been previously published. The number of available density estimates has also proliferated due to methodological progress, notably the use of camera traps with the identification of individual cats in the resulting images enabling a type of mark-recapture analysis (McGregor et al., 2015b; Stokeld et al., 2015). The oldest estimate of local density included in our analysis was from the late 1970s, but most estimates were much more recent, with the median year of study being 2011. We included older estimates because there is no reason for cat densities to have changed over the past 30 or so years (except in cases where cats were eradicated from islands). Nevertheless, we checked this assumption by regressing density estimates against the year of study, and confirmed no relationship.

For every site-based density estimate, we noted source, site location, the estimation method (see next paragraph), land-use (conservation reserve or otherwise, as noted by the data contributors, with conservation reserve including various types of relatively low-intensity pastoralism, defence land, some types of Crown land, etc.), and whether the site was on an island or the Australian mainland. From the locational data, we also subsequently determined mean annual rainfall (spatial resolution: 0.05 degrees) (Australian Bureau of Meteorology, 2016b), mean annual temperature (spatial resolution: 0.025 degrees) (Australian Bureau of Meteorology, 2016a), mean tree cover (spatial resolution: 500 m) within a 5-km radius (Hansen et al., 2003) (available at http://glcf.umd.edu/data/vcf/), topographic ruggedness (standard deviation of elevation [spatial resolution: 90 m] within a 5-km radius) (Jarvis et al., 2008), and for density estimates from islands, island area. We also noted whether the introduced red fox *Vulpes vulpes*, a potential competitor and mediator of cat density (Glen and Dickman, 2005), was present at the site. We did not consider whether the site was also within the range of the dingo or wild dog *Canis familiaris*, because this species occurs almost ubiquitously across the Australian mainland.

The quality and precision of the individual density estimates that we collated vary. Some density estimates were based on very intensive and rigorous studies undertaken over several years, and corrected for potential biases; but others were derived from shorter studies over smaller areas, and may not have considered potential biases. Only some studies included measures of variability around the site-based density estimate. We excluded only one published estimate, where that estimate was reported incidentally to the main focus of the paper, and for which no methodological basis was described (Ridpath, 1991). Estimation methods included partial or complete removal of cats from a bounded area; spatially and temporally replicated spotlight transects; intensive observation studies based on radio-tracking, tracking and capture-mark-recapture from live trapping; and analyses based on camera trapping with various trap array designs and replication. Given the heterogeneity of data sources, we note the potential for commensurate heterogeneity in reliability, and we therefore examined the influence of estimation method (i.e. Removal, Camera traps, Spotlighting, Capture-based) on the density estimates (see Section 2.2.1).

Typically, each study supplied a single density estimate for our analysis, with some exceptions: in one study, two adjacent sites exposed to contrasting management (i.e. foxes controlled in one site, but not the other) were sampled simultaneously, and we used the site information as independent estimates because we considered them to be sufficiently distinct. In seven studies, we used estimates from the same site when they were sampled in contrasting climatic conditions (i.e. wet and dry periods in the arid and semi-arid zones). However, to avoid excessive leverage from individual sites, we capped the number of estimates used in our analysis from a single site at two; if data were available from a site over many years we averaged the density estimates over the periods of time with similar climatic conditions (e.g. Mahon et al., 1998). The median duration of studies was 1 year; most estimates

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were based on a single year of sampling, but 27 estimates were based on 2–9 years of sampling (Table B1).

2.1.3. Feral cats in highly modified environments

We separately estimated the number of cats living in areas with highly modified environments (urban environments, intensive farm sites, rubbish dumps). We define these as unowned cats that rely largely on food resulting from human activity. Estimating the number of feral cats in highly modified landscapes is important for two reasons. First, there is evidence of genetic exchange between feral cats in natural and highly modified environments (Denny et al., 2002; Denny, 2005), suggesting a division between feral cats living in these two environments is artificial. Second, a recent analysis showed that urban areas in Australia support a disproportionately high number of threatened animal species (Ives et al., 2016); feral cats living in these modified environments may therefore impose substantial impacts on threatened species, even if much of their diet is anthropogenic in origin. Note that by definition, and in analyses here, the extent of highly modified environments and the extent of natural environments sum to the total land area of Australia.

The density and grouping behaviour of feral cats in highly modified environments is hyper-variable, and related to the extent of food subsidy (Liberg et al., 2000). Urban areas can support a moderate background density of solitary cats. However, at localised sites with rich food subsidies (such as rubbish dumps, intensive farm sites) cats shift from being solitary to living in groups, or 'colonies' (Kerby and MacDonald, 1988; Macdonald et al., 1987). Accordingly, we considered that feral cats living in highly modified environments comprised two components: (i) solitary cats living in urban areas and other extensive modified environments without localised rich sources of 'supplied' food, and (ii) groups of cats closely associated with small discrete areas offering particularly rich food sources. Our analyses considered these two components separately. There are relatively few estimates of cat density or abundance in highly modified environments in Australia, so we augmented these records with information on density and colony size from similar environments in Europe, north America and South Africa (see Appendix C for details).

We used the Catchment Scale Land Use of Australia Data (ABARES, 2015) to derive the total area of highly modified environments, as well as the number and area of intensive farm sites across the country that potentially offer rich anthropogenic food subsidies large enough to support feral cat colonies. We sourced data on the number of rubbish dumps across the country from the National Waste Management Database (Geoscience Australia, 2012). Further information on methods is provided in Appendix C.

2.2. Analysis

2.2.1. Feral cats in natural environments

We analysed cat density data separately for islands and the mainland (including Tasmania: see Fig. 4a for justification for including the Tasmanian mainland with the Australian mainland). Starting with the mainland, we developed a model of cat density as a function of six explanatory variables: mean annual rainfall; mean annual temperature; tree cover; ruggedness; fox presence; land-use (conservation or not). We constructed least-squares linear regression models incorporating all combinations of the variables, as well as an interaction between rainfall and temperature, giving a total of 40 models. Cat density was log-transformed prior to analysis, to ensure normality of model residuals. Models were evaluated using the second-order form of Akaike's Information Criterion (AIC_c), which is appropriate for small sample sizes. The final model was based on multi-model averaging of the entire candidate set, with each model weighted according to w_i, the Akaike weight, equivalent to the probability of a particular model being the best in the candidate set (Burnham and Anderson, 2003). Because of multi-collinearity among some of the explanatory variables, and the problems this presents for multi-model averaging, we standardized each explanatory variable prior to analysis by dividing by its standard deviation (Cade, 2015). The final model was used to predict cat density across the Australian mainland and Tasmania (excluding areas of intensive land use). We checked whether different estimation methods (Removal, Camera traps, Spotlighting, Capture-based) affected site estimates for cat density by comparing the model residuals for each method after fitting the best model of cat density from all periods (dry to wet; see below).

To estimate cat densities on islands smaller than Tasmania (i.e. <64,519 km^2), we used predictions of the mainland model, but also added a term representing island size (the natural logarithm of island area [km^2]). After Tasmania, Australia's next largest island is 5,786 km^2 (Melville Island). However, it was necessary to correct for the absence of cats from some islands. Islands known to be free of cats were allocated a density of zero. Islands known to have cats present were allocated densities according to the island density model. For the remaining islands, where cat presence was uncertain, we developed a model of the probability of cats being present as a function of island area (log-transformed) as there was a clear positive relationship between island size and cat presence, using a generalized linear model with binomial errors. To correct density for uncertain cat presence on islands, we multiplied predicted density on islands by the predicted probability of cat presence.

To estimate the total population of feral cats in Australia, we predicted density (and hence cat population size) for every 1×1 km cell across the mainland, Tasmania and islands (excluding heavily modified areas), then calculated the sum of the population estimates across all cells. We characterised the uncertainty of the total cat population by bootstrapping the dataset 10,000 times, and recalculating the population based on each random selection of the data. We report the 2.5% and 97.5% quantiles for the 10,000 values of the total population.

Marked variation in the local and regional abundance of feral cats - associated with rainfall - is a feature of arid and semi-arid Australia (Burrows and Christensen, 1994; Dickman, 2014; Read and Bowen, 2001; Rich et al., 2014). To characterise the variation in feral cat density and total population size driven by inter-annual rainfall variability in the arid and semi-arid zone, the modelling process was repeated using three sets of cat density data: (1) using all density observations, with those from the same site averaged; (2) excluding density observations following average to dry periods in the arid and semi-arid zone (where interannual variation in rainfall is very high); and (3) excluding density observations following wet periods in the arid and semi-arid zone. Hence, the three sets of cat density data differ only for the semi-arid and arid sites; the same observations from the temperate and monsoon tropical sites (where interannual variation in rainfall is relatively low) appear in all three sets. These provided approximations of the long-term average feral cat density, and the rainfall-driven lower and upper bounds, respectively.

2.2.2. Feral cats in highly modified environments

To estimate the population size of solitary feral cats living in highly modified environments within a plausible range, we multiplied the total area of such modified environments in Australia with the mean, minimum and maximum densities of cats (from the collated studies; Table C1) living in comparable environments in other countries. To estimate the additional number of cats living colonially at discrete sites with rich food subsidies, we multiplied the number of such sites across Australia by the mean, minimum and maximum colony size determined from the collated studies carried out in Australia and other countries (Table C1). We combined the statistics of the colonial cats with those of the solitary cats to generate a population size estimate for feral cats in highly modified environments, with a range based on the minimum and maximum reported densities and colony sizes.

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2.2.3. Relating modelled spatial variation in cat density with extent of decline in the Australian mammal fauna

Previous studies have provided estimates of the extent of loss in the Australian mammal fauna assemblages ('fauna attrition index') for every Australian bioregion (Burbidge et al., 2008; McKenzie et al., 2007). We used our modelled variation in cat density after wet periods to derive a mean estimate of density in each of these bioregions, and then correlated, across all bioregions, this mean with the corresponding index of regional decline in Australia's non-flying, native mammal fauna. We repeated the analysis using all available observed site-based densities, rather than predicted density.

3. Results

3.1. Cat-free areas

3.1.1. Predator exclosures

There are 19 predator exclosures in Australia designed to protect self-sustaining mammal populations, although three of these are currently compromised (i.e. with many feral predators inside the fenced area). The 16 areas from which feral cats (and other introduced predators) are effectively excluded range in size from 0.5 to 78 km^2, with a total area of 274 km^2 (i.e. 0.0036% of the Australian land area) (Table A1).

3.1.2. Islands

Feral cats are known to be present on 98 Australian islands including Tasmania (1.8% of all Australian islands), with a total area of 90,042 km^2 (92.4% of the total area of Australian islands). Excluding Tasmania, cats are present on islands with a total area of 25,523 km^2 (77.4% of the area of all other islands) (Tables A2, A3). Cats are known to be absent from 592 islands (10.9% of the island tally) with a total area of 4,911 km^2 (5.0% of the total island area, including Tasmania, or 14.9% of the total area of islands excluding Tasmania) (Table A4). Cat presence/absence is unknown for an additional 4,758 islands of size >1 ha, totalling 2,535 km^2. Because of uncertainty due to lack of sampling, the number of islands without feral cats is therefore between 592 and 5,350 islands, covering 4,911 km^2 to 7,446 km^2, and representing 0.06 to 0.1% of the total Australian land area (7.69 million km^2, including all islands).

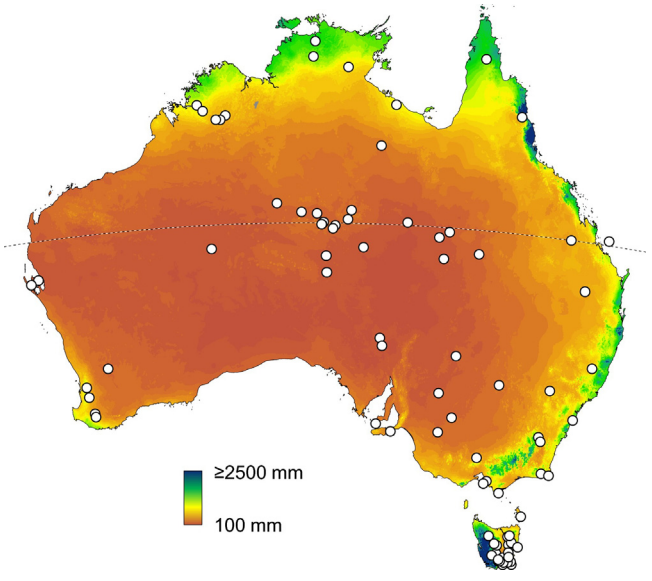

Fig. 1. Locations of feral cat density observations. There are 78 sites on the Australian and Tasmanian mainland in natural vegetation, and 13 sites on islands smaller than Tasmania (including Macquarie Island, not shown on map). The map background shows mean annual rainfall (Australian Bureau of Meteorology, 2016b). The dashed line indicates the Tropic of Capricorn.

Feral cats are much more likely to be present on larger islands. Only ten (of the 40) Australian islands larger than 100 km^2 (and none larger than 1,000 km^2) are likely or assumed to be without feral cats. Australia's largest cat-free island is the sub-Antarctic Heard Island (at 365 km^2) (Table A4).

3.2. Feral cats in natural environments

Using density observations from all periods (dry–wet) at 78 sites on the mainland and Tasmania and 13 sites on smaller islands (Fig. 1; Table B1), and extrapolating our statistical model of cat density across the areas of Australia with relatively natural environments (7.63 million km^2), we estimate the total Australian (mainland and islands) feral cat population in natural environments to be 2.07 million (95% CI: 1.40–3.45 million) (Fig. 2a). This is equivalent to a mean density of 0.27 cats km^{-2} (95% confidence interval [CI]: 0.18–0.45 cats km^{-2}) (Fig. 2b). Following periods of average to low rainfall in the arid and semi-arid zone, the total population is lower at 1.39 million (95% CI: 0.98–2.17 million) (Fig. 2a), equivalent to 0.18 cats km^{-2} (95% CI: 0.13–0.28 cats km^{-2}) (Fig. 2b). Following periods of high rainfall in the arid and semi-arid zone, the total populations is considerably higher at 5.56 million (95% CI: 2.51–10.91 million) (Fig. 2a), equivalent to 0.73 cats km^{-2} (95% CI: 0.33–1.43 cats km^{-2}) (Fig. 2b). Finally, we estimate that feral cats on islands smaller than Tasmania contribute only 0.5% of Australia's feral cat population in natural environments.

The models of cat densities showed that there was a clear negative relationship between mean annual rainfall and cat density on the mainland and Tasmania, when using observations from arid/semi-arid areas during wet periods only (Table 1b; Fig. 3b). However, when observations from arid/semi-arid areas during dry periods only were included or modelled separately, there was little evidence of this relationship

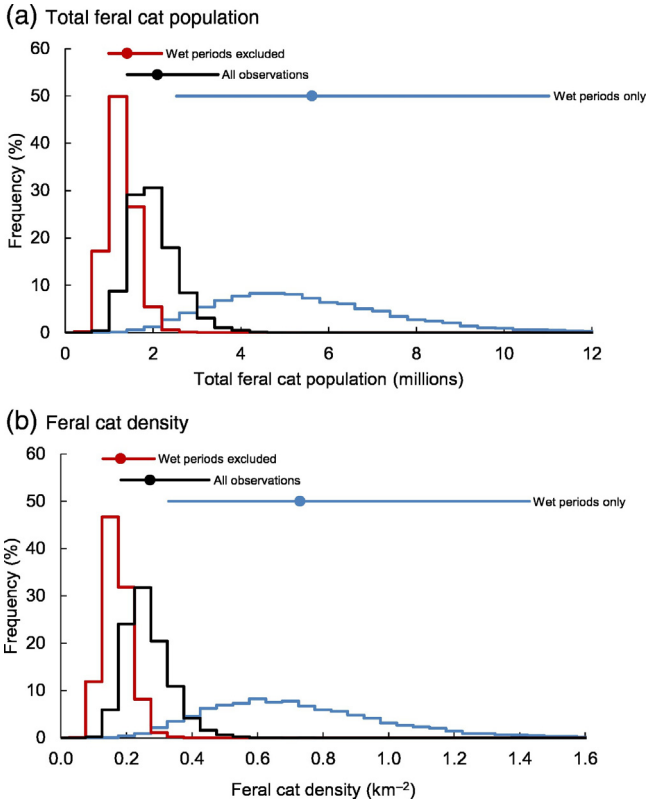

Fig. 2. Uncertainty in (a) the total feral cat population, and (b) feral cat density estimates, based on bootstrapping of the dataset 10,000 times. At the top of each panel is the mean (filled circle) and 95% confidence bounds (lines), shown separately for analyses with observations from wet periods excluded, all observation, and observations from wet periods only.

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Table 1
Highly ranked models explaining variation in feral cat density in natural environments on the mainland and Tasmania, and the results of the model selection procedure. The models are shown ranked in ascending order of the model selection criterion, AIC_c. ΔAIC_c is the difference between the model's AIC_c value and the minimum AIC_c value in the candidate set. w_i is the Akaike weight, or the probability of the model being the best in the candidate set. Models with limited support ($\Delta AIC_c > 2$), or lower support than the null model, are not included in the table.

Model	ΔAIC_c	w_i	R^2
(a) All observations included			
log(rainfall) * temperature	0.0	0.10	0.09
log(rainfall)	0.1	0.09	0.03
Null model	0.1	0.09	0.00
(b) Observations from wet periods only			
log(rainfall) * temperature	0.0	0.35	0.21
log(rainfall) * temperature + fox	1.6	0.16	0.21
log(rainfall) * temperature + ruggedness	1.6	0.15	0.21
(c) Observations from wet periods excluded			
log(rainfall) + fox	0.0	0.23	0.21
log(rainfall) + cover	1.3	0.12	0.23
log(rainfall) * temperature	1.5	0.11	0.23
log(rainfall) + temperature + ruggedness	1.8	0.09	0.22

(Table 1a, c; Fig. 3a, c). The negative relationship between a site's mean annual rainfall and cat density was relatively weak ($R^2 = 0.21$ for observations from wet periods only), though it suggested an order of magnitude difference in density between the most arid and most mesic sites in some years (Fig. 3b). We found little support for other predictors of cat density, i.e. no other predictors consistently appeared in the best models (Table 1). Of particular conservation implication, we found no consistent difference in cat density inside and outside conservation reserves. Adding a binary variable representing 'conservation reserve vs. unreserved' to the best model of cat density (density ~ log[rainfall] * temperature) decreased support for that model (using all available observations from the mainland and Tasmania). There was very clear evidence of an island area effect, with the smallest islands tending to have two orders of magnitude greater density of cats than mainland and Tasmanian sites (Fig. 4a, b). There was no evidence that estimation method (Removal, Camera traps, Spotlighting, Capture-based; see Table B1) was important: there were no significant differences between the model residuals (i.e. residuals of the best model of cat density from all periods [dry–wet]) associated with each estimation method. The spatial variation in the modelled density of feral cats across Australia is shown in Fig. 5.

3.3. Feral cats in highly modified environments

The mean cat density in highly modified landscapes was 8.2 cats km^{-2} (range: 0.8–32; n = 10; Table C1). The mean colony size was 26 (range: 3–81; n = 35) (Table C1). Note that the mean colony sizes from Australian and non-Australian studies were similar (25 and 26 respectively). The area of highly modified environments in Australia was assessed as 53,768 km^2; the constituent areas ranged in size from 0.02 to 2,543 km^2 (with this latter area being Melbourne) (Table C2). In addition, there were 10,370 sites with the potential to provide large food subsidies to feral cats (mean area of each site: 0.22 km^2; Table C3). Applying the spatial extent of heavily modified environments to the cat density and colony size estimates, gives the total number of feral cats in highly modified environments in Australia as 0.71 million, with a plausible minimum to maximum range of 0.07–2.56 million (Table 2).

3.4. Relationship between regional-level cat density and attrition of Australian mammals

There was a very strong positive relationship ($R^2 = 0.63$) between modelled cat density following wet periods and the attrition rate reported for native non-flying mammals (Fig. 6a). The relationship between observed cat density and the mammal faunal attrition rate was weaker ($R^2 = 0.22$; Fig. 6b).

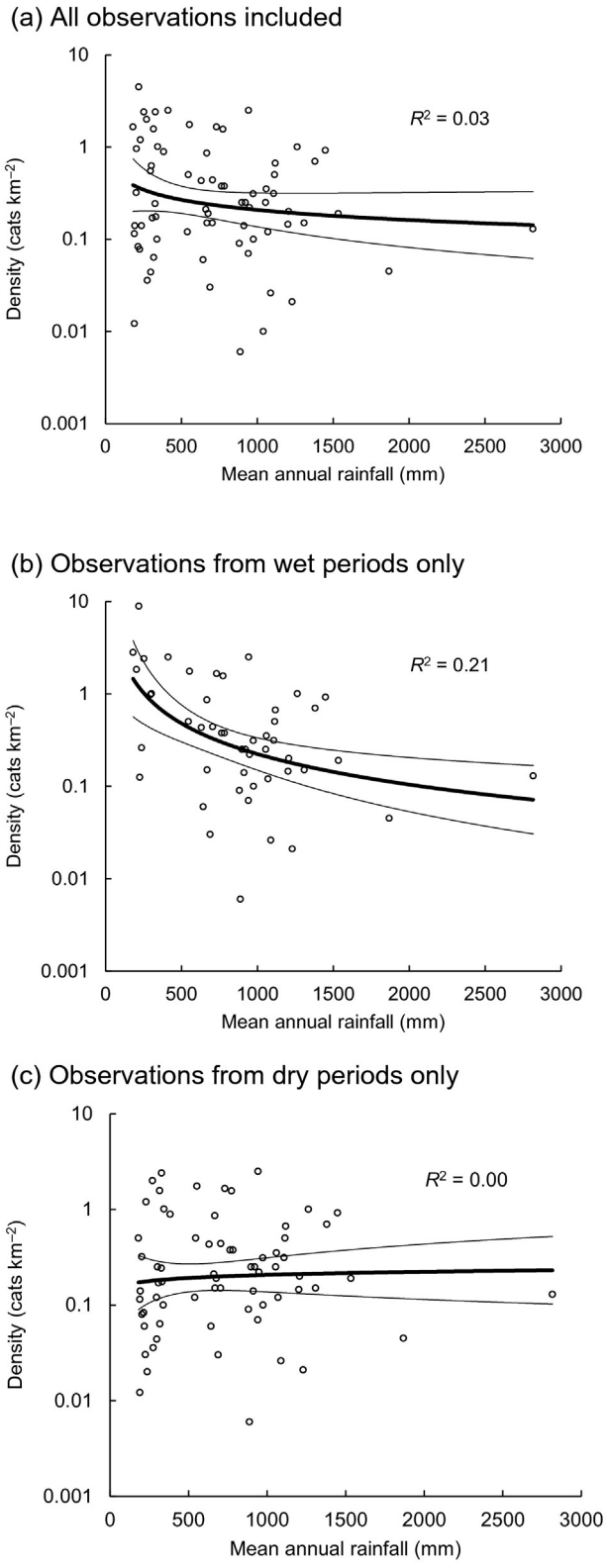

Fig. 3. Modelled relationships between cat densities and mean annual rainfall (mainland and Tasmanian sites only). The data and model shown in panel (a) relates to observations from all years. For semi-arid and arid sites, in panel (b) dry to average years have been excluded, and in panel (c) wet years have been excluded. The bold lines indicates the predicted relationships, and the thin lines indicate 95% confidence intervals.

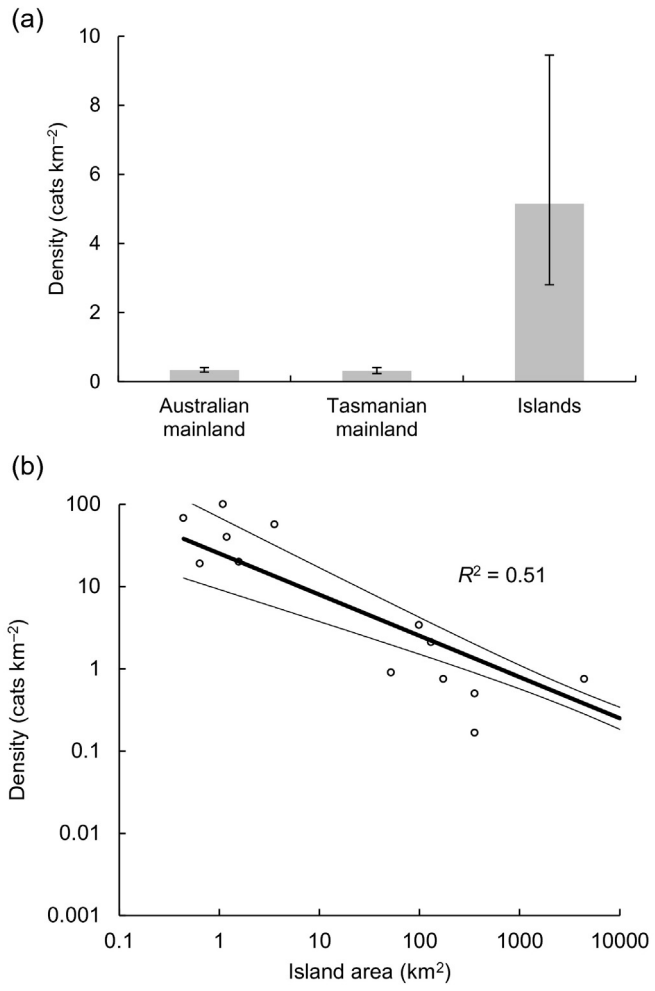

Fig. 4. (a) Variation in site-based estimates of feral cat densities in largely natural environments for the Australian mainland, Tasmanian 'mainland' and islands smaller than Tasmania. Bars are means, and whiskers standard errors. The data were log-transformed prior to analysis. (b) Modelled relationship between cat density and island area (for islands smaller than Tasmania), using observations from all periods (dry–wet). The bold line indicates the predicted relationships, and the thin lines indicate 95% confidence intervals.

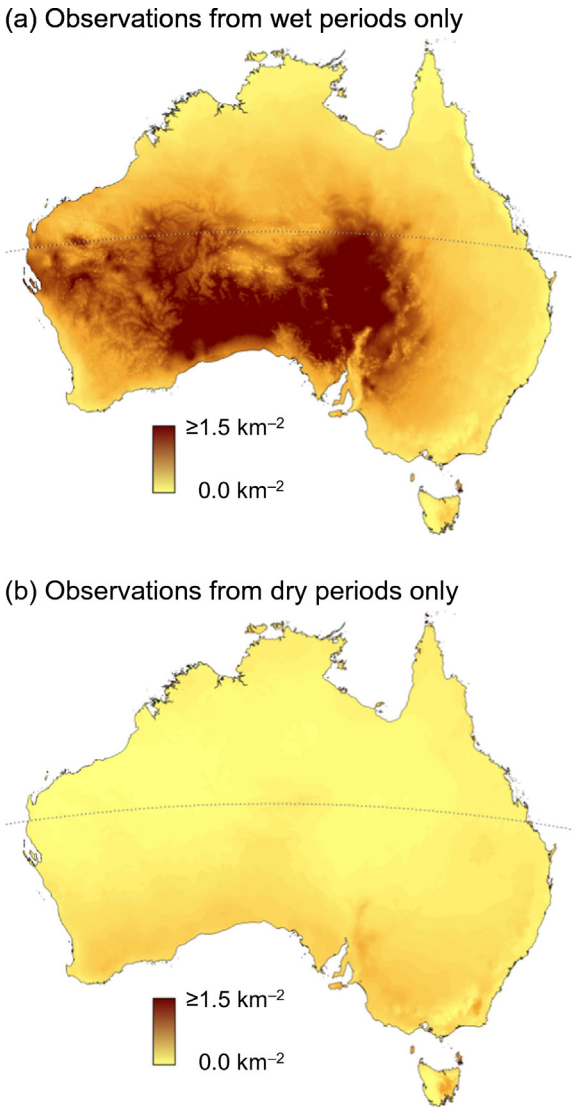

Fig. 5. The modelled density of cats throughout Australia, based on observations from (a) wet periods only, and (b) dry periods only. As predictors, the regression model includes mean annual rainfall, mean annual temperature, tree cover, ruggedness and fox presence/absence. For islands smaller than Tasmania, island area was also included as a predictor of density. The dashed lines indicates the Tropic of Capricorn.

4. Discussion

In little over 200 years, the feral cat has colonised all of mainland Australia and most of its large islands. We estimate that it is now absent from only some, mostly small, islands (with a total area of 4,911 km^2 to 7,446 km^2, or 0.06–0.1% of the total Australian land area), and that it has been removed and excluded (through fencing) from a further 274 km^2 (or 0.004%) of the total Australian land area. Thus, feral cats are likely present across >99.8% of Australia's land area. Cats may also be absent or at very low densities in a small range of unsuitable habitats, of very limited extent. A priority for management is to ensure, through appropriate biosecurity mechanisms, that this very small proportion of the Australian land mass that is currently without cats (mostly small islands) remains without cats.

By extrapolating modelled density (based on 91 field studies from across the continent) we estimate the population of feral cats in natural environments in Australia fluctuates from 1.4 million (CI: 1.0–2.2 million) following broadscale drought, to 5.6 million (CI: 2.5–11 million) following periods of widespread, high rainfall (Fig. 2). Combining these estimates with the estimate for feral cats in highly modified environments (0.7 million), gives an overall feral cat population size for Australia that fluctuates between 2.1 and 6.3 million, depending on the rainfall conditions. This population estimate is notably lower than the widely-used figures of 15–20 million (Anon, 2012; Department of the Environment Water Heritage and the Arts, 2008; McLeod, 2004; Pimentel et al., 2001). However, we consider our estimate to be more robust: the estimate for feral cats in natural environments is based on a large and representative set of site-based estimates. The estimate for feral cats in highly modified environments is less well-evidenced, however it aligns with other information. For example, RSPCA shelters take in 65,000 cats each year (RSPCA, 2011) which is about 9% of our estimate for the population of feral cats in highly modified environments; there have been no attempts to estimate the percentage of the unowned cat population that is rescued each year, but 9% is plausible.

We found that feral cat density across Australia varies widely, from 0 to 100 cats km^{-2}. Cat densities were higher on islands than on the mainland, and much higher on smaller rather than larger islands. This is most likely due to relatively abundant food resources on some islands (notably those with colonially-nesting seabirds) plus ongoing inputs of food from washed-up marine life (typically with higher perimeter:area ratio on smaller islands), and, in many cases, the absence of other mammalian predators. On the Australian mainland and Tasmania, density

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Table 2
Summary of the estimation for the number of feral cats living in highly modified environments, including estimates generated from the mean, minimum and maximum densities and colony sizes derived from a literature review.
(Source data are provided in Appendix C.)

	Spatial extent	Mean (cats km^{-2})	Minimum (cats km^{-2})	Maximum (cats km^{-2})
Highly modified landscapes	53,768 km^2			
Feral cat density		8.2	0.8	32
Population size estimate		440,898	43,014	1,720,576
Sites with large food subsidies	10,370 sites			
Colony size		26	3	81
Population size estimate		269,600	31,100	840,000
Total cats in modified landscapes		710,518	74,124	2,560,546

variation was associated mostly with annual rainfall (with higher density at sites with lower average annual rainfall), although this relationship was episodic, being evident only during wet periods. The increase in feral cat density in arid and semi-arid areas during extensive rainfall events is probably driven by the rapid (and transitory) pulse in prey species, including of introduced rodents and rabbits, following rain (Letnic and Dickman, 2010; Pavey et al., 2008). Other environmental and locational variables had little influence on cat density, including tenure (conservation versus other land uses), habitat type (tree cover), ruggedness, and the presence or absence of foxes. However, we note this analysis was conducted at a continental scale, and these variables may well be influential at local scales. Of particular note, the similarity of cat densities between reserved and unreserved areas indicates that for cat-susceptible wildlife, the Australian reserve system is unlikely to provide sufficient conservation security, and that they will continue to disappear from reserves (e.g. Woinarski et al., 2010) unless those reserves are managed with intensive control of feral cats.

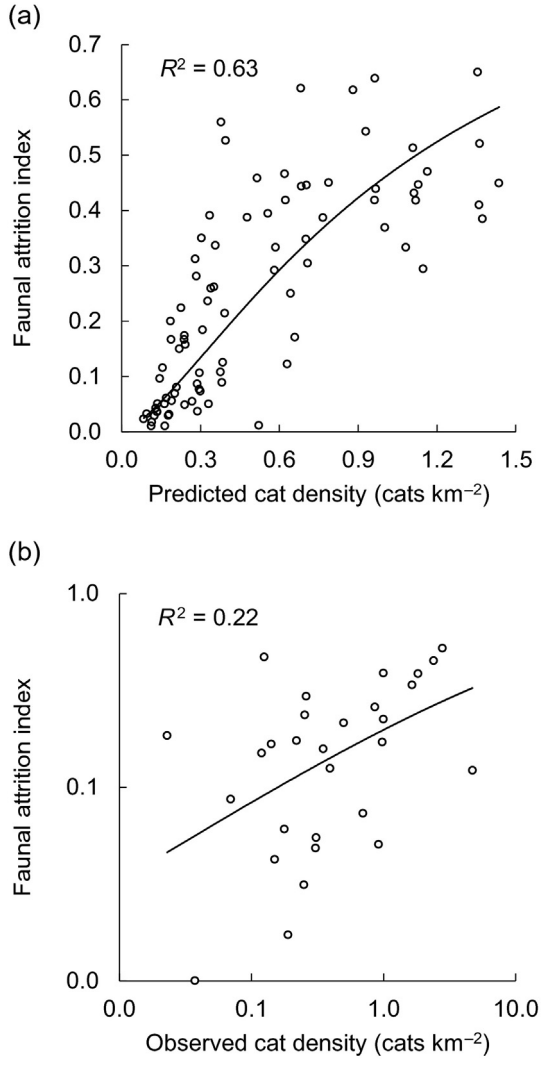

Fig. 6. Relationships between the regional attrition of native, non-flying mammals (Burbidge et al., 2008) and the (a) predicted and (b) observed feral cat densities in each bioregion following a wet period. The regression lines are linear regressions of the form: Faunal attrition index (FAI) ~ density, with FAI logit-transformed and density log-transformed prior to analysis.

Although our estimate of the national population size of feral cats is considerably lower than formerly proposed, this does not mean that the impacts of feral cats on Australian wildlife are any less profound than previously suggested. The evidence of marked detrimental impacts of feral cats is irrefutable, with a large and increasing number of compelling cases of positive responses of threatened mammal species to exclusion (or effective control) of feral cats and to translocation to islands without cats (see references in Moseby et al., 2015; Moseby et al., 2011; Short, 2009). The strong positive correlation described here across Australian bioregions between the modelled and observed density of feral cats and the extent of decline in native mammal fauna (Fig. 6) provides some further evidence of the potential impacts of feral cats, but we recognise that this observed relationship does not necessarily demonstrate causality, and that many factors may be implicated in the extinction and decline of Australian mammal fauna.

Notwithstanding the observed strong correlation between modelled cat density and native mammal decline, we note that cat population size or density per se does not necessarily relate to impacts. There is now substantial evidence that even very small numbers of feral cats can have significant negative impacts upon threatened species (Moseby et al., 2015; Short, 2016; Vázquez-Domínguez et al., 2004), because cats may continue to target favoured prey irrespective of their density, and because cats respond more strongly to hunting stimuli than satiation cues, leading them to surplus kill at times (Adamec, 1976; Peck et al., 2008; Woods et al., 2003). Moreover, the high reproductive capacity of cats means that cat densities can rapidly increase in the event of brief irruptions of more common prey. The higher cat density may cause extra pressure on rare species, especially via prey-switching when densities of common prey fall (Rich et al., 2014). These episodic pulses of elevated predation pressure may be a feature of much of arid and semi-arid Australia.

Our estimate of the total feral cat population provides context for the high profile Australian Government conservation target to kill two million feral cats by 2020 (Commonwealth of Australia, 2015). It makes this target more challenging, given that such a cull would represent a far higher proportion of the pre-cull cat population than originally envisaged. To some extent, focus on the cull target and even a population estimate is tangential to the main conservation issue of the role of feral cats as a key factor in the decline (and in some cases, extinction) of Australian animal species, and the mechanisms to manage that impact. For example, it may be more beneficial for Australian biodiversity if relatively few feral cats are eradicated from small areas of high conservation value while cats remain widespread and abundant elsewhere, than if the feral cat population was more substantially reduced overall but

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not eradicated from those important areas. Indeed, many Australian native mammal species occur now only in very small areas in which feral cats have been excluded, or on islands from which feral cats have been eradicated or not yet invaded. Hence, the national population size of feral cats, and the extent of its reduction, is not necessarily an important parameter for conservation management.

There have been few attempts to estimate the total population size of feral cats across entire countries and these have been carried out using less well-evidenced approaches. Harris et al. (1995) derived a figure of 813,000 feral cats in Great Britain by extrapolating from questionnaire-based surveys of farmers and field surveys of feral cats in samples of just four urban areas. In the United States, feral cat population estimates (in both natural and modified environments) range from 30 million (Loss et al., 2013) to 60–100 million (Jessup, 2004). The most evidenced estimate (Loss et al., 2013) was based on probability distributions for the cat population size, based on input data from just five studies. Another recent estimate, of 1.4 to 4.2 million feral cats for southern Canada (Blancher, 2013) was derived by modelling of regional estimates in media reports and then modelling of these reports against human population densities. In contrast, estimates for the population size of pet cats across entire countries are more accurate, based on extensive questionnaire surveys of households, and usually carried out by the pet food or veterinary industry. The most recent pet cat population estimate in Australia is 3.3 million (Animal Health Alliance, 2013); the analogous figure for the UK is 7.4 million (Pet Food Manufacturers Association, 2015); and for the USA it is 74 million (American Veterinary Medical Foundation, 2016).

Feral cats occur, and are a conservation problem, across much of the world. The densities in natural environments reported here for Australia (0.2–0.7 cats km^{-2}) are lower than those reported elsewhere (e.g. 2.3–10.1 cats km^{-2} in Great Britain, Europe, New Zealand, United States; 0.6–1.9 for southern Canada) (Langham and Porter, 1991; Liberg, 1980; Macdonald et al., 1987; Warner, 1985). To some extent, this comparison is constrained by marked variation in the methods used for density estimation. However, our study suggests that this influence of estimation method is probably relatively modest. The inter-continental difference in cat densities is probably due to the relatively low human population density (and hence availability of supplementary food) in rural and remote areas of Australia and/or to Australia's typically lower productivity (Orians and Milewski, 2007). Our results indicate that the severe losses of Australia's native mammals are not due to exceptionally high densities of feral cats. Instead, the relatively high impacts of cats on native wildlife in Australia may be because many Australian species have relatively low reproductive outputs (Geffen et al., 2011; Sinclair, 1996; Yom-Tov, 1985) and/or may be unusually susceptible to novel predators (Salo et al., 2007), and also because much of the Australian landscape has been, and continues to be, subjected to a range of other pervasive landscape changes (notably predation from introduced red foxes, changed fire regimes and broad-scale habitat change due to introduced herbivores). These changes probably contribute to reduced shelter availability for terrestrial native mammals and consequently more efficient hunting by feral cats (reviewed in Doherty et al., 2015b).

4.1. Priorities for further research

Our modelling did not detect any significant influence of the estimation method involved in the site-based density estimates that we collated. This was a surprising result; to better understand potential biases associated with estimation method, it would be useful for future studies to attempt to compare a range of density estimate approaches at individual sites. The estimate for the feral cat population in natural environments in Australia could be improved by additional site-based density estimates, particularly for habitats that have been little sampled to date, such as rainforests, heathlands, wetlands and rugged areas. Our estimate of feral cat population size in highly modified environments is based on limited evidence, and its precision could be substantially improved with further site-based estimates of densities, and information on the locations and frequencies of cat colonies in urban, peri-urban and rural areas. We also currently have very little understanding of the nature and extent of the impacts of feral cats in highly modified environments on threatened species, although there is potential for considerable impact (Ives et al., 2016). It would also be valuable to characterise the exchange between feral cats living in highly modified environments with those living in more natural environments.

More broadly, a research focus directed towards understanding the relationship between cat density and their impacts in a range of different environments, and how this relationship is affected by other threats and environmental drivers (like climate), will help provide the evidence base needed to effectively manage feral cats (Department of the Environment, 2015; Doherty and Ritchie, 2016; Norbury et al., 2015). Additional monitoring and research is also required into the extent to which local, regional and national management actions lead to reductions in feral cat populations, and the duration of such responses.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2016.11.032.

References

ABARES, 2015. Catchment scale land use of Australia - update March 2015. http://data.daff.gov.au/anrdl/metadata_files/pb_luausg9abll20150415_11a.xml (accessed 16 April 2016).

Abbott, I., 2002. Origin and spread of the cat, *Felis catus*, on mainland Australia, with a discussion of the magnitude of its early impact on native fauna. Wildl. Res. 29, 51–74.

Abbott, I., 2008. The spread of the cat (*Felis catus*) in Australia: re-examination of the current conceptual model with additional information. Conservation Science Western Australia. 7, 1–17.

Abbott, I., Burbidge, A., 1995. The occurrence of mammal species on the islands of Australia: a summary of existing knowledge. CALM Science 1995, 259–324.

Adamec, R.E., 1976. The interaction of hunger and preying in the domestic cat (*Felis catus*): an adaptive hierarchy? Behav. Biol. 18, 263–272.

American Veterinary Medical Foundation, 2016. U.S. pet ownership statistics. https://www.avma.org/KB/Resources/Statistics/Pages/Market-research-statistics-US-pet-ownership.aspx (accessed 16 April 2016).

Animal Health Alliance, 2013. Pet ownership in Australia 2013 summary. http://animalmedicinesaustralia.org.au/wp-content/uploads/2014/08/Pet-Ownership-in-Australia-2013-Summary-ONLINE-VER.pdf (accessed 16 April 2016).

Anon, 2012. Stopping the slaughter: fighting back against feral cats. Wildlife Matters Summer 2012 (13), 4–7.

Australian Bureau of Meteorology, 2016a. Average annual and monthly maximum, minimum, and mean temperature. http://www.bom.gov.au/jsp/ncc/climate_averages/temperature/index.jsp (accessed 16 April 2016).

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Australian Bureau of Meteorology, 2016b. Average annual, seasonal and monthly rainfall. http://www.bom.gov.au/jsp/ncc/climate_averages/rainfall/index.jsp (accessed 16 April 2016).

Banks, S.C., Hoyle, S.D., Horsup, A., Sunnucks, P., Taylor, A.C., 2003. Demographic monitoring of an entire species by genetic analysis of non-invasively collected material. Anim. Conserv. 6, 101–107.

Bengsen, A.J., Butler, J.A., Masters, P., 2012. Applying home-range and landscape-use data to design effective feral-cat control programs. Wildl. Res. 39, 258–265.

Blancher, P., 2013. Estimated number of birds killed by house cats (*Felis catus*) in Canada. Avian Conservation and Ecology 8, 3.

Burbidge, A.A., Manly, B.F.J., 2002. Mammal extinctions on Australian islands: causes and conservation implications. J. Biogeogr. 29, 465–473.

Burbidge, A.A., McKenzie, N.L., Brennan, K.E.C., Woinarski, J.C.Z., Dickman, C.R., Baynes, A., Gordon, G., Menkhorst, P.W., Robinson, A.C., 2008. Conservation status and biogeography of Australia's terrestrial mammals. Australian Journal of Zoology 56, 411–422.

Burnham, K.P., Anderson, D.R., 2003. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer, New York.

Burrows, N., Christensen, P., 1994. Hunting the hunter. Landscape 10, 36–41.

Cade, B.S., 2015. Model averaging and muddled multimodel inferences. Ecology 96, 2370–2382.

Caughley, G., Grigg, G.C., 1981. Surveys of the distribution and density of kangaroos in the pastoral zone of South Australia, and their bearing on the feasibility of aerial survey in large and remote areas. Australian Wildlife Research 8, 1–11.

Commonwealth of Australia, 2015. Threatened Species Strategy. Commonwealth of Australia, Canberra.

Copley, P., 1991. Feral and Domestic Cats in South Australia. The Impacts of Cats on Native Wildlife. Australian National Parks and Wildlife Service, Canberra.

Denny, E.A., 2005. Ecology of Free-living Cats Exploiting Waste Disposal Sites: Diet, Morphometrics, Population Dynamics and Population Genetics. PhD thesis. University of Sydney.

Denny, E.A., Dickman, C.R., 2010. Review of Cat Ecology and Management Strategies in Australia. Invasive Animals Cooperative Research Centre, Canberra.

Denny, E., Yakovlevich, P., Eldridge, M.D.B., Dickman, C., 2002. Social and genetic analysis of a population of free-living cats (*Felis catus* L.) exploiting a resource-rich habitat. Wildl. Res. 29, 405–413.

Department of the Environment, 2015. Threat Abatement Plan for Predation by Feral Cats. Commonwealth of Australia, Canberra.

Department of the Environment Water Heritage and the Arts, 2008,. Threat Abatement Plan for Predation by Feral Cats. DEWHA, Canberra.

Dickman, C.R., 1996. Overview of the Impacts of Feral Cats on Australian Native Fauna. Australian Nature Conservation Agency, Canberra.

Dickman, C.R., 2014. Measuring and managing the impacts of cats. In: Glen, A.S., Dickman, C.R. (Eds.), Carnivores of Australia: Past, Present and Future. CSIRO Publishing, Collingwood, pp. 173–195.

Doherty, T.S., Ritchie, E.G., 2016. Stop jumping the gun: A call for evidence-based invasive predator management. (Conservation Letters).

Doherty, T.S., Bengsen, A.J., Davis, R.A., 2015a. A critical review of habitat use by feral cats and key directions for future research and management. Wildl. Res. 41, 435–446.

Doherty, T.S., Dickman, C.R., Nimmo, D.G., Ritchie, E.G., 2015b. Multiple threats, or multiplying the threats? Interactions between invasive predators and other ecological disturbances. Biological Conservation 190, 60–68.

Domm, S., Messersmith, J., 1990. Feral cat eradication on a barrier reef island. Australia. Atoll Research Bulletin 338, 1–4.

Geffen, E., Rowe, K.C., Yom-Tov, Y., 2011. Reproductive rates in Australian rodents are related to phylogeny. PLoS One 6, e19199.

Geoscience Australia, 2012. National Waste Management Database. http://www.ga.gov.au/metadata-gateway/metadata/record/gcat_a66ac3ca-5830-594b-e044-00144fdd4fa6/National+Waste+Management+Database (accessed 1 February 2016).

Glen, A.S., Dickman, C.R., 2005. Complex interactions among mammalian carnivores in Australia, and their implications for wildlife management. Biol. Rev. 80, 387–401.

Gordon, G., 1991. Feral Cats in Queensland. The Impact of Cats on Native Wildlife. Australian National Parks and Wildlife Service, Canberra.

Hansen, M.C., DeFries, R.S., Townshend, J.R.G., Carroll, M., Dimiceli, C., Sohlberg, R.A., 2003. Global percent tree cover at a spatial resolution of 500 m: first results of the MODIS vegetation continuous fields algorithm. Earth Interactions 7, art10.

Hardman, B., Moro, D., Calver, M., 2016. Direct evidence implicates feral cat predation as the primary cause of failure of a mammal reintroduction programme. Ecological Management & Restoration 17, 152–158.

Harris, S., Morris, P., Wray, S., Yalden, D., 1995. A Review of British Mammals: Population Estimates and Conservation Status of British Mammals Other than Cetaceans. Joint Nature Conservation Committee, Peterborough, UK.

Hayde, K.A., 1992. Ecology of the Feral Cat *Felis catus* on Great Dog Island. BSc (Hons) thesis. University of Tasmania.

Hohnen, R., Tuft, K., McGregor, H.W., Legge, S., Radford, I., Johnson, C.N., 2016. Occupancy of the invasive feral cat varies with habitat complexity. PLoS One 11 (9), e0152520. http://dx.doi.org/10.1371/journal.pone.0152520.

Hone, J., Buckmaster, T., 2014. How many are there? The use and misuse of continental-scale wildlife abundance estimates. Wildl. Res. 41, 473–479.

Ives, C.D., Lentini, P.E., Threlfall, C.G., Ikin, K., Shanahan, D.F., Garrard, G.E., Bekessy, S.A., Fuller, R.A., Mumaw, L., Rayner, L., Rowe, R., Valentine, L.E., Kendal, D., 2016. Cities are hotspots for threatened species. Glob. Ecol. Biogeogr. 25, 117–126.

Jarvis, A., Reuter, H.I., Nelson, A., Guevara, E., 2008. Hole-filled SRTM for the globe Version 4, available from the CGIAR-CSI SRTM 90m Database. http://srtm.csi.cgiar.org (accessed 1 February 2016).

Jessup, D., 2004. The welfare of feral cats and wildlife. J. Am. Vet. Med. Assoc. 225, 1377–1383.

Jones, E., Coman, B.J., 1982. Ecology of the feral fat, *Felis catus* (L.), in South-Eastern Australia III. Home ranges and population ecology in semiarid North-west Victoria. Wildl. Res. 9, 409–420.

Kerby, G., MacDonald, D.W., 1988. Cat society and the consequences of colony size. In: Turner, D., Bateson, P. (Eds.), Domestic Cat: The Biology of its Behavior. Cambridge University Press, Cambridge, pp. 67–82.

Kutt, A., 2012. Feral cat (*Felis catus*) prey size and selectivity in north-eastern Australia: implications for mammal conservation. J. Zool. 287, 292–300.

Langham, N., Porter, R., 1991. Feral cats (*Felis catus* L.) on New Zealand farmland. I. Home range. Wildl. Res. 18, 741–760.

Letnic, M., Dickman, C., 2010. Resource pulses and mammalian dynamics: conceptual models for hummock grasslands and other Australian desert habitats. Biol. Rev. 85, 501–521.

Liberg, O., 1980. Spacing patterns in a population of rural free roaming domestic cats. Oikos 336-349.

Liberg, O., Sandell, M., Pontier, D., Natoli, E., 2000. Density, spatial organisation and reproductive tactics in the domestic cat and other felids. In: Turner, D., Bateson, P. (Eds.), The Domestic Cat: The Biology of its Behaviour. Cambridge University Press, Cambridge, pp. 119–147.

Loss, S.R., Will, T., Marra, P.P., 2013. The impact of free-ranging domestic cats on wildlife of the United States. Nat. Commun. 4, 1396.

Macdonald, D.W., Apps, P.J., Carr, G.M., Kerby, G., 1987. Social dynamics, nursing coalitions and infanticide among farm cats, *Felis catus*. Advances in Ethology 28, 1–66.

Mahon, P.S., Banks, P.B., Dickman, C.R., 1998. Population indices for wild carnivores: a critical study in sand-dune habitat, south-western Queensland. Wildl. Res. 25, 11–22.

McGregor, H., Legge, S., Jones, M., Johnson, C., 2014. Landscape management of fire and grazing regimes alters the fine-scale habitat utilisation by feral cats. PLoS One 9, e109097.

McGregor, H., Legge, S., Jones, M.E., Johnson, C.N., 2015a. Feral cats are better killers in open habitats, revealed by animal-borne video. PLoS One 10, e0133915.

McGregor, H.W., Legge, S., Potts, J., Jones, M.E., Johnson, C.N., 2015b. Density and home range of feral cats in north-western Australia. Wildl. Res. 42, 223–231.

McGregor, H.W., Legge, S., Jones, M.E., Johnson, C.N., 2016. Extraterritorial hunting expeditions to intense fire scars by feral cats. Scientific Reports 6, 22559.

McKenzie, N.L., Burbidge, A.A., Baynes, A., Brereton, R.N., Dickman, C.R., G, G., Gibson, L.A., Menkhorst, P.W., Robinson, A.C., Williams, M.R., Woinarski, J.C.Z., 2007. Analysis of factors implicated in the recent decline of Australia's mammal fauna. J. Biogeogr. 24, 597–611.

McLeod, R., 2004. Counting the Cost: Impact of Invasive Animals in Australia. Cooperative Research Centre for Pest Animal Control, Canberra, Australia.

Medina, F.M., Bonnaud, E., Vidal, E., Tershy, B.R., Zavaleta, E.S., Donlan, C.J., Keitt, B.S., Corre, M., Horwath, S.V., Nogales, M., 2011. A global review of the impacts of invasive cats on island endangered vertebrates. Glob. Chang. Biol. 17, 3503–3510.

Moseby, K.E., Read, J.L., Paton, D.C., Copley, P., Hill, B.M., Crisp, H.A., 2011. Predation determines the outcome of 10 reintroduction attempts in arid South Australia. Biol. Conserv. 144, 2863–2872.

Moseby, K.E., Peacock, D.E., Read, J.L., 2015. Catastrophic cat predation: a call for predator profiling in wildlife protection programs. Biol. Conserv. 191, 331–340.

Newton, A.C., 2011. Implications of Goodhart's Law for monitoring global biodiversity loss. Conserv. Lett. 4, 264–268.

Norbury, G.L., Pech, R.P., Byrom, A.E., Innes, J., 2015. Density-impact functions for terrestrial vertebrate pests and indigenous biota: guidelines for conservation managers. Biol. Conserv. 191, 409–420.

Orians, G.H., Milewski, A.V., 2007. Ecology of Australia: the effects of nutrient-poor soils and intense fires. Biol. Rev. 82, 393–423.

Pavey, C., Eldridge, S.R., Heywood, M., 2008. Population dynamics and prey selection of native and introduced predators during a rodent outbreak in arid Australia. J. Mammal. 89, 674–683.

Peck, D.R., Faulquier, L., Pinet, P., Jaquemet, S., Le Corre, M., 2008. Feral cat diet and impact on sooty terns at Juan de Nova Island, Mozambique Channel. Animal Conservation 11, 65–74.

Pet Food Manufacturers Association, 2015. Pet population 2015. http://www.pfma.org.uk/pet-population-2015 (accessed 16 April 2016).

Pimentel, D., McNair, S., Janecka, J., Wightman, J., Simmonds, C., O'Connell, C., Wong, E., Russel, L., Zern, J., Aquino, T., 2001. Economic and environmental threats of alien plant, animal, and microbe invasions. Agric. Ecosyst. Environ. 84, 1–20.

Read, J., Bowen, Z., 2001. Population dynamics, diet and aspects of the biology of feral cats and foxes in arid South Australia. Wildl. Res. 28, 195–203.

Rich, M., Nolan, B., Gentle, M., Speed, J., 2014. Lessons in feral cat control. Can adaptive management provide the solution? A case study from Astrebla Downs National Park, western Queensland. 16th Australasian Vertebrate Pest Conference 2014. Brisbane.

Ridpath, M.G., 1991. Feral mammals and their environment: landscape, ecology and man in the Northern Lowlands. In: Haynes, C.D., Ridpath, M.G., Willaims, M.A.J. (Eds.), Monsoonal Australia. AA Balkema, Rotterdam, pp. 169–191.

RSPCA, 2011. A review of trap-neuter-return (TNR) for the management of unowned cats. kb.rspca.org.au/afile/462/80/ (accessed 16 April 2016).

Salo, P., Korpimäki, E., Banks, P.B., Nordström, M., Dickman, C.R., 2007. Alien predators are more dangerous than native predators to prey populations. Proc. R. Soc. Lond. B Biol. Sci. 274, 1237–1243.

Short, J., 2009. The Characteristics and Success of Vertebrate Translocations within Australia. Wildlife Research and Management Pty Ltd, Perth, WA (Australian Government Department of Agriculture, Fisheries and Forestry Canberra).

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Short, J., 2016. Predation by feral cats key to the failure of a long-term reintroduction of the western barred bandicoot (*Perameles bougainville*). Wildl. Res. 43, 38–50.
Short, J., Rakai, L., Ingram, J., 2013. Control of feral cats at Shire rubbish tips to assist with the protection of the red-tailed phascogale. Project # SUS2.ECO.03.010; Final Report to SWCC, June 2013.
Sinclair, A., 1996. Fertility control of mammal pests and the conservation of endangered marsupials. Reprod. Fertil. Dev. 9, 1–16.
Stokeld, D., Frank, A., Hill, B., Low Choy, J., Mahney, T., Stevens, A., Young, S., Gillespie, G., 2015. Multiple cameras required to reliably detect feral cats in northern Australian tropical savanna: an evaluation of sampling design when using camera traps. Wildl. Res. 42, 642–649.
Vázquez-Domínguez, E., Ceballos, G., Cruzado, J., 2004. Extirpation of an insular subspecies by a single introduced cat: the case of the endemic deer mouse *Peromyscus guardia* on Estanque Island, Mexico. Oryx 38, 347–350.
Wallach, A., Ramp, D., 2015. Let's give feral cats their citizenship. The Conversation, e45165.
Warner, R.E., 1985. Demography and movements of free-ranging domestic cats in rural Illinois. J. Wildl. Manag. 49, 340–346.
Woinarski, J.C.Z., Armstrong, M., Brennan, K.E.C., Fisher, A., Griffiths, A.D., Hill, B., Milne, D.J., Ward, S., Watson, M., Wunderlich, S., Young, S., 2010. Monitoring indicates rapid and severe decline of native small mammals in Kakadu National Park, northern Australia. Wildl. Res. 37, 116–126.
Woinarski, J., Legge, S., Fitzsimmons, J., Traill, B., Burbidge, A., Fisher, A., Firth, R., Gordon, I., Griffiths, A., Johnson, C., McKenzie, N., Palmer, C., Radford, I., Rankmore, B., Ritchie, E., Ward, S., Ziembicki, M., 2011. The disappearing mammal fauna of northern Australia: context, cause and response. Conserv. Lett. 4, 192–201.
Woinarski, J.C.Z., Burbidge, A.A., Harrison, P.L., 2014. The Action Plan for Australian Mammals 2012. CSIRO Publishing, Melbourne.
Woinarski, J.C.Z., Burbidge, A.A., Harrison, P.L., 2015a. Ongoing unraveling of a continental fauna: decline and extinction of Australian mammals since European settlement. Proc. Natl. Acad. Sci. 112, 4531–4540.
Woinarski, J.C.Z., Morris, K., Ritchie, E.G., 2015b. Draft national targets for feral cat management; towards the effective control of feral cats in Australia – targets with teeth. National Feral Cat Management Workshop. PestSmart Toolkit Publication. Invasive Animals Cooperative Research Centre, Canberra.
Woods, M., McDonald, R.A., Harris, S., 2003. Predation of wildlife by domestic cats *Felis catus* in Great Britain. Mammal Rev. 33, 174–188.
Yip, S.J., Dickman, C.R., Denny, E.A., Cronin, G.M., 2014. Diet of the feral cat, *Felis catus*, in central Australian grassland habitats: do cat attributes influence what they eat? Acta Theriol. 59, 263–270.
Yom-Tov, Y., 1985. The reproductive rates of Australian rodents. Oecologia 66, 250–255.
Ziembicki, M., Woinarski, J., Webb, J., Vanderduys, E., Tuft, K., Smith, J., Ritchie, E., Reardon, T., Radford, I., Preece, N., Perry, J., Murphy, B., McGregor, H., Legge, S., Leahy, L., Lawes, M., Kanowski, J., Johnson, C., James, A., Griffiths, T., Gillespie, G., Fisher, A., Frank, A., Burbidge, A., 2014. Stemming the tide: progress towards resolving the causes of decline and implementing management responses for the disappearing mammal fauna of northern Australia. Therya. 6, 169–225.

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