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A global review of the impacts of invasive cats on island endangered vertebrates

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Abstract

Cats are generalist predators that have been widely introduced to the world's ~179 000 islands. Once introduced to islands, cats prey on a variety of native species many of which lack evolved defenses against mammalian predators and can suffer severe population declines and even extinction. As islands house a disproportionate share of terrestrial biodiversity, the impacts of invasive cats on islands may have significant biodiversity impacts. Much of this threatened biodiversity can be protected by eradicating cats from islands. Information on the relative impacts of cats on different native species in different types of island ecosystems can increase the efficiency of this conservation tool. We reviewed feral cat impacts on native island vertebrates. Impacts of feral cats on vertebrates have been reported from at least 120 different islands on at least 175 vertebrates (25 reptiles, 123 birds, and 27 mammals), many of which are listed by the International Union for the Conservation of Nature. A meta-analysis suggests that cat impacts were greatest on endemic species, particularly mammals and greater when non-native prey species were also introduced. Feral cats on islands are responsible for at least 14% global bird, mammal, and reptile extinctions and are the principal threat to almost 8% of critically endangered birds, mammals, and reptiles.

Keywords: *Felis catus*, feral cats, impact, islands, predation

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Introduction

Domestication of the cat took place around 9000 years ago from the Near Eastern wildcat (*Felis silvestris lybica*) (Randi & Ragni, 1991; Serpell, 2000; Vigne *et al*., 2004; Driscoll *et al*., 2007). Since then domestic cats (*Felis silvestris catus*) have traveled with humans to most corners of the globe including many remote islands where they have become feral (Fitzgerald, 1988).

Feral cats on islands are dietary generalists feeding on many types of native and introduced prey, including vertebrates (mainly mammals, birds, and reptiles) and invertebrates (chiefly insects) with much of the variation explained by prey availability (Fitzgerald & Turner, 2000; Nogales & Medina, 2009; Bonnaud *et al*., 2011). As many native island species have reduced behavioral, morphological, and life-history defenses against mammalian predators, and because islands have a disproportionate share of global terrestrial biodiversity (Kier *et al*., 2009), feral cats are thought to have been a major driver of biodiversity loss causing extinctions of insular endemic birds and mammals and local extinctions of island breeding seabirds (e.g. Veitch, 1985; Dowding & Murphy, 2001; Medway, 2004; Keitt *et al*., 2006; Wolf *et al*., 2006; Knowlton *et al*., 2007). In addition to direct impact of predation, indirect impacts, such as apparent competition, food competition, or transmission of disease have also been reported or suggested (Nishimura *et al*., 1999; Phillips *et al*., 2007; Rayner *et al*., 2007). Feral cats can also influence other ecological process by their predation upon nectivorous and frugivorous vertebrates especially disruption of native seed dispersal systems (Nogales *et al*., 1996) or secondary long-distance dispersal of invasive plants (Bourgeois *et al*., 2004).

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Cats can be eradicated from islands (Nogales *et al.*, 2004) after which threatened species can recover (Aguirre-Muñoz *et al.*, 2008). However, cats have been eradicated from fewer than 100 islands (Nogales *et al.*, 2004; Campbell *et al.*, 2011), but have likely been introduced to at least 5% of the worlds' 179 000 small and medium sized islands (B. Tershy, unpublished data). The current rate of cat eradications from islands is not having a significant impact on the thousands of islands where invasive cats likely threaten native wildlife. Consequently, to maximize their biodiversity benefits, future cat eradications will have to be prioritized and to do so effectively, conservation biologists must have a better understanding of the impacts of feral cats on native island species.

There have been no global reviews of feral cat impacts on islands. Information the impact of feral cats is scattered with qualitative reviews of impacts on mainland or large islands of continental origin (Australia: Dickman, 1996; New Zealand: Taylor, 2000; Dowding & Murphy, 2001; Gillies & Fitzgerald, 2005; Great Britain: Dyczkowski & Yalden, 1998; Woods *et al.*, 2003) and partial reviews by Fitzgerald (1988) and Fitzgerald & Turner (2000). Here, we review the literature on the impacts of feral cats on island animals and use meta-analysis techniques to help predict which types of threatened native island species are most impacted by feral cats and under what conditions are they most impacted.

Materials and methods

Data collection

We compiled data from published and gray literature covering most of the world's insular regions where impacts by feral cats were documented. To drive conservation action, we included only prey species that have been assigned to one of the five most threatened categories by the IUCN 2008 Red List: vulnerable, endangered, critically endangered, extinct in the wild, and extinct. Furthermore, we also included those cases of endemic subspecies that have become extinct on the only island where they lived, although other subspecies survive elsewhere. Invertebrates were often found in the diet of feral cats on islands, but none of the invertebrates recorded were listed as threatened in the IUCN (2008) Red List of Threatened Species, so our results discuss vertebrates exclusively. Moreover, only cases that clearly reported feral cat impact on species on specific islands were included.

We defined impact as any inference that cats had caused a decline in the population abundance or geographical distribution of a native insular species. While many publications and internal reports do not quantify the magnitude of a population decline, there is often strong inference of a decline due to feral cat predation (Dickman, 1996). Furthermore, many of these considerations of impact are anecdotal and thus alone should be interpreted with care. For this reason, three different classes of impact were considered following the suggestions established in each studied case: mixed (when the cat effects had been compounded by other factors), high (when there was high evidence of a severe effect of cats on species populations), and strong (when the extinction of a particular taxon on a specific island was attributed to feral cats). All islands have been included with the exception of Great Britain, Australia and the two largest islands of New Zealand, where feral cat impacts have been reviewed elsewhere (see Dickman, 1996; Taylor, 2000; Woods *et al.*, 2003; Gillies & Fitzgerald, 2005).

Our database includes 229 separate cases, each of which consists of a unique island-prey species combination for which we found evidence of feral cat impacts. For each case, we recorded the species affected; its taxonomic classification (class/family), provenance (insular endemic or present on continents), and IUCN status; degree of impact reported by feral cats and evidence on which this categorization was based; island characteristics including origin (oceanic/land-bridge), size, elevation, latitude, longitude, region, ocean, and presence of other exotic predators or prey; and published or gray literature source(s). The degree of cat impact in each case was coded as 0.01 if cats and potential prey coexisted with no apparent negative effects on the prey; 0.5 if cats had mixed or complex effects (see above); 0.9 if cats had severe effects on prey; and 1 if cats completely extirpated the prey population (Jones *et al.*, 2008).

Data analysis

We used meta-analysis to determine the effect size and significance of feral cat effects on prey species by class (Mammalia, Aves, Reptilia), endemicity (insular only or insular + continental), and selected island characteristics across the 229 separate cases in our database. Formal meta-analysis involves weighting of individual cases based on each study's variance and/or sample size. As no variance or sample size data exist for our data (each is a single case of a feral cat–prey species interaction associated with a categorical degree of impact), we conducted two types of analyses: (i) unweighted meta-analyses, which simplify to traditional ANOVA or ordinary least squares (OLS) regression analyses; and (ii) weighted meta-analyses using bootstrapping and 5000 randomizations each to generate results robust to violations of parametric assumptions, and using weights assigned to each of our 229 cases. We assigned weights *sensu* Jones *et al.* (2008), who developed a categorical series of qualitative weights assigned to each case based on the type and strength of evidence provided for the case.

For our first analysis, of the effect of prey taxonomic class on severity of feral cat impact, we did both unweighted ANOVA and weighted nonparametric (bootstrapped) analyses. They produced nearly identical results, with no effect on outcome and a minor difference in effect size. For this reason, and because the unweighted analyses increase power and allow inclusion of both multiple independent variables and interac-

tion terms, we proceeded with unweighted analyses of the remaining relationships. Only when results of an analysis were marginally significant or marginally nonsignificant did we check by running a weighted analysis. Fail-safe numbers are reported only for traditional meta-analyses and indicate how many additional cases reporting no effect would need to be included to eliminate a significant overall effect size.

Results

General analysis

Impacts of feral cats upon vertebrates have been described on at least 120 different islands around the world (Fig. 1). A total of 175 threatened taxa (25 reptiles, 123 birds, and 27 mammals) were impacted by cats on islands based on their status in the 2008 IUCN Red List (Table 1; see Supporting information, Appendices S1–S4). Of the reptiles, 16 taxa were endemics and 9 natives. The most important groups affected were the iguanas (14 taxa), and lizards (6 taxa), plus four turtles and one snake. Cats impacted 48 taxa of endemic birds in four main groups: landbirds (61 taxa, 49%) mostly belonging to Passeriformes and Psittacidae; seabirds (45 taxa, 36%), especially burrowing petrels, albatrosses, and penguins. Waterbirds and shorebirds were the groups with fewest species affected (11 and 6, respectively). Of the 27 mammal taxa impacted by cats, four were endemic. Fifteen taxa (55.6%) were rodents while eight were marsupials, two soricomorphs, one chiropteran, and one primate.

Studies documenting the impacts of feral cats on threatened island taxa were not evenly distributed, with more studies on birds in the Pacific and more studies on reptiles in the Caribbean (Fig. 1). Reptile impacts were dominated by iguanas in West Indies and Fiji, and giant lizards in the Canary Islands. Bird impacts were dominated by passerines and petrels throughout the Pacific and mammal impacts dominated by rodents in Baja California and Galapagos.

Based on our database, feral cats on islands have contributed to 33 (13.9%) of the 238 global bird, mammal, and reptile extinctions (including species extinct in the wild but extant in captivity) recorded by the IUCN Red List (Table 2; Fig. 2; Appendices S1–S4). They have also contributed to 38 (8.2%) of the 464 critically endangered birds, mammals, and reptiles (Fig. 2; Appendices S1–S4).

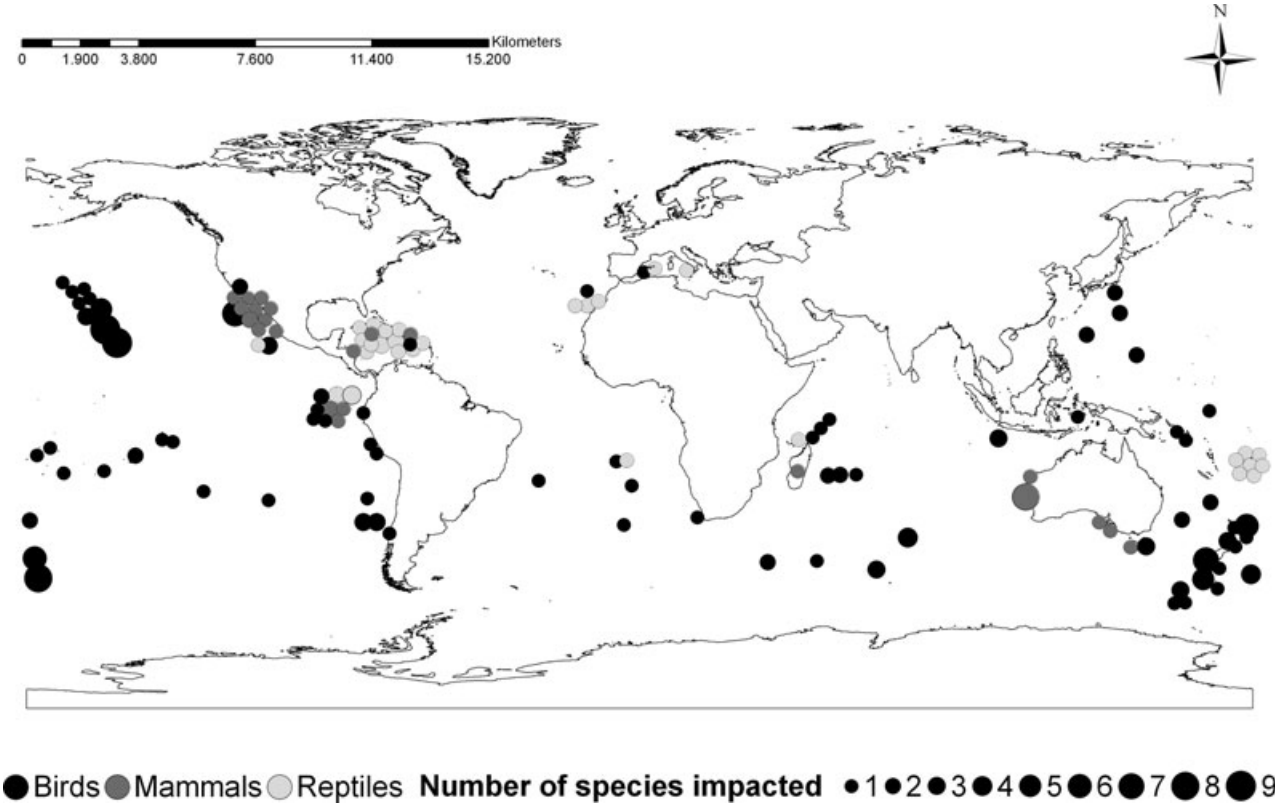

Fig. 1 Islands where impacts of feral cats (*Felis silvestris catus*) have been described. Light gray spots, reptiles; dark gray spots, birds; black spots, mammals.

Table 1 Number of species and taxa of the different prey groups affected by feral cats (*Felis catus*) on islands, according to the five most critical categories of the IUCN 2008 Red List of Threatened Species: EX, extinct; EW, extinct in the wild; CR, critically endangered; EN, endangered; VU, vulnerable. Number of subspecies is indicated in brackets

Groups	EX	EW	CR	EN	VU	Total	Total taxa
Reptiles	1 (1)	–	9 (1)	4 (2)	2 (5)	16 (11)	25
Birds	11 (9)	2 (–)	24 (1)	32 (2)	37 (5)	106 (17)	123
Mammals	4 (5)	–	3 (–)	7 (–)	8 (–)	22 (5)	27
Total	16 (15)	2 (–)	36 (2)	43 (4)	47 (10)	144 (31)	175

The effect of feral cats was considered as mixed in the 69.4% of the 229 cases, while 16.2% and 14.4% of the impacts were high and strong, respectively (see Supporting information). Strong impact levels were most common for birds and mammals. On >75% of islands with recorded feral cat other introduced predators such as rats, mongoose, stoats, weasels, dogs or pigs, were also present.

Meta-analysis

Feral cats on islands have strong negative overall impacts on reptiles, birds, and mammals ($N = 229$, fixed-effects unweighted meta-analysis $P < 0.05$, Rosenthal's fail-safe number = 5778; effect sizes: mammals 0.6088, birds 0.5484, and reptiles 0.5290). For insular endemic species and subspecies ($N = 213$), the overall severity of cat impacts varied by taxonomic class (ANOVA, $F = 3.30$, $P = 0.039$), with cat impacts significantly greater on mammals than on birds (Tukey's *post hoc* $P = 0.028$) (Fig. 3). When continental species that also occur on islands were included in the analysis, there were no significant differences of cat impact between vertebrate classes.

Across vertebrate classes, feral cats on islands have larger impacts on insular endemic species than on continental species (ANOVA, $F = 6.32$, $P = 0.013$) (Fig. 4a). This pattern appeared consistent in each vertebrate class but did not differ significantly among them (class × provenance interaction, $P > 0.05$) (Fig. 4b).

To examine the influence of introduced alternate prey species on the severity of cat impacts on native prey, we

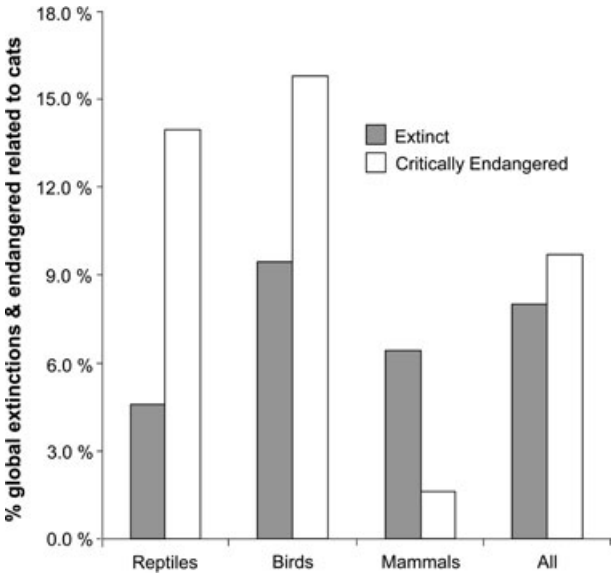

Fig. 2 Percent of all extinctions recorded by the IUCN 2008 Red List (including species extinct in the wild, but extant in captivity) that were caused, at least in part, by feral cats on islands (filled bars). Percent of all critically endangered species for which cats are a significant threat (open bars).

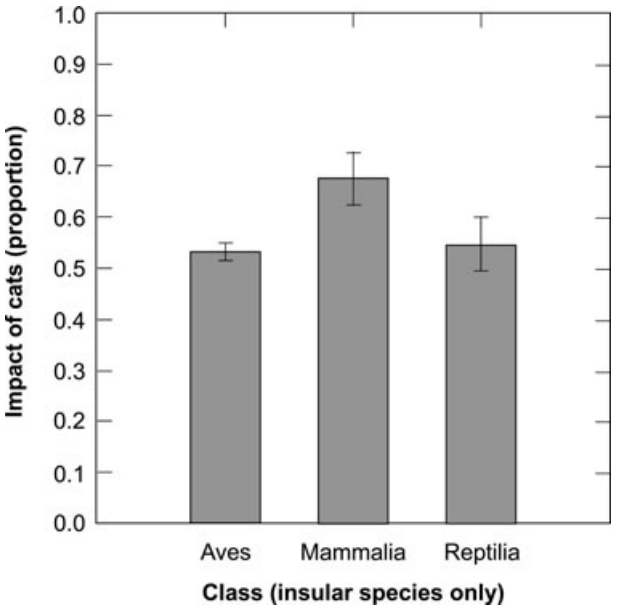

Fig. 3 Meta-analysis effect sizes of overall cat impacts on each vertebrate class in our database, including only those prey species limited to islands (213 of 229 cases). For all three prey classes, mean effect of feral cats is significantly >0 ($P < 0.05$), where effects range from 0.01 (no apparent effect) to 1 (complete extirpation). When continental prey species are excluded, mammals are significantly more affected by cats than are birds (see text for details). Bars are ±1 SE.

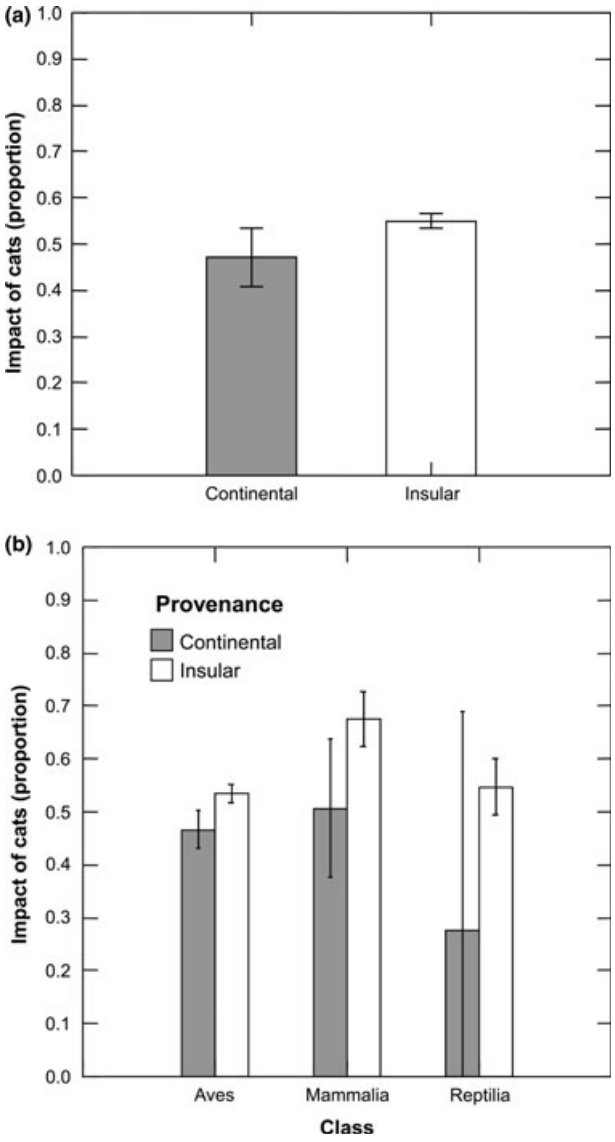

Fig. 4 Effect of provenance (insular endemics vs. continental species) on severity of cat impacts (a) across the three taxonomic classes and (b) by class. Bars are ±1 SE.

looked at islands with and without rabbits or mice. We excluded islands with rats from this analysis because rats were both an alternative prey for cats and a predator of native species. Mice too can be predators on insular endemic vertebrates, but were not excluded from the analysis because they are much less significant predators than rats. The presence of alternative prey significantly increased the impact of feral cats on birds, the only class where sample size was large enough for a meaningful test ($N = 166$, ANOVA, $F = 4.24$, $P = 0.041$) (Fig. 5).

The impact of feral cats on islands was not significantly affected by island size, origin (oceanic or land-bridge), or latitude (OLS regressions, $P > 0.05$).

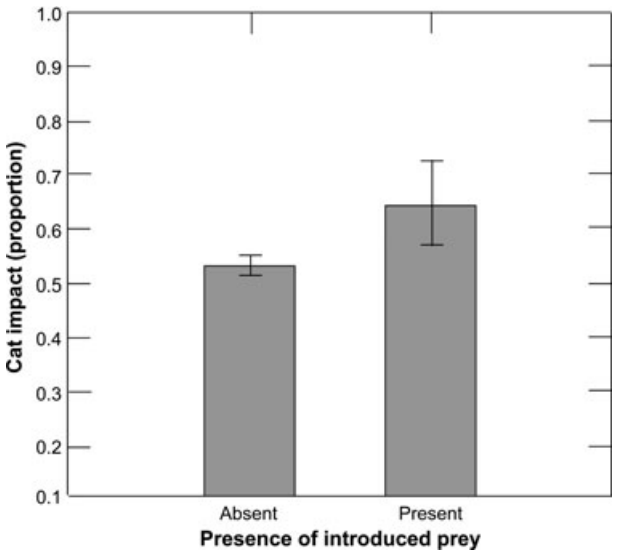

Fig. 5 Effect on cat impact severity of the presence of alternative introduced prey (rabbits or mice). Bars are ±1 SE. See text for details.

Discussion

This is the first study that attempts to quantify the global impact of an invasive species on insular biodiversity. Our review demonstrates that feral cats have contributed to at least 14% of the modern bird, mammal, and reptile extinctions (Table 2) and have to the endangerment of at least 8% of critically endangered birds, mammals, and reptiles (Fig. 2). These are absolute minimum values because they are derived from our database of studies, yet the impacts of cats on many, perhaps most species, have not been studied. For this same reason, it is difficult to interpret the uneven spatial distribution of studies (Fig. 1), however, we suspect that it is more reflective of research effort than the distribution of actual impacts.

Our meta-analysis suggests that feral cats on islands have the largest negative impacts on insular endemic species, especially endemic mammals (Fig. 4b), and these impacts are exacerbated by the presence of invasive cat prey species such as mice and rabbits as predicted by Courchamp *et al.* (2000) (Fig. 5). Other invasive predatory mammals, such as rats, pigs, mongoose compounded the impacts of cats on native insular species (Towns *et al.*, 2006; Jones *et al.*, 2008).

Insular endemic species are more likely to have lost behavioral, morphological, and life-history defenses against predators than are island populations of species that also occur on continents (Beauchamp, 2004; Fullard *et al.*, 2004; Yamaguchi & Higuchi, 2005). Likewise, cats may affect insular mammals more than birds because nonvolant mammals cannot exchange genetic material

Table 2 Taxa driven to global extinction with the direct participation of feral cats on islands

Order	Species	Island	Country
Reptiles (2)	*Leiocephalus eremitus*	Navassa	West Indies, USA
	Podarcis sicula sanctistephani	San Stephano	Italy
Birds (22)	*Anthornis melanocephala*	Mangere	New Zealand
	Bowdleria rufescens	Mangere	New Zealand
	Cabalus modestus	Mangere	New Zealand
	Caracara lutosa	Guadalupe	Mexico
	Chaunoproctus ferreorostris	Peel	Japan
	Coenocorypha barrierensis	Little Barrier	New Zealand
		Stewart	New Zealand
		Herekopare	New Zealand
	Colaptes auratus rufipileus	Guadalupe	Mexico
	Corvus hawaiensis	Hawai'i	Hawai'i, USA
	Cyanoramphus novaezelandiae erythrotis	Macquarie	Australia
	Microgoura meeki	Choiseul	Solomon Islands
	Pipilio maculates consobrinus	Guadalupe	Mexico
	Porzana sandwichensis	Hawai'i	Hawai'i, USA
	Pterodroma cervicalis cervicalis	Raoul	New Zealand
	Regulus calendula obscurus	Guadalupe	Mexico
	Sceloglaux albifacies	Stewart	New Zealand
	Sephanoides fernandesis leyboldi	Alejandro Selkirk	Chile
	Thryomanes bewickii brevicauda	Guadalupe	Mexico
	Traversia lyalli	Stephens	New Zealand
	Turnagra capensis minor	Stephens	New Zealand
	Xenicus longipes	Stephens	New Zealand
		Kapiti	New Zealand
	Zenaida graysoni	Socorro	Mexico
	Zoothera terrestris	Peel	Japan
Mammals (9)	*Chaetodipus baileyi fornicatus*	Dirk Hartog	Australia
	Geocapromys thoracatus	Little Swan	Honduras
	Nesoryzomys darwini	Santa Cruz	Galápagos, Ecuador
	Nesoryzomys indefessus	Santa Cruz	Galápagos, Ecuador
		Baltra	Galápagos, Ecuador
	Oryzomys galapagoensis galapagoensis	San Cristóbal	Galápagos, Ecuador
	Oryzomis nelson	María Madre	Mexico
	Peromyscus guardia harbinsoni	Granito	Mexico
	Peromyscus guardia mejiae	Mejía	Mexico
	Peromyscus maniculatus cineritius	San Roque	Mexico

as easily as birds can with populations on other islands or the mainland to maintain evolved defenses against predation. The presence of abundant introduced exotic prey has been shown in a number of cases to subsidize introduced predator populations, allowing them to grow and then more severely impact relatively scarce native prey (Courchamp *et al*., 1999, 2000). This is the case of *Cyanorhamphus novaezelendiae erythrotis*, a parakeet that coexisted on Macquarie Island with cats until rabbits were introduced (Taylor, 1985). Introduced prey subsidies (Roemer *et al*., 2002) could explain our finding of increased cat impacts on native prey when exotic rodents or rabbits are also present.

Eradication of feral cats from islands is quite feasible on islands under 1000 ha, and eradication attempts from island an order of magnitude larger have been successful, but cats have been eradicated from only two islands >10 000 ha (Nogales *et al*., 2004). Cat eradication is planned on several islands >10 000 ha (see Campbell *et al*., 2011). In most of the papers reviewed, different conservation actions were proposed to reduce the impact of feral cats on islands where they were introduced. Of the total conservation priorities, eradication and control of feral cat populations were the most important actions proposed (31% and 29%, respectively). Cat eradication can result in dramatic recoveries of threatened vertebrates. For example, the iguana (*Cyclura carinata*) in Long Cay, West Indies (Mitchell *et al*., 2002), the rodent (*Peromyscus pseudocrinitus*) in Coronados Island, Gulf of California (Rodríguez-Moreno *et al*., 1999), and the bird (*Philesturnus*

carunculatus rufusater) in Little Barrier Island, New Zealand (Gillies & Fitzgerald, 2005). Yet there have been fewer than 100 cat eradications from islands (Nogales *et al.*, 2004; Campbell *et al.*, 2011) and there are likely thousands of islands where feral cats negatively impact native vertebrates (B. Tershy, unpublished data). Thus, more effective cat eradication techniques are needed, as are guidelines for selecting islands where cat eradication will have the largest impact. Our review suggests that cats have negative impacts on a wide range of native vertebrates, that endemic island species are particularly vulnerable compared to species that also occur on continents, that endemic island mammals may be the most vulnerable, and that introduced alternate prey species such as mice and rabbits increase the risk to native species.

Conclusions

1. Cats have contributed to a minimum of 14% of all bird, mammal, and reptile extinctions and the decline of at least 8% of critically endangered birds, mammals, and reptiles. Cats can be eradicated from many islands and our results suggest that the most vulnerable species are island endemics, particularly mammals and that introduced alternate prey (rodents and rabbits) increase the impacts of feral cats.
2. Our review undoubtedly underestimated the impact of cats on native species due to the lack of studies on numerous islands of the world and on numerous endangered species particularly in Asia, Indonesia, Polynesia, and Micronesia.
3. Existing studies suffered from uneven geographic coverage of vertebrate orders (e.g. clumping of reptile studies in the Caribbean and mammal studies in the Eastern Pacific) and limited quantification of impacts or controlled experimental design.
4. More research on the impacts of feral cats on island animals can improve these guidelines and thus improve the prioritization of islands for cat eradication.
5. More studies are needed that quantify changes in the survival, reproductive success, or population size of native vertebrates following cat eradication.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Endangered reptile species affected by the predation of feral cats (*Felis catus*) on islands.
Appendix S2. Endangered bird species affected by the predation of feral cats (*Felis catus*) on islands.
Appendix S3. Endangered mammal species list affected by the predation of feral cats (*Felis catus*) on islands.
Appendix S4. References not listed in main manuscript.

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