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ORIGINAL PAPER

Underlying impacts of invasive cats on islands: not only a question of predation

Félix M. Medina · Elsa Bonnaud · Eric Vidal · Manuel Nogales

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Abstract The domestic cat has been introduced on most islands worldwide, where it has established feral populations and is currently known to be one of the worst invasive mammalian predators. Predation is the strongest deleterious effect of cats on wildlife, inducing a direct negative impact on population size and dynamics, breeding success and changes in species assemblages. Direct predation is not the only damaging impact on native wildlife, since cats can be responsible for other poorly-documented underlying ecological impacts, like competition, hybridization, disease transmission, ecological process alteration, and behavioral change. Here, we pinpoint relevant examples of these ecological impacts, by searching for accurate data from published literature. We used electronic databases covering most of the world islands where the effects of cats were documented. Knowledge of these impacts can be of great importance to preserve insular ecosystem functions and persistence of endangered native species. We emphasize that direct predation processes should not be the only factor considered in the management of invasive cats on islands.

Keywords Competition · Diseases · Ecological process disruption · *Felis silvestris catus* · Hybridization

F. M. Medina (✉)
Servicio de Medio Ambiente, Cabildo Insular de La Palma, Avenida Los Indianos 20, 2°,
38700 Santa Cruz de La Palma, Canary Islands, Spain
e-mail: felix.medina@cablapalma.es

F. M. Medina · M. Nogales
Island Ecology and Evolution Research Group (IPNA-CSIC), Astrofísico Francisco Sánchez 3,
38206 La Laguna, Tenerife, Canary Islands, Spain

E. Bonnaud
Ecologie, Systématique and Evolution, UMR CNRS 8079 Univ. Paris Sud, 91405 Orsay, France

E. Vidal
IMBE, Institut Méditerranéen de Biodiversité et d'Ecologie Marine et Continentale, AMU/CNRS/IRD/
UAPV/Aix-Marseille Université, BPA5, 98848 Noumea cedex, New-Caledonia

Introduction

Among invasive species, mammals are known to be the most detrimental group, threatening native species through predation, grazing, competition for resources, habitat loss, and introduction and spread of diseases and parasites (e.g. Courchamp et al. 2003). The domestic cat (*Felis silvestris catus*) has been introduced on most islands worldwide, where it has established feral populations leading to a heavy impact on native island species (Dickman 1996; Fitzgerald and Turner 2000; Courchamp et al. 2003; Medina et al. 2011). Continuous release of house cats into the wild leads to a large reservoir of breeding animals for feral populations, increasing their survival success even in the most severe environmental conditions (Potter 1991). Three different status groups of cats are known: (i) house cats living with people that provide food, rest and shelter; (ii) feral cats independent of humans that reproduce and predate in the wild, and (iii) stray or roaming cats linked to one or several households but living and predating mostly in the wild (see Liberg et al. 2000 for details). Thus, working on cats and their impacts requires considering these different statuses and the source-sink dynamics between them.

Predation has been considered the strongest deleterious impact of cats on wildlife (Fitzgerald and Turner 2000), in the case of both (i) house cats in urban and suburban habitats (Woods et al. 2003; Baker et al. 2005) and (ii) stray and feral cats in natural environments (Dickman 1996; Fitzgerald and Turner 2000). The direct impact of cat predation can (i) decrease population size and population dynamics (*Microtus arvensis* in Sweden, Hansson 1988), (ii) affect assemblage structure of numerous prey species (several bird species in Britain, Sims et al. 2008), and (iii) negatively affect breeding success (*Pterodroma macroptera* and *Procellaria aequinoctialis* on Marion Island, van Rensburg and Bester 1988; *Loxioides bailleui* on Hawai'i, Pletschet and Kelly 1990). Two reviews to highlight the impact of cat predation on islands were published recently. The first discussed analyses of feral cat diet on islands and showed that at least 248 different species were predated (27 mammals, 113 birds, 34 reptiles, 3 amphibians, 2 fish, and 69 invertebrates) (Bonnaud et al. 2011). The second concluded that feral cats preyed on at least 175 endangered vertebrates (25 reptiles, 123 birds and 27 mammals) and are at least in part responsible for 14 % of global bird, mammal and reptile extinctions, currently affecting 8 % of critically endangered birds, mammals and reptiles (Medina et al. 2011).

Although direct predation by cats has been highly destructive, their impact can be exacerbated through indirect negative effects on native island wildlife. Indirect effects appear when the impact of one species on another is mediated by a third species, as occurs in apparent competition (Wootton 1994). Sub-lethal or non-consumptive effects of predators can also affect the fitness of prey, leading to changes in their ecological and behavioral constraints (Cresswell 2008; Bonnington et al. 2013). In the same way, predator presence can strongly increase prey's perception of predation risk to seriously affect prey population dynamics, independently of the predation process (Zanette et al. 2011). The ability of naive island prey to identify predation risk, and to develop or alter their behavior to avoid introduced predators, largely depends on their ability to discriminate cues of predator presence (Lima 1998). For many prey species, sensitivity to predator-derived odors, sounds and visual cues is crucial to their survival.

Therefore, the global effect of predators on prey populations may be much greater than predation alone, particularly if the prey response to predator impact (direct or indirect) leads to a decrease in reproductive success and/or an increase in mortality (Lima 1998; Beckerman et al. 2007).

Cats are one of the most studied invasive mammalian predators, information about their other ecological impacts besides predation is available, although scattered (e.g. Bonnington et al. 2013). The main purpose of this contribution is to review the literature to highlight further potential effects of cats on islands, other than direct predation, and assess the need to study predator impact more thoroughly.

Methods

We compiled data from published literature using electronic databases (Webspire, Web of Knowledge, Ovid SP, Inist, Blackwell Publishing, Science Direct) covering the world's insular regions where impacts by cats were documented, combining (as a Boolean search) the key words: cat(s), feral cat(s), *Felis catus*, *Felis silvestris catus*, island(s), diet, predation, impact, indirect, and native species. References cited in the papers found were examined for additional sources. Even after the most complete review possible ($n = 149$ studies), a quantitative analysis of each impact studied was not possible, due to the low number of cases described. We thus decided to pinpoint and illustrate the most relevant cases to show the need to study these interactions more deeply.

The effects of feral cats on island species are usually compounded by the presence of other introduced predators. Often, other factors such as habitat destruction, fishing, pollution or persecution are more deleterious for some species than cat predation itself (Medina et al. 2011). For this reason, some examples were included in this paper where cats were not the main predator species involved, to discuss similar impacts found for cats.

Results and discussion

We gathered examples of (i) predator–prey mechanisms: competition and ecological process alteration and (ii) non-predator–prey mechanisms: hybridization, and disease transmission. Behavioral changes can be induced by both predator–prey and non-predator–prey mechanisms (see text and Fig. 1). From the studies reviewed, a total of 29 species (3 plants, 4 reptiles, 16 birds and 6 mammals) have been indirectly affected by cats in 23 different places worldwide (Table 1). Food competition, transmission of diseases and changes in behavior were the most frequent indirect impact described in the studied cases. Most took place on islands ($n = 26$) and 14 species affected by cat presence are currently threatened (IUCN 2012). From these endangered species, six are considered as a critically endangered, mainly affected by competition for food (Table 1).

Competition

Introduced animals compete with native species for food and habitat when individuals feed on the same limited resources. Exploitation is one of the simplest ways to compete using up the common resources (Krebs and Davies 1993). In contrast, apparent competition occurs when an alternative prey species in the diet of a food-limited predator reduces the other's equilibrium abundance, whether or not they directly compete (Holt 1977). Due to cat predation, some specific interactions can be indirectly modified, those related to hyperpredation and mesopredator release have been extensively studied as apparent competition and trophic cascade effects, respectively (Courchamp et al. 1999, 2000a; Russell and Le Corre 2009). The examples encountered dealt with exploitative competition and more frequently between

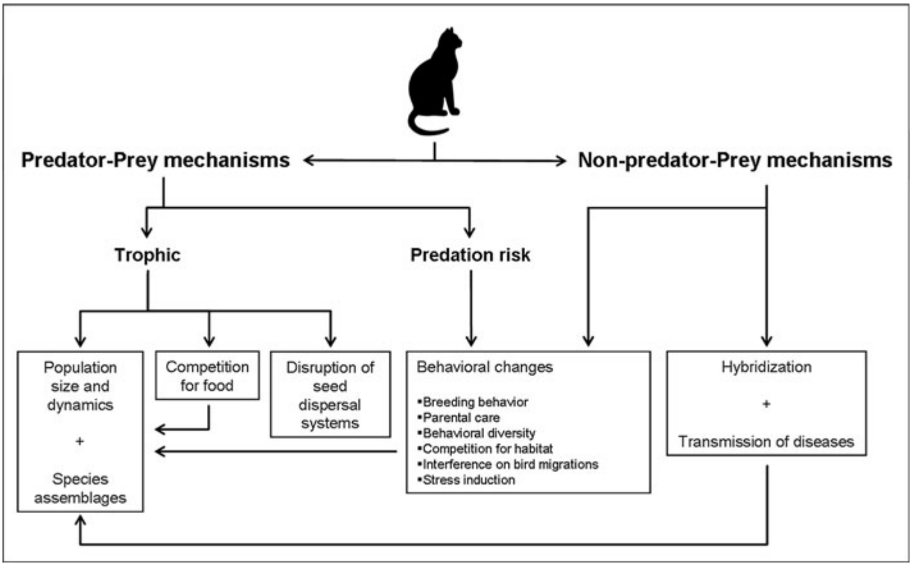

Fig. 1 Impacts of feral cats (*Felis silvestris catus*) on island species

closely-related species, though in some cases it can occur between different animal groups. Competition between species has a strong influence on their abundance and distribution overall when resources are limiting (Glen and Dickman 2005, 2008).

Competition for food

The Iriomote cat (*Prionailurus iriomotensis*) is an endemic felid species on Iriomote Island (Ryukyu archipelago, Japan) currently threatened by habitat restriction and competition with feral cats. When studying the diet of these two species, Watanabe et al. (2003) found that feral and Iriomote cats shared some prey species, leading to possible inter-specific competition for food resources. However, to accurately assess the quantitative impact of this competition process is generally difficult. In the same way, Phillips et al. (2007) found a high level of dietary overlap between feral cats and the endemic island fox (*Urocyon littoralis clementae*) on San Clemente Island, California. Despite this extensive dietary overlap and the relatively narrow niche breadth of these two species, cats and foxes coexist (Phillips et al. 2007). A similar case was found for native mammals like the chuditch (*Dasyurus geoffroii)* in Australia, also coexisting with feral cats. Both of these species showed a high level of diet similarity (Dickman 1996; Glen et al. 2009), even if the chuditch is also a common prey for cats (Glen et al. 2010).

More surprisingly, feral cat trophic competition can also occur among distant taxa like reptiles and birds. On Isla Todos Santos Sur, in northwest Mexico, feral cats compete for food resources with an endemic subspecies of kingsnake (*Lampropeltis zonata herrerae*), by preying on lizards and skinks that constitute its primary prey (Donlan et al. 2000). In Australia, a dietary overlap between one bird, the endemic letter-winged kite (*Elanus scriptus*), and three different introduced mammals (dingo, *Canis familiaris*; European red fox, *Vulpes vulpes*; and cat) was described. Although dietary overlap between these species was especially high during rodent outbreaks, strong competition for food was observed,

Table 1 Species affected by non-direct predation by feral cats on islands

Species	Group	Location	Region	IUCN Category	Geographical features	Other introduced predators	Indirect impact	References
Plants								
Cneorum tricoccon	Plant	Balearic Islands	Mediterranean	–	Continental fragments	Martens, genets and weasels	Disruption seed dispersion	Riera et al. (2002)
Daphne rodriguezii	Plant	Balearic Islands	Mediterranean	VU	Continental fragments	Martens, genets and weasels	Disruption seed dispersion	Traveset and Riera (2005)
Neochamaelea pulverulenta	Plant	Canary Islands	Atlantic Ocean	–	Oceanic island	Rats, mice and dogs	Disruption seed dispersion	Valido (1999)
Reptiles								
Caledoniscincus austrocaledonicus	Skink	New Caledonia	Pacific Ocean	LC	Oceanic island	Rats, mice, dogs, pigs and minas	Stress response	Gerard et al., unpublished
Lampropeltis zonata herrerae	Snake	Isla Todos Santos Sur (Mexico)	Pacific Ocean	CR	Continental fragments	Rats and dogs	Trophic competition	Donlan et al. (2000)
Podarcis erhardii	Lizard	Naxos (Greece)	Mediterranean	CR	Continental fragments	Martens	Reduction of behavioral diversity	Li (2012)
Tropidurus spp.	Lizard	Galapagos Islands	Pacific Ocean	–	Oceanic islands	Rats, mice, dogs and stoats	Reduction of behavioral diversity	Stone et al. (1994)
Birds								
Anthornis melanura	Landbird	New Zealand	Pacific Ocean	LC	Continental fragments	Rats, stoats, ferrets, weasels and brushtail possums	Change in parental care	Massaro et al. (2008)
Catharacta skua	Seabird	Kerguelen Islands	Sub-Antarctic Ocean	LC	Oceanic island	Rats and mice	Trophic competition	Courchamp et al. (2003)
Charadrius falklandicus	Shorebird	Falkland (Malvinas) Islands	Pacific Ocean	LC	Oceanic island	Dogs and foxes	Reduction of behavioral diversity	St Clair et al. (2010)
Columbina passerine socorroensis	Landbird	Isla Socorro (Mexico)	Pacific Ocean	–	Oceanic island	Mice	Reduction of behavioral diversity	Rodríguez-Estrella et al. (1991)

Table 1 continued

Species	Group	Location	Region	IUCN Category	Geographical features	Other introduced predators	Indirect impact	References
Corvus hawaiiensis	Landbird	Hawaii, Hawaiian Islands	Pacific Ocean	EW	Oceanic island	Rats and mice	Transmission of diseases	Work et al. (2000, 2002)
Elanus scriptus	Landbird	Australia	Pacific Ocean	NT	Mainland	Several	Trophic competition	Pavey et al. (2008)
Fregata aquila	Seabird	Ascension Island	Atlantic Ocean	VU	Oceanic island	Rats, mice and dogs	Interference in movement	Ashmole et al. (1994)
Nesochen sandvicensis	Landbird	Maui, Hawaiian Islands	Pacific Ocean	VU	Oceanic island	Rats and mice	Transmission of diseases	Work et al. (2000, 2002)
Numenius tahitiensis	Shorebird	Phoenix Islands	Pacific Ocean	VU	Oceanic island	Rats, dogs and mongoose	Interference in migration	Marks and Redmond (1994)
Phalacrocorax harrisi	Seabird	Isabela, Galapagos	Pacific Ocean	VU	Oceanic island	Rats and dogs	Transmission of diseases	Deem et al. (2010)
Puffinus yelkouan	Seabird	Port-Cros	Mediterranean	VU	Continental fragments	Rats and mice	Interference in movement	Bonnaud et al. (2009)
Spheniscus mendiculus	Seabird	Isabela, Galapagos	Pacific Ocean	EN	Oceanic island	Rats and dogs	Transmission of diseases	Deem et al. (2010)
Sterna fuscata	Seabird	Ascension Island	Atlantic Ocean	LC	Oceanic island	Rats, mice and dogs	Interference in movement	Ashmole et al. (1994)
Sula dactylatra	Seabird	Ascension Island	Atlantic Ocean	LC	Oceanic island	Rats, mice and dogs	Interference in movement	Ashmole et al. (1994)
Sula sula	Seabird	Farquhar Atoll, Seychelles	Indian Ocean	LC	Oceanic island	Rats and owls	Change in breeding behavior	Feare (1984)
		O′ahu, Hawaiian Islands	Pacific Ocean	-	Oceanic island	Rats and mice	Transmission of diseases	Work et al. (2000, 2002)

Table 1 continued

Species	Group	Location	Region	IUCN Category	Geographical features	Other introduced predators	Indirect impact	References
Todiramphus gambieri	Landbird	Niau, Tuamotu archipelago	Pacific Ocean	CR	Oceanic island	Rats and dogs	Trophic competition	Zarzoso-Lacoste, (2013)
Mammals								
Dasyurus geoffroii	Marsupial	Australia	Pacific Ocean	NT	Mainland	Several	Trophic competition	Dickman (1996), Glen et al. (2009)
							Habitat competition	Dickman (1996)
Macropus eugenii	Marsupial	Australia	Pacific Ocean	LC	Mainland	Several	Stress response	Mella et al. (2010)
Monachus schauinslandi	Monk seal	Kauai, Hawaiian Islands	Pacific Ocean	CR	Oceanic island	Rats and mice	Transmission of diseases	Honnold et al. (2005)
Prionailurus bengalensis euptilura	Feline	Tsushima Island	Japan, Pacific Ocean	LC	Oceanic island	Rats, mice and dogs	Hybridization	Murayama (2008)
							Transmission of diseases	Nishimura et al. (1999)
Prionailurus iriomotensis	Feline	Iriomote Island	Japan, Pacific Ocean	CR	Oceanic island	Rats	Trophic competition	Watanabe et al. (2003)
							Habitat competition	Watanabe et al. (2003)
							Hybridization	Izawa et al. (1991)
Urocyon littoralis clementae	Carnivore	San Clemente Island, California	Pacific Ocean	CR	Continental fragments	Rats and mice	Trophic competition	Phillips et al. (2007)

IUCN categories (IUCN 2012): *DD* data deficient, *LC* least concern, *NT* near threatened, *VU* vulnerable, *EN* endangered, *CR* critically endangered, *EW* extinct in the wild particularly between kites, red foxes and cats (Pavey et al. 2008). On Niau Island, Tuamotu Archipelago (Pacific), feral cats have been shown to strongly compete for reptiles with the endemic and critically endangered Tuamotu kingfisher (*Todiramphus gambieri*) (Zarzoso-Lacoste 2013). Another striking example appeared on the Kerguelen Islands where cats and skuas (*Catharacta skua*) compete for a primary shared prey (petrels). This food competition severely decreased the reproductive success of skuas (Courchamp et al. 2003), despite the availability of mice and rabbits as alternative prey (Chapuis et al. 2001).

The reviewed studies only provided evidence of negative effects and did not address specific impacts on native species caused by food competition. In these cases, cat impact strength could depend on other factors such as structural complexity of habitat, degree of human interference, and distribution and abundance of shared prey species (Glen and Dickman 2005; Glen et al. 2009). More thorough studies are required to clarify interactions between native and invasive species due to competition for food resources.

Competition for habitat

Extensive overlap in resources use (space and food) between species (e.g. mammalian carnivores) helps to explain the small degree of habitat competition derived from inverse relationships in their abundance and distribution (Glen and Dickman 2005, 2008). However, cats can strongly compete for habitat since they can spread rapidly from their introduction site, generally linked to human settlements, and can survive in almost all habitats (Medina and Nogales 2007). Currently, Iriomote cat in Japan (Watanabe et al. 2003) and *Dasyurus* spp. in Australia (Dickman 1996) are endangered and approaching potential extinction due to range restrictions caused by feral cat presence.

Cat presence can also affect species movements, activity patterns and even island recolonization and establishment (Ashmole et al. 1994). On Ascension Island (South Atlantic), cats kill many birds like sooty terns (*Sterna fuscata*), masked boobies (*Sula dactylatra*) and frigate birds (*Fregata aquila*). They also negatively affect the population dynamics of these bird species in limiting or even preventing their settlement even a strong inconspicuous effect (Ashmole et al. 1994). On Port-Cros Island in the Mediterranean Basin, the predation risk for prospecting Yelkouan shearwaters (*Puffinus yelkouan*) was four times higher than for breeding birds (Bonnaud et al. 2009). This result can explain why (i) despite the high number of shearwaters killed on this island, their breeding population remained stable for 20 years (Bonnaud et al. 2009), and (ii) when cats were eradicated, the number of breeding pairs rapidly increased by recruiting new breeding birds (Bonnaud et al. 2010).

Alteration of ecological processes

Ecological interactions can be severely disturbed by biological invasions, particularly in island ecosystems where native populations are small in size and have evolved in isolation (Vitousek et al. 1997). According to the reviewed literature, interference with bird migration and disruption of seed dispersal systems were the most documented ecological alterations.

Bird migration interference

Stopovers play an important role in the migration of many bird species. During stopovers, site selection generally depends on refueling rate, or foraging intensity. However, predation risk (represented by cat presence) is sometimes more decisive in site selection than fuel load (Dierschke 2003), because it could modify their stopover behavior (birds staying and resting less) during migration events (Dierschke 2003). Therefore, cat presence alone, without any significant predation effect, can itself decrease bird survival during migration (Lank and Ydengerg 2003). For example, cat presence affected bristle-thighed curlew (*Numenius tahitiensis*) distribution on the Phoenix Islands (Marks and Redmond 1994). These curlews tend to live only on uninhabited islets without introduced predators, thus allowing them a safer molting period, when a high percentage of adults become flightless and more vulnerable (Marks and Redmond 1994).

Disruption of seed dispersal systems

An invasive species can alter species interactions in a very complex but specific way, for example when introduced predators disrupt some native seed dispersal systems that include frugivorous animals (Traveset and Richardson 2011). This phenomenon was described for at least six native and two introduced plants, when studying cat predation on frugivorous lizards in the Canary Islands in both coastal habitats and thermophilous woodland (Nogales et al. 1996). This secondary dispersal process can cause disruption of the seed dispersal and ecological processes of native plant species.

A complex ecological effect has been linked to the rarity of endemic giant lizards (*Gallotia simonyi*, *G. bravoana*, and *G. intermedia*) in the Canary Islands due to cat predation (Medina and Nogales 2009). The Canary endemic plant *Neochamaelea pulverulenta* (Cneoraceae) is dispersed by giant lizards but different seed sizes are dispersed by different-sized lizards. Currently, smaller seeds are sub-optimally dispersed by the population of smaller endemic lizards (*G. galloti*). As the biggest lizards are more easily preyed on by cats, their population has drastically decreased leading to a low dispersal of bigger seeds. This new dispersal process, boosting small seed dissemination, is strongly suspected to have an impact on the survival and evolution of this plant species (Valido 1999).

Likewise, the disappearance of an endemic lizard (*Podarcis lilfordi*) from some of the Balearic Islands, partially due to cat predation, will probably limit seedling recruitment and plant regeneration in the remaining population of the endemic plant *Daphne rodriguezii*, which is exclusively dispersed by this endemic lizard (Traveset and Riera 2005). A similar case was also described in the mutualistic systems between the plant *Cneorum tricoccon* and the endemic lizard *Podarcis pityusensis* in the Balearics (Riera et al. 2002), where other introduced carnivores, like pine martens (*Martes martes*), genets (*Genetta genetta*) and weasels (*Mustela nivalis*), threaten this endemic lizard.

Another striking example deals with the dispersion of an exotic plant species, Hottentot fig (*Carpobrotus edulis*) on Porquerolles Island (Mediterranean Basin). Feral cats were found to secondarily disperse these seeds, when eaten by introduced rats (Bourgeois et al. 2004). The germination rate after being consumed by rats and secondly by cats was not significantly different to those not consumed. However, these seeds were dispersed over a much larger distance. Thus, introduced cats, eating introduced rats, increase the invasive success of this invasive plant in Mediterranean insular ecosystems (Bourgeois et al. 2004).

Behavioral changes

Cat predation can induce selective pressure on native species, reducing life history traits (Beckerman et al. 2007; Bonnington et al. 2013) and leading to behavioral changes.

Hunting behavior can also modify species interactions when, for example, predators flush out prey species making them more vulnerable to other predators (Wootton 1994). In addition, some experimental studies demonstrated that cat odor can induce a stress response in their prey. Mella et al. (2010) provided evidence that cat urine odor induces an increase in the ventilatory frequency of tammar wallabies (*Macropus eugenii*). Several studies also showed that rodents (rats and mice) exhibit behavioral responses when confronted with cat odor, especially defensive and avoidance behavior, (Dielenberg and McGregor 2001) even if they have never been in contact with it before (Bramley et al. 2000). However, Dickman (1992) reported the opposite with predator-naive mice.

In general, in the absence of predators, native species develop different behavior, being less distrustful and protective (e.g. Blumstein and Daniel 2005; Sih et al. 2010). Invasive predators and competitors had definite impacts on native species behavior, causing changes in their habitat use or activity patterns (Parker et al. 1999). They also led to a possible loss of behavioral diversity, considered as an overlooked component of biological diversity (Stone et al. 1994; Delibes and Blázquez 1998). Breeding, flocking and parental care of prey species were the behaviors most reported in the reviewed studies as being affected by cats on islands.

Breeding behavior

On Farquhar Atoll, South Island, Seychelles, the red-footed booby (*Sula sula*) breeds in taller *Casuarina* trees, rather than in shorter *Pemphis* and *Scaveola* bushes where it breeds on many other islands. Cats have good climbing abilities and their presence and predation pressure can affect the breeding behavior of this bird species (Feare 1984).

Parental care behavior

Cats can also have indirect impacts through lethal trait-mediated effects reducing, for example, provisioning rates (Bonnington et al. 2013). Nevertheless, in some cases, species are able to respond to an increased risk of predation by changing parental care behavior (Massaro et al. 2008). For example, the endemic New Zealand bellbird (*Anthornis melanura*) spends more time on the nest during the incubation period to better protect its eggs against several predators (cats; rats *Rattus exulans*, *R. rattus*, *R. norvegicus;* mustelids *Mustela erminea*, *M. furo*, *M. nivalis;* and brushtail possum *Trichosurus vulpecula*) (Massaro et al. 2008).

Reduction of behavioral diversity

When a new predator is introduced on islands, the selective forces acting on insular organisms can shift. For example, Stone et al. (1994) found higher wariness in native species as a result of predation pressure. Thus, behavioral diversity can be reduced when organisms lose their evolved behavior. In the Galapagos archipelago, lava lizards (*Tropidurus* spp.) are common prey for cats and an increase in lizard wariness and cat presence were linked (Stone et al. 1994 but see Delibes and Blázquez 1998). On Isla Socorro, Mexico, cats preyed on the endemic Socorro ground dove *Columbina passerina socorroensis* (Rodríguez-Estrella et al. 1991). These authors considered that the endemic dove's habitual tameness was affected by cat predation. In the same way, the presence of an introduced predator induced changes in prey species behavior regarding tolerance to predation or disturbance risk. For example, in the Falkland (Malvinas) Islands, the variation in flight initiation distance of a small ground-nesting shorebird (the two-banded plover *Charadrius falklandicus*) varied in response to human proximity according to the presence or absence of feral cats. However, other variables like human activity and reproductive traits could also influence this behavior (see St Clair et al. 2010). On Naxos (Cyclades, Greece), cats have a strong negative impact on Aegean wall lizards (*Podarcis erhardii*), which adapted their anti-predator behavior by extending their flight initiation distance, increasing their tail autotomy capacity, and staying closer to refugia (Li 2012). In a recent study, an endemic New-Caledonian skink (*Caledoniscincus austrocaledonicus*) was shown to exhibit an aversion for cat-scented retreat sites and to significantly select those free of predator odors (Gerard et al., unpublished).

Hybridization

Domestic cats were derived from the wildcats, *F. silvestris*, composed of five distinct interfertile subspecies (Driscoll et al. 2007). Hybridizations between wildcats and domestic cats are common and were found in the genetic admixture present in European, African and Asian wildcat populations (Driscoll et al. 2007). However, in some cases like African wild cats (*F. s. lybica*) the observed level of genetic introgression was low (Wiseman et al. 2000). The hybridization of Scottish wildcats (*F. s. silvestris*) with domestic cats is one of the best studied cases, which currently represents one of the main threats for the endangered population of Scottish wildcats (Kitchener et al. 2005). These hybrids are widespread in Scotland and only some "relatively" pure populations still remain. To distinguish hybrid from pure individuals, different aspects of their biology (morphological and pelage: Daniels et al. 1998; Kitchener et al. 2005, craniological differentiation: Yamaguchi et al. 2004) must be taken into account.

Furthermore, man-made hybrids between domestic house cats and other species belonging to different genera of the Felidae family have been bred, like the Asian leopard cat (*Prionailurus bengalensis*), Geoffroy's cat (*Leopardus geoffroyii*), or the serval (*Leptailurus serval*) (see Markula et al. 2009). On Japanese islands, hybridization is still an issue hindering the preservation of the endemic Tsushima leopard cat (*Prionailurus–Felis–Bengalensis euptilura*) (Murayama 2008) and Iriomote cat (Izawa et al. 1991). Introgression with traits from domestic cats has been a threat for wild species conservation and current management plans depend on the ability to distinguish the native species from domestic cats (Daniels et al. 1998).

Transmission of diseases

In a review about feral cat control, Robertson (2008) reported that from a human perspective the main issues surrounding feral cats are those related to public health, spread of disease to other species and public nuisance. Cats carry and suffer from many viral and bacterial diseases as well as a considerable number of other endo- and ectoparasites (Kitchener 1991). Some of these diseases and parasites affect humans (Robertson 2008), livestock and wild carnivores (Macdonald et al. 2000).

One of the most studied diseases transmitted by feral and house cats is the Feline Immunodeficiency Virus (FIV) (Courchamp et al. 2000b), which has occurred, for example, in natural populations of wildcats in Scotland (Daniels et al. 1999). Another example is the FIV transmission from domestic cats to the endangered leopard-cat in the wild, *P. –F.– bengalensis euptilura* on Tsushima, Japan. This subspecies was positive to

FIV antibody, certainly due to contact with the domestic and feral cat populations, being the only other felidae present on this island that contained sero-positive individuals (Nishimura et al. 1999). Similar cases appeared on islands, where cats introduced FIV and other diseases such as feline leukemia virus and toxoplasmosis (Duffy and Capece 2012). Regarding conservation perspectives, FIV has been used as a biological control of feral cat populations on islands (see Nogales et al. 2004 and references therein). However, this virus appeared to be a poor control agent due to its low transmission rates and long lasting sero-positivity (Courchamp et al. 2000b).

The parasite *Toxoplasma gondii* infects native species and affects their populations; e.g. nene goose (*Nesochen sandvicensis*), red-footed booby (*S. sula*), 'alala (*Corvus hawaiiensis*) (Work et al. 2000, 2002), and even a monk seal (*Monachus schauinslandi*, Honnold et al. 2005) as described in the Hawaiian Islands (Danner et al. 2007). In the Galapagos, the prevalence of antibodies to *T. gondii* in two threatened avian marine species, Galapagos penguins (*Spheniscus mendiculus*) and flightless cormorants (*Phalacrocorax harrisi*), was higher on an island with cats (Isabela) than one without cats (Fernandina), providing indications of disease-related risks associated with the feral cat population in the archipelago (Deem et al. 2010). Cats can also act as reservoirs and zoonotic vectors of the Nipah Virus that infects pigs in Malaysia (Epstein et al. 2006).

Conclusions

A large amount of research has been mainly focused on the obvious direct effects of invasive mammal predation upon particular endangered species, and the associated large number of publications reflects this interest. Nevertheless, the other ecological processes involved, much less studied, are more complex to evaluate but can have a strong effect on the conservation of native species on islands (Table 1). Due to these overlooked impacts, cat control or eradication can be planned even when their predation rate on native species is low. Even if an accurate understanding of all invasive predator impacts is not needed to determine whether or not control or eradication should go ahead (Grantham et al. 2009), we strongly recommend taking into account the different biotic interactions driven by these predators. Changes in prey numbers or dynamics after predator removal should not only be attributed to their release from predation, but also to being freed from non-direct predation impacts. The extent to which feral cat presence is identified as a risk by naive island prey still remains to be investigated, and also how the adaptive or non-adaptive prey responses are modified (leading to consequences in their dynamics and survival). Due to the lack of studies focused on these often overlooked impacts of invasive species on islands, we consider that these highlighted cases should arouse interest in improving scientific knowledge of this research area.

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