Population impacts of free-ranging domestic cats on mainland vertebrates

Scott R Loss[1*] and Peter P Marra[2]

Domestic cats (*Felis catus*) have contributed to at least 63 vertebrate extinctions, pose a major hazard to threatened vertebrates worldwide, and transmit multiple zoonotic diseases. On continents and large islands (collectively termed "mainlands"), cats are responsible for very high mortality of vertebrates. Nevertheless, cat population management is traditionally contentious and usually involves proving that cats reduce prey population sizes. We synthesize the available evidence of the negative effects of cats on mainland vertebrates. More than a dozen observational studies, as well as experimental research, provide unequivocal evidence that cats are capable of affecting multiple population-level processes among mainland vertebrates. In addition to predation, cats affect vertebrate populations through disease and fear-related effects, and they reduce population sizes, suppress vertebrate population sizes below their respective carrying capacities, and alter demographic processes such as source–sink dynamics. Policy discussions should shift from requiring "proof of impact" to a precautionary approach that emphasizes evidence-driven management to reduce further impacts from outdoor cats.

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Invasive mammalian predators have catastrophic impacts on biodiversity; such predators have been implicated in 58% of modern vertebrate extinctions and threaten the continued existence of 600 additional species (Doherty *et al*. 2016). For example, the introduction of invasive rats (*Rattus* spp) on many islands around the world has led to the extinction or decline of many amphibians, reptiles, and birds (Harper and Bunbury 2015), and the introduction of the invasive red fox (*Vulpes vulpes*) in Australia has contributed to the extinction of several rat-kangaroo species (Short 1998). The domestic cat (*Felis catus*) is among the most ubiquitous and environmentally damaging invasive predators on Earth.

In a nutshell:

- Free-ranging domestic cats are increasingly the focus of policy and management attention as well as controversy due to their substantial environmental impacts and their popularity as pets
- We synthesize the evidence that cats affect mainland vertebrate populations through predation, fear, and disease
- Rather than requiring proof of declines in vertebrate prey populations, cat population management and policy decisions should be based on scientific evidence demonstrating that cats often do affect vertebrate populations
- Efforts to manage outdoor cat populations should include rigorous monitoring that allows evaluation of success and ongoing assessment of harm to wildlife, cats, and humans

[1]*Department of Natural Resource Ecology and Management, Oklahoma State University, Stillwater, OK* [*]*(scott.loss@okstate.edu);* [2]*Migratory Bird Center, Smithsonian Conservation Biology Institute, National Zoological Park, Washington, DC*

Domestic cats (hereafter "cats") descended from the wildcat (*Felis silvestris*) and were domesticated in Asia's Fertile Crescent over 10,000 years ago (Driscoll *et al*. 2007). Similar to other domesticated species, cats have no native range and they are now among the most popular pets worldwide. Pet cats that have been abandoned or that are allowed outdoors have resulted in large, growing, free-ranging cat populations (Lepczyk *et al*. 2010) (Figure 1, a–d). Cats have contributed to 26% of reptile, bird, and mammal extinctions (Doherty *et al*. 2016) and pose a global risk to threatened and endangered vertebrates (Bellard *et al*. 2016). These impacts are most severe on islands without native predators (Medina *et al*. 2011). However, even in continental areas with comparable native predators such as the wildcat in Eurasia and Africa, domestic cat densities often far exceed those of native cats (Beutel *et al*. 2017). Human provisioning of food, vaccinations, and shelter frees cat populations from constraints of prey availability and disease, and cats carry multiple diseases that affect both wildlife and humans (Gerhold and Jessup 2013).

Despite substantial data-supported impacts, decisions about managing free-ranging cat populations are increasingly the focus of public controversy, likely due to the popularity of cats as pets. For instance, in New York, a decade-long conflict over human-supported cat colonies near a breeding population of endangered piping plovers (*Charadrius melodus*) recently reached federal court (Brulliard 2016). The controversial Trap-Neuter-Return (TNR) method – where cats are trapped, sterilized, and released, and for which evidence of effectiveness is severely limited – has led to policy conflicts in many jurisdictions (Marra and Santella 2016). The controversy surrounding cats, along with the magnitude of their adverse environmental impacts, makes cat population management one of the most challenging conservation, animal welfare, and public health issues of our time.

The cat management debate often revolves around the degree to which cats cause wildlife mortality and whether that mortality reduces wildlife population sizes. Overwhelming evidence for such impacts on islands has led to many successful cat eradications, with subsequent recovery of persisting species (Nogales *et al.* 2004). On mainlands (continents and large islands, such as those constituting New Zealand and the UK), cat impacts on vertebrate populations remain the subject of heated debate. Rigorous quantitative studies clearly show that cats kill a huge number of vertebrates on mainlands (Blancher 2013; Loss *et al.* 2013). Nevertheless, conclusively determining population impacts is complicated by the challenge of disentangling the effects of cats from other natural and human drivers of population trajectory and identifying whether various mortality sources are compensatory or additive (Panel 1). Because of these complications, feral cat advocacy groups and other organizations often argue that evidence for cat impacts on mainland vertebrates is lacking (Alley Cat Allies 2017; RSPB 2017). We perceive this as a major factor limiting public and political will toward initiating steps to reduce cat populations and revisiting policies like TNR that appear largely ineffective and facilitate expansion of cat populations and their associated predation and disease transmission.

Here, we synthesize evidence that cats negatively influence mainland vertebrate populations. We first outline a framework for the direct and indirect mechanisms for these effects and review studies showing evidence for these impacts on mainland vertebrates. We then argue that policy discussions should shift from requiring proof of impact to a precautionary approach that weighs the substantial evidence that cats impact mainland vertebrates and recognizes that evidence-driven management is needed to reduce further impacts on biodiversity and human health.

Figure 1. *(a) Abundant free-ranging cat populations exist throughout the world. Contributing factors include: (b) cat owners allowing pets to roam free (this cat is identified as a pet by its collar), (c) Trap-Neuter-return (TNR) programs, such as this TNR colony in Ottawa, Canada, subsidizing cats with food and shelter despite limited evidence that such programs consistently reduce populations, and (d) countless informal feeding and sheltering operations supporting cats on public and private land.*

Framework for cat impacts

The debate over whether cats impact vertebrates usually focuses on whether they reduce prey abundance. The most obvious mechanism by which cats influence abundance – and on which research and policy debates have focused – is by directly reducing survival due to predation (Figure 2a). However, the specter of predation can also create a "landscape of fear" that indirectly affects survival and reproduction by altering prey stress responses and foraging, movement, and/or defense behaviors (Preisser *et al.* 2005). Cats also transmit diseases that directly kill infected individuals and have sublethal behavioral or physiological effects that indirectly affect survival and/or reproduction (Figure 2b).

Two factors are relevant when inferring potential cat-associated impacts. First, such effects are often defined based on declines in population abundance. Yet, more subtle impacts are also possible, including suppression of abundance below carrying capacity (Loss *et al.* 2012) and alteration of demographic processes such as source–sink dynamics (Figure 2c). Second, cats can simultaneously exert more than one impact mechanism. Focusing on a single mechanism, as is often done with cat predation, will result in an underestimation of impacts.

Predation mortality

Research on population impacts of cats has largely focused on predation. Dozens of studies have investigated cat diets, and quantitative syntheses of these data estimate that cats annually kill hundreds of millions of birds in Canada (Blancher 2013) and hundreds of millions (reptiles and amphibians) to billions (birds and mammals) of vertebrates in the US (Loss *et al.* 2013). These studies illustrate the magnitude of cat-induced mortality in mainland vertebrates and suggest an obvious need for policy and management to reduce this mortality. However, large-scale estimates do not address whether mortality is additive or compensatory (Panel 1), and inferring predation impacts ideally requires intensive local-scale, species-specific research.

Panel 1. Quantifying impacts of cats on vertebrate populations

Linking cause to effect in population ecology is extremely difficult and is fraught with uncertainty. In cat policy and management debates, this uncertainty is often conflated with the conclusion that cats have no impacts on vertebrates and so cat management is unnecessary. Here, we discuss the problems associated with assessing the population impacts of cats to support our call to shift from a proof of impact focus to a weight of evidence approach to managing cat impacts.

Identifying all factors affecting populations

Identifying the many natural and human-related factors driving population trends for vertebrates is inherently challenging, and this makes it hard to separate impacts of cats versus other factors. For instance, although predation is an obvious mechanism by which cats affect vertebrates, the fear and disease effects are less obvious and many have only recently emerged. This challenge is compounded for migratory species, for which movements and the factors affecting them during all stages of their annual cycle are usually unknown. Thus, when cats cause mortality for a migratory species, it is difficult to link that mortality to population-level processes across the species' entire annual cycle.

Measuring population responses

Even given identification of all factors affecting populations, unbiased measurement of population responses to these factors remains a substantial challenge. Small abundance declines are difficult to detect even with large-scale, long-term monitoring schemes, such as those for birds in many countries. Even large declines may go unnoticed for species without such monitoring programs and for migratory species with annual cycles extending across multiple countries and continents. Furthermore, accurate modeling of population responses often requires estimation of cause-, age-, and sex-specific mortality, information that is challenging to gather in an unbiased manner at relevant spatiotemporal scales (Loss *et al*. 2012).

Determining whether mortality is compensatory or additive

A frequently misunderstood aspect of the debate about the impacts of cats – and of human-caused mortality sources broadly – relates to whether mortality is additive or compensatory. This dichotomy is often boiled down to whether animals would have soon died from other causes if not killed by cats (compensatory mortality) or would not have soon died (additive mortality). Under this definition, an often-cited example of supposed compensatory effects is a study showing that birds depredated by cats were in poorer physical condition than those killed by window-collision, suggesting the birds would have soon died if not killed by cats (Baker *et al*. 2008).

However, this simplified definition – and the crude assessment of bird body condition to infer whether predation mortality is compensatory – overlooks substantial mechanistic complexity associated with determining whether mortality is compensatory or additive. A more mechanistically accurate definition is that mortality is compensatory when demographic processes, such as a density-dependent increase in reproduction, make up for any losses and is additive when such processes do not fully compensate for losses. Furthermore, population responses are more nuanced, falling along a continuum from overcompensatory (ie density-dependent processes compensate more than necessary) to overadditive (ie a mortality source causes mortality from other sources to increase). Determining the nature of population response requires estimation of: (1) the survival rate in the absence of the mortality source, (2) the mortality rate specific to the mortality source, and (3) the correlation between (1) and (2) (Péron 2013). As discussed above, major difficulties exist in estimating (1) and (2), and the compounding effect of these challenges makes it nearly impossible to conclusively determine the degree to which mortality is additive or compensatory.

A minimum of 15 local- to national-scale studies illustrate that cat predation can be a substantial mortality source for mainland vertebrates (WebTable 1). In the UK, pet cats caused at least 30% of mortality for house sparrows (*Passer domesticus*), as estimated by prey returned to owners (Churcher and Lawton 1987). In Australia, DNA analysis of the remains of woylies (*Bettongia penicillata*) revealed that feral cats were responsible for 65% of mortality for this rare marsupial (Marlow *et al*. 2015) (Figure 3a). In Florida, video cameras showed that greater than 70% of nest predation events for northern mockingbirds (*Mimus polyglottos*) were attributed to cats (Stracey 2011). Several studies have compared predation to prey abundance, to generate estimates of impact. In the UK, Baker *et al*. (2008) estimated that pet cats depredated a large percentage of populations of the house sparrow (10–30%), common blackbird (*Turdus merula*) (40–70%), Eurasian wren (*Troglodytes troglodytes*) (70–100%), dunnock (*Prunella modularis*) (80–410%), and great tit (*Parus major*) (100–890%). Also in the UK, Thomas *et al*. (2012) estimated that numbers of birds depredated by pet cats exceeded estimated adult bird abundance for 14 of 36 species–study site combinations. These studies strongly indicate the investigated populations were sinks, requiring immigration from other areas to remain sustainable.

Population modeling studies have evaluated how cat predation affects prey population dynamics or persistence. In New Zealand, models showed that predation by pet cats led to a high probability of population extinction for the native silvereye (*Zosterops lateralis*) (37–99% and 40–99% after 50 and 100 years, respectively) and non-native common blackbird (68–100% and 88–100% after 50 and 100 years, respectively) (Van Heezik *et al*. 2010). In Washington, DC, cats were responsible for 47% of known predation events for fledgling gray catbirds (*Dumetella carolinensis*) (Balogh *et al*. 2011). When considering differences in cat populations among study sites and incorporating predation rates into population models, this study illustrated that cats likely caused catbird populations to be sinks. Similar research in Oregon found that cats killed at least 37% of fledgling spotted towhees (*Pipilo maculatus*), a mortality rate that – when modeled – increases the probability of towhee populations being sinks (Smith *et al.* 2016).

Research also shows correlative associations between cat populations and prey populations. These studies generally assume predation to be the mechanism behind observed associations. In the UK, density of the wood mouse (*Apodemus sylvaticus*) (Baker *et al.* 2003) and abundance of several songbird species (Sims *et al.* 2008) were inversely related to cat abundance and density, respectively. Species richness of native birds in urban areas was inversely related to outdoor cat density across Great Britain (Sims *et al.* 2008) and outdoor cat abundance in California (Crooks and Soule 1999) and Illinois (Belaire *et al.* 2014). Large-scale correlational studies indicate cats likely drive population declines and extinctions for multiple mainland prey species. A study analyzing conilurine rodent declines across Australia found that range overlap with medium-to-high feral cat densities best predicted decline for small species, as well as for species of all sizes in areas without invasive red foxes and common rabbits (*Oryctolagus cuniculus*) (Smith and Quin 1996). Also in Australia, Fisher *et al.* (2014) determined that the best predictor of range decline for tropical marsupials was small body mass within the preferred range of small predators. Because red foxes were absent from tropical Australia, the authors concluded that the declines were driven by feral cats and exacerbated by reductions in understory vegetation, which improve the hunting success of cats.

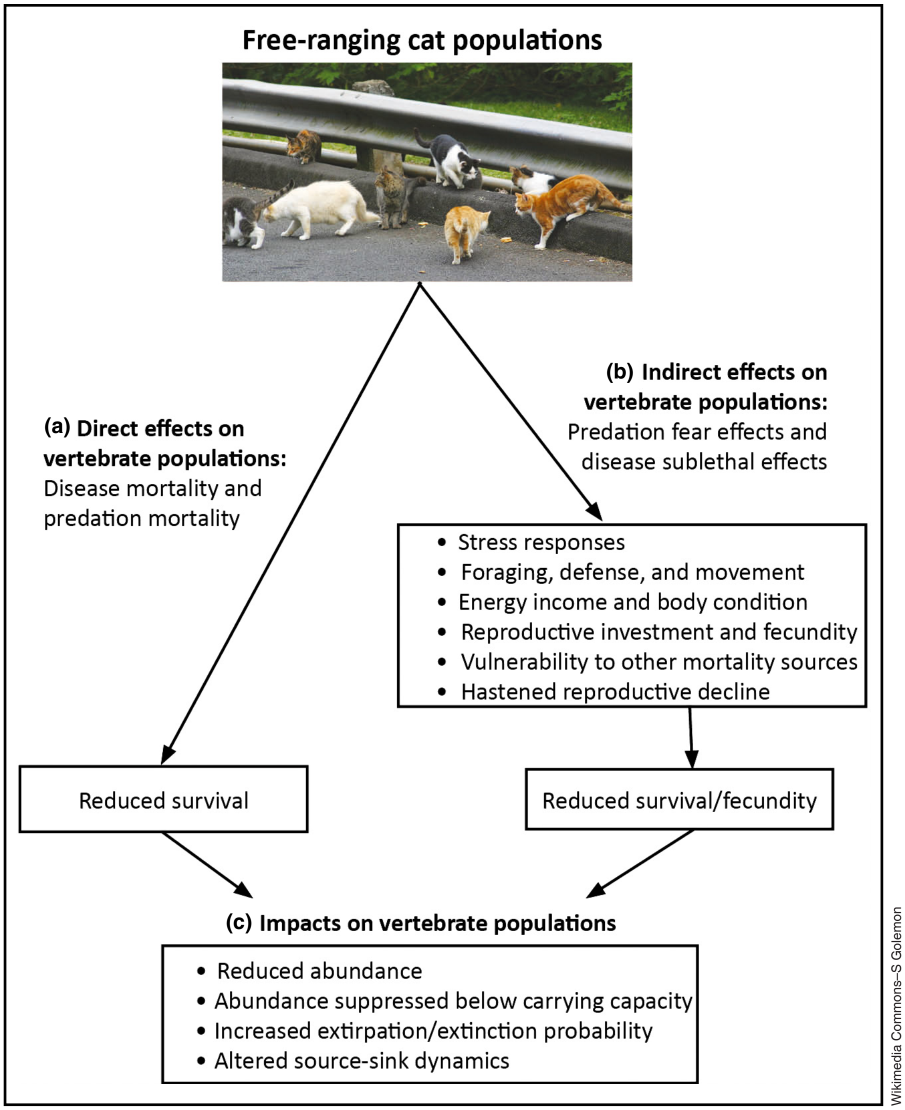

Figure 2. *Mechanisms of free-ranging cat impacts on vertebrate populations include: (a) mortality from predation and disease directly reducing survival and (b) "fear effects" of predation and sublethal effects of disease indirectly reducing survival and/or reproduction through altered physiological and/or behavioral effects. (c) Independently or cumulatively, these mechanisms have been shown to reduce population abundance, suppress abundance below carrying capacities, increase extinction/extirpation probability, and alter source–sink dynamics.*

Recent experimental research provides the most compelling evidence to date that cat predation reduces mainland prey populations. Frank *et al.* (2014) conducted an enclosure study in Australia to evaluate population persistence of the native long-haired rat (*Rattus villosissimus*) under predator-accessible and predator-proof treatments. Rat populations persisted throughout the study in predator-proof areas, which were surrounded by a 2-m-high electrified fence. However, populations declined to extinction in predator-accessible areas, which were surrounded by a 0.9-m-high non-electrified fence. Notably, time to extinction was related to the numbers of cat detections. In the predator-accessible area with frequent cat detections, the rat population went extinct within 3 months, likely due to a substantial decline in adult survival from cat predation. In the predator-accessible area with infrequent cat detections, decline to extinction occurred over 16 months, likely attributable to reduced juvenile recruitment.

Fear effects

Cats also indirectly affect prey populations by influencing stress responses, foraging and defense behaviors, energy income and body condition, reproductive investment and output, and vulnerability to other predators. Such "fear effects" of predators can have even greater impacts on

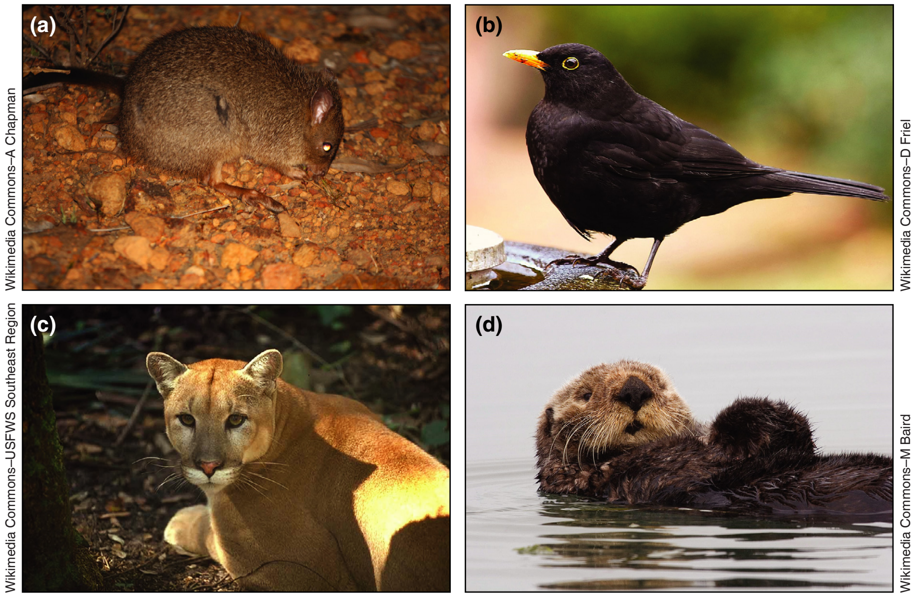

Figure 3. *Vertebrates with mainland populations affected by cats. (a) In Australia, 65% of woylie mortality was from cat predation. (b) In the UK, 40–70% of common blackbirds were killed by cat predation; this species was also shown to experience elevated nest predation from other predators due to cat fear effects. (c) In Florida, one cat with feline leukemia virus caused the death of five Florida panthers. (d) In California, 16% of sea otters were directly killed by toxoplasmosis; severely infected sea otters were also more likely to be shark attack victims, suggesting additional indirect mortality caused by the disease.*

prey populations than predation (Preisser *et al.* 2005). A growing body of research suggests unexpected ways that the fear of cats affects mainland vertebrate populations. Using a bird population model including a direct effect of cat predation and an indirect effect of fear on fecundity, Beckerman *et al.* (2007) illustrated that fear effects can reduce bird abundance by 95% even with predation mortality below 1%. Relevant to cat suppression of prey populations below their carrying capacity, fear effects were so intense that the authors concluded that low predation rates could, in some instances, reflect prey populations already reduced by cat-associated decreases in prey fecundity.

Several empirical studies provide support for fear effects of cats (Table 1). In the UK, the presence of a "cat model" (taxidermy mount of an adult cat) increased common blackbird alarm calling and aggression, reduced nestling provisioning, and elevated nest predation by other predators (Bonnington *et al.* 2013) (Figure 3b). The authors concluded that increased third-party predation occurred due to agitation behaviors drawing attention to the nest, reduced energy for defense against other predators, and/or the need for adults to spend more time away from the nest after defending against cats. Likewise, in high-density colonies of barn swallows (*Hirundo rustica*) in Denmark, exposure to high levels of cat predation risk early in life hastened reproductive decline during senescence late in life (Balbontín and Møller 2015). Given low observed predation, the authors concluded this effect was indirectly caused by cats elevating swallow stress responses, which reduced egg production. Fear of cats also affects prey foraging, which can influence survival and reproduction, especially under harsh environmental conditions. In Poland, avian use of new bird feeders was slower with cats present, suggesting predation risk influences detection and use of new food sources (Tryjanowski *et al.* 2015). In Tennessee, tufted titmice (*Baeolophus bicolor*) and Carolina chickadees (*Poecile carolinensis*) avoided bird feeders more when a cat model (plush toy cat) was present. This effect was greatest when cat models faced toward feeders, suggesting that birds respond

Table 1. Studies providing evidence for cat impacts on mainland vertebrate populations through "fear effects"*

Species/group impacted	*Cat type*	*Location*	*Evidence*	*Impact description*	*Reference*
Common blackbird	Model	Sheffield (UK)	Experimental	Presentation of cat model increased alarm calling and direct aggression, reduced nestling provisioning, and increased nest predation by other species	Bonnington *et al.* (2013)
Barn swallow	Unspecified free-ranging	Kraghede (Denmark)	Cat presence observations	In medium-high density colonies, cat predation risk early in life elevated rate of reproductive decline during senescence late in life	Balbontín and Møller (2015)
Granivorous birds	Unspecified free-ranging	Poland	Cat presence observations	Use of new bird feeders slower with cats present	Tryjanowski *et al.* (2015)
Carolina chickadee	Model	Tennessee (US)	Experimental	Avoidance of bird feeders greater with cat model; avoidance greatest with cat model facing toward feeders	Freeberg *et al.* (2016)

Notes: *indirect effects on survival or reproduction due to alteration of physiology and/or behaviors in response to predation pressure.

to cat presence and body orientation when assessing predation risk in foraging contexts (Freeberg *et al.* 2016).

Disease effects

Domestic cats carry and transmit multiple zoonotic diseases that affect vertebrates (Gerhold and Jessup 2013). Many of these (eg rabies, plague, toxoplasmosis) are of public health concern given their association with human illness and mortality. Cat-transmitted diseases can generate direct mortality in infected vertebrates and have sublethal behavioral or physiological effects that indirectly affect survival and/or reproduction. A noteworthy example of a cat-transmitted disease directly reducing a critically endangered vertebrate population occurred when a single cat infected with feline leukemia virus likely caused the death of five Florida panthers (*Puma concolor coryi*) (Brown *et al.* 2008) (Figure 3c).

The most studied cat-transmitted disease is toxoplasmosis, which results from infection by the protozoan *Toxoplasma gondii*. Wild and domestic cats are the only definitive hosts for this pathogen, and infected domestic cats shed millions of *T gondii* oocysts into the environment in their feces (Dubey 1995). Wildlife contract *T gondii* by ingesting infected prey or oocysts directly from sources such as water and soil. Environmental transmission from oocysts deposited by free-ranging cats is likely a primary source of infection for wildlife and humans (Kreuder *et al.* 2003; Hill *et al.* 2011). For many vertebrates, *T gondii* infection was previously considered to be asymptomatic, but accumulating evidence indicates symptoms are more subtle and more common than previously thought (Flegr 2007). Substantial mortality from toxoplasmosis has been documented for marsupials, marine mammals, and neotropical primates (Gerhold and Jessup 2013), and population impacts appear likely. Perhaps most strikingly, *T gondii* was a primary cause of death for 16% of southern sea otters (*Enhydra lutris nereis*) found on beaches in California (Kreuder *et al.* 2003) (Figure 3d). Furthermore, sea otters with severe infections were more likely to be attacked by sharks, suggesting that *T gondii* has sublethal behavioral effects that indirectly lead to additional mortality. Because infection rates were highest in coastal areas with large amounts of freshwater runoff, the authors concluded that otters were likely infected by ingesting oocysts in runoff, and ultimately, by fecal deposition by urban cat populations. They also concluded that combined direct and indirect effects of toxoplasmosis were likely reducing and/or suppressing otter populations.

A proposed paradigm shift

On the basis of evidence reviewed here – including at least 14 observational studies from four countries, an experimental study attributing cat predation with population decline of a native prey species (WebTable 1), and emerging research into fear and disease effects of cats (Table 1) – we conclude that there is overwhelming evidence demonstrating that cats affect mainland vertebrate populations. Uncertainty remains about the exact magnitude of those impacts; also, because research thus far has disproportionately occurred in the US, Europe, Australia, and New Zealand, an improved understanding of the magnitude and extent of cat impacts will require further investigation in other regions. This uncertainty and research gap may lead to continued claims that there is insufficient evidence to warrant cat population management, as advocated by organizations that downplay cat impacts (RSPB 2017) or promote the continued existence of free-ranging cat populations regardless of impacts (Alley Cat Allies 2017). However, this uncertainty reflects the challenge of linking cause to effect in population ecology (Panel 1) and is emblematic of scientific inquiry, in which theories and hypotheses are falsifiable but not provable.

We argue that discussion about cat population management should shift toward a weight of evidence approach used hand-in-hand with the precautionary principle. This principle allows ameliorative management even when uncertainty exists about the risk or magnitude of a harmful effect (Foster *et al.* 2000). Calver *et al.* (2011) discussed the use of precaution when deciding whether to manage the impacts of outdoor pet cats. They concluded that sufficient data exist on cat impacts to trigger precautionary measures, and the risk of vertebrate population declines and extinctions, along with uncertainty regarding the role of cats, provides a rationale for strong levels of precaution. As we illustrate, there is now more than sufficient evidence indicating that management decisions regarding cats in mainland areas – including outdoor pet cats and unowned feral/semi-feral cats – should ascribe to the precautionary principle and assume that impacts on vertebrates are likely. Moreover, under most interpretations of the principle, proponents of a potentially harmful activity bear the burden of proof in showing a lack of effect. The management debate would be greatly reshaped by considering the weight of evidence that cats do affect mainland vertebrate populations and assuming that these impacts are likely unless evidence is provided that conclusively suggests otherwise.

Precautions may be advisable even in instances when cats appear to have little impact on vertebrates. In addition to the challenge of linking cause to effect in population ecology, estimates of cat impacts are likely to be conservative because although cats can exert multiple direct and indirect effects simultaneously, most research has focused only on predation. Vertebrate mortality from cats could also have difficult-to-detect indirect effects on other species (eg by affecting food supplies for predators or competitors) or ecosystem services (eg by reducing pollinator or seed disperser populations). Finally, an increased focus on the individual welfare of wild animals, in addition to population-level processes, should be considered for vertebrates affected by cats. Individual cat welfare is often the only consideration in cat management discussions, yet similar considerations should be recognized for the wildlife that cats injure or kill (Mcruer *et al.* 2017).

Management and policy implications

The case for the harmful effects of cats on mainland vertebrates consists of their clear potential to affect populations through predation, fear, and disease effects, and also their broad range of impacts, including reduced abundance, population suppression below carrying capacity, and alteration of demographic processes such as source–sink dynamics. Given these impacts, effective and humane approaches to reducing and eradicating mainland cat populations are warranted. Notably, programs to introduce cats for control of pest species (eg Norway rats, *Rattus norvegicus*) are increasingly being implemented in major cities (Christensen 2016). We strongly discourage efforts to purposefully increase cat populations because they are certain to harm wildlife populations and facilitate disease transmission to animals and humans. Further, cats may be incapable of causing long-term reductions in invasive pest populations (Glass *et al.* 2009).

Decisions about managing cats should ideally incorporate public judgments on acceptability of alternative approaches. However, widespread public agreement may be elusive because attitudes about management vary widely depending on country, cat ownership, and group membership (eg wildlife enthusiasts versus TNR supporters) (Wald *et al.* 2013; Hall *et al.* 2016). Moreover, opinions about cat impacts and efficacy of cat management do not always align with evidence and, for some groups, appear unlikely to change even with information-based education campaigns (McDonald *et al.* 2015). Further sociological research is required to determine successful approaches to educate the public about cat impacts and gain broad acceptance of effective management programs. In the meantime, depending solely on public opinion without considering scientific evidence could lead to management outcomes that continue to harm biodiversity and public health.

For pet cats, restricting outdoor access or only allowing cats outdoors with restraint (eg on leashes and in open-air enclosures), as well as enacting and enforcing legislation requiring licensing and prohibiting abandonment, will reduce outdoor cat populations and a key source of individuals sustaining feral and semi-feral populations. Notably, these steps are widely endorsed by wildlife conservation, animal welfare, and veterinary organizations. Management approaches for feral and semi-feral cats are more controversial and range from TNR to removal with adoption and/or euthanasia. TNR in particular is promoted as a panacea despite negligible evidence for its widespread effectiveness, minimal understanding of TNR program characteristics that lead to success in reducing populations, and its facilitation of predation, disease, and often inhumane conditions for cats. Additionally, modeling indicates a high sterilization rate is necessary for TNR to initiate consistent declines in cat population sizes (eg 71–94% of cats; Foley *et al.* 2005). Assuming a conservative estimate of 30–80 million cats in the continental US (Loss *et al.* 2013), this equates to 21–75 million cats requiring sterilization on a national scale. This rate exceeds the capacity and goals of organizations attempting to reduce populations solely using non-lethal means (eg Million Cat Challenge 2017) and illustrates the need for alternative and/or complementary approaches.

Nonetheless, recognizing that TNR currently receives some public support, we call for a substantial increase in rigor for monitoring and regulatory oversight if this approach continues to be implemented. First, colonies should only remain if located in areas of low biodiversity importance as determined by wildlife professionals (Marra and Santella 2016). Second, rather than relying on anecdotal observations, scientific principles of study design should be used to determine whether TNR achieves population reduction goals and to track harmful effects to wildlife, cats, and humans. Third, adaptive management based on rigorous monitoring will help to refine management and guide implementation of alternative approaches if TNR is ineffective at reducing cat populations or causes harm to wildlife, cats, or humans. These steps will require collaboration among conservation scientists, veterinary professionals, and cat and wildlife advocates. These collaborations will facilitate the trust building, expertise sharing, and capacity enhancement needed to address the pressing global problem of overabundant cat populations.

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