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The Effects of Feral Cats on Insular Wildlife: The Club-Med Syndrome

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ABSTRACT: Domestic cats have been introduced to many of the world's islands where they have been particularly devastating to insular wildlife which, in most cases, evolved in the absence of terrestrial predatory mammals and feline diseases. We review the effects of predation, feline diseases, and the life history characteristics of feral cats and their prey that have contributed to the extirpation and extinction of many insular vertebrate species. The protozoan *Toxoplasma gondii* is a persistent land-based zoonotic pathogen hosted by cats that is known to cause mortality in several insular bird species. It also enters marine environments in cat feces, where it can cause the mortality of marine mammals. Feral cats remain widespread on islands throughout the world, and are frequently subsidized in colonies which caretakers often assert have little negative effect on native wildlife. However, population genetics, home range, and movement studies all suggest that there are no locations on smaller islands where these cats cannot penetrate within two generations. While the details of past vertebrate extinctions were rarely documented during contemporary time, a strong line of evidence is emerging that the removal of feral cats from islands can rapidly facilitate the recolonization of extirpated species, particularly seabirds. Islands offer unique, mostly self-contained ecosystems in which to conduct controlled studies of the effects of feral cats on wildlife, having implications for continental systems. The response of terrestrial wildlife such as passerine birds, small mammals, and herptiles still needs more thorough long-term monitoring and documentation after the removal of feral cats.

KEY WORDS: domestic cats, *Felis catus*, invasive species, island naïveté, mesopredator release, toxoplasmosis

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INTRODUCTION

Domestic cats (*Felis catus*) have been introduced to nearly all of the world's inhabited islands as well as numerous uninhabited ones which previously had depauperate mammal faunas or none at all (Medina et al. 2011). Although many of their founding populations were small, high fecundity (van Aarde 1983), wide-ranging movements (Edwards et al. 2001), and the ability to proliferate in a wide variety of habitats (van Aarde 1979, Smucker et al. 2000, Medina and Nogales 2007, Hess et al. 2007a) have resulted in rapid population growth (van Aarde 1979, 1984), enabling cats to establish themselves ubiquitously on many islands. On inhabited islands, feral cat populations have also been supplemented by additional releases of unwanted pets and further subsidized by feeding (Winter 2003).

Cats are typically apex predators on islands because their predators, such as coyotes (Crooks and Soulé 1999) and dogs (Warner 1985), have either not been introduced or occur in small numbers. In addition, other leading causes of cat mortality such as cars and humans (Warner 1985) are less significant on islands lacking extensive human development. Cats also face few competitors because other mesopredators such as raccoons and opossums have remained absent from many islands. This lack of competition and predation may be responsible for rapid population growth and dense populations on some islands (van Aarde 1979,

Domm and Messersmith 1990), as well as high survival relative to continental environments (Warner 1985, Kaeuffer et al. 2004, Danner et al. 2010, Schmidt et al. 2007).

Conversely, the native faunas of remote islands were rarely prey of mammalian predators. The consequential lack of coevolution between predators and prey is thought to result in character release, including reduced predatory defenses, which has been termed 'prey naïveté' (reviewed in Sih et al. 2010). In addition to prey naïveté, animals on isolated islands are also often highly susceptible to continental pathogens (Wikelski et al. 2004). These two phenomena, prey naïveté and susceptibility to disease, can be lumped more broadly into 'island naïveté'. While exploring the Galápagos Islands, Charles Darwin was probably the first to conceptualize island naïveté and predict the devastating effects that would follow (see Lomolino 2010).

On many islands, mesopredator release of cats is coupled with island naïveté of prey: the conditions that favor the proliferation of cats on islands; the ease of obtaining naïve prey and the factors favoring high reproduction and survival rates, including the absence of competitors and larger predators, and limited anthropogenic mortality all lead to a life of leisure relative to continental situations. The consequence has been devastating for native wildlife, including the decline, extirpation, and extinction of numerous

vertebrate populations, particularly ground-nesting and burrowing landbirds and seabirds, as well as many herptile and small mammal species. Similar effects are also manifested in continental environments, particularly for shrub-nesting birds in suburban areas (van Heezik et al. 2010).

In this paper, we present recent evidence and mechanisms by which cats have proliferated and devastated insular vertebrate species. Our focus is primarily on Hawai'i, which serves as a model system, although we use examples from around the world. Specifically, we document predation and feline disease transmission to naïve insular fauna. While evidence of mesopredator release is harder to quantify, we present life history and ecological characteristics that have made cats successful invaders on islands. We then explore evidence of vulnerability to cat predation and the responses of bird populations to feral cats and their removal.

LINES OF EVIDENCE

Diet and Predation

Cats on islands are known to consume a wide variety of vertebrate prey, consisting of over 248 species on 40 islands, including 27 mammals, 113 birds, 37 herptiles, 2 fish, as well as 69 invertebrates (Bonnaud et al. 2011). Of these, 3 mammals, 29 birds, and 3 reptiles are considered threatened species by the IUCN (IUCN 2012). The diet of feral cats, as measured by the contents of digestive tracts, differs strongly by location, even within islands of Hawai'i (Hess et al. 2007a). The diet of feral cats from Mauna Kea, from Hawai'i Volcanoes National Park (HAVO), and the island of Kaho'olawe differed markedly in those that consumed birds, ranging from <30% to nearly 70% of digestive tracts (Figure 1). The proportion of cat digestive tracts containing small mammals, birds, and invertebrate prey varies markedly even over short distances of 25 km within HAVO, suggesting that cats are not especially selective, but consume prey species according to relative availability, perhaps subsisting on invertebrates in the scarcity of vertebrate prey (Hess et al. 2007b).

Videographic evidence of predation by cats on endangered species has confirmed that cats do not merely scavenge carcasses of dead birds, but depredate live birds, particularly nestlings. On Mauna Kea, four occasions of depredation have been recorded on endangered palila (*Loxioides bailleui*) nestlings, a forest-dwelling finch-billed honeycreeper that nests in woodland tree canopies (Laut et al. 2003, Lindsey et al. 2009). An estimated 11% of palila nests are depredated annually by feral cats (Hess et al. 2004). Ground-nesting landbirds and burrow-nesting seabirds such as the endangered Hawaiian petrel (*Pterodroma sandwichensis*) are particularly vulnerable to depredation by cats (Hu et al. 2001). Feral cats were recorded at three Hawaiian petrel nest burrows in 2007 and in 2008 at HAVO (Figure 2). While only one nestling depredation event was recorded on video in 2008, 5 other adult depredation events were found during the two-year period (USGS and NPS, unpubl. data).

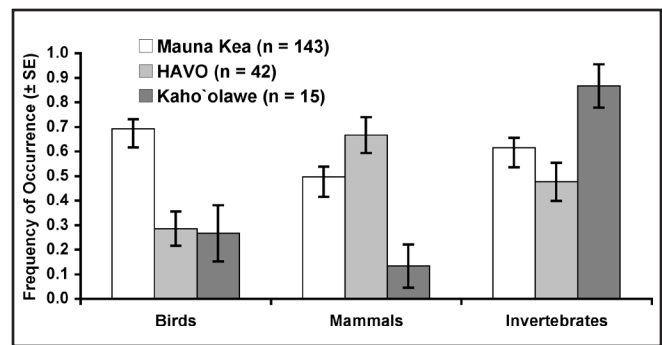


Figure 1. Frequency of occurrence (\pm SE) of three prey types from digestive tracts of feral cats from Mauna Kea, Hawai'i Volcanoes National Park (HAVO), and the Island of Kaho'olawe, Hawai'i 1998-2005.



Figure 2. A feral cat (*Felis catus*) taking an endangered Hawaiian petrel (*Pterodroma sandwichensis*) nestling from its burrow on Mauna Loa, Hawai'i Island during a nighttime video segment illuminated by infrared light. The nestling, which is entirely covered in downy feathers, is held upside down by the cat and its head is facing the left side of the frame.

Disease

Although cats are well-known to be highly efficient predators, the effects of feline diseases on insular wildlife are not as well understood. Toxoplasmosis, however, has caused mortality in several endangered terrestrial and marine species and has perhaps the greatest effect of all feline diseases on other species of wildlife. Toxoplasmosis is a zoonotic disease caused by the protozoan *Toxoplasma gondii*. Felids are the definitive hosts of *T. gondii*, and domestic cats are generally the only felid species that inhabit most of the world's islands. The sexual phase of the *T. gondii* life cycle occurs only in the gut of cats, during which, environmentally resistant oocysts are shed in cat feces. Other warm-blooded species that ingest *T. gondii* oocysts or tissue cysts may become intermediate hosts of the pathogen. Comparative evidence from cat-free islands demonstrates that the prevalence of toxoplasmosis is related to the presence of cats (Dubey et al. 1997). Antibodies to *T. gondii* were found in 11

(0.9%) of 1,264 pigs on Ossabaw Island southeast of Savannah, GA, an island with only one known cat, whereas *T. gondii* antibodies were found in 31 (18.2%) of 170 feral pigs from mainland Georgia in the presence of widespread cats.

The environmental resistance of *T. gondii* oocysts makes them persistent not only in soils (Dubey et al. 2011), but oocysts are also capable of sporulating in seawater (Lindsay et al. 2003), where they may infect a wide variety of marine mammals (Jessup and Miller 2011). Marine mammals known to be killed by toxoplasmosis include the endangered Hawaiian monk seal (*Monachus schauinslandi*) (Honnold et al. 2005), spinner dolphins (*Stenella longirostris*) (Migaki et al. 1990), and southern sea otters (*Enhydra lutris nereis*) (Miller et al. 2002). Sea otter mortality has led to a California ban of flushable cat litter and spurred research into terrestrial deposition of oocysts that make their way into the marine environment. In the Morro Bay watershed of California, only 3 (0.9%) samples of feces from 326 cats contained *T. gondii*-like oocysts, but because of the large number of oocysts shed during initial infection, the environmental oocyst burden based on the estimated tonnage of cat feces deposited outdoors in this area was 94 to 4,671 oocysts/m² (9 to 434 oocysts/ft²) (Dabritz et al. 2007).

In the terrestrial environment of Hawai'i, toxoplasmosis has been known to kill the endangered Hawaiian goose (*Branta sandvicensis*), the critically endangered Hawaiian crow (*Corvus hawaiiensis*), red-footed booby (*Sula sula*), and Erkel's francolin (*Francolinus erckelii*), an introduced game bird (Work et al. 2000, 2002). Because surveillance for the pathogen is limited and diagnostic testing is not routinely performed on asymptomatic individuals, the prevalence of toxoplasmosis is still little known among wildlife species. In feral cats from Mauna Kea, Hawai'i, the overall prevalence was 37% based on IgG antibodies to *T. gondii*, indicating past exposure, whereas 7% of cats had active infections as indicated by IgM antibodies (Danner et al. 2007). Worldwide, overall seroprevalence in cats ranges from 5.4-74.2% depending on location and diagnostic method, and several studies have found seroprevalence to be related to cats' ages, suggesting cumulative exposure over time (Dubey et al. 2009). Humans are also affected by *T. gondii*, which may cause severe developmental disabilities in fetuses of infected mothers and mortality in immunocompromised individuals. The overall age-adjusted seroprevalence from 1988-1994 was 22.5% (95% CI: 21.1-23.9) in humans (Jones et al. 2001).

Feline immunodeficiency virus (FIV) and feline leukemia virus (FeLV) both primarily concern the welfare of free-ranging cats, their effects on domestic cats, and other species of wild felids. Because islands generally lack other species of wild felids, viral pathogens have not been as thoroughly researched as *Toxoplasma* in this context. One study noted, however that, "...domestic cat FIV spillover into populations of wild felids could have potentially devastating consequences" (Franklin et al. 2007). Other feline diseases may also have implications for wildlife.

Home Range and Movements

The home range and movements of feral cats is surprisingly large on islands, with strong implications for the potential to affect wildlife over broad areas. Goltz et al. (2008) found the mean home range of male cats to be 14.2 km² on Mauna Kea, Hawai'i, with a maximum of 20.5 km², whereas the mean home range of females was 7.7 km². Cats made mean daily movements ≤ 6 km, and maximum daily movements of ≤ 25 km. The home ranges of males were larger than that of females in 8 Pacific region studies (Goltz et al. 2008). Other studies found home range size related to body mass; however, body mass is generally related to gender in cats (Nowak 2005). The maximum home range reported in the literature was 22.1 km² in a semiarid woodland environment of central Australia (Edwards et al. 2001). Guttilla and Stapp (2010) determined home-range area and overlap and characterized the long-range movements of 14 sterilized and 13 intact radio-collared cats on Santa Catalina Island, CA, from 2002 to 2004. This study also found that male home ranges were significantly larger than those of females, but there were no significant differences in home-range areas or overlap between sterilized and intact cats. Cats regularly moved between natural habitats in the interior of the island and human-populated areas regardless of sex or treatment status, suggesting that cats may be able to take advantage of subsidies provided by humans, but then also feed in areas beyond human influence.

Population Genetics

While telemetry studies are capable of documenting movement within generations, they cannot address the intergenerational spread of cats or more complex issues of population dynamics such as source and sink metapopulation structure. Population genetics can address these issues, and although genetics have not yet been widely applied to the field of invasive species, one study has demonstrated the application and the magnitude of intergenerational movements in feral cats on Hawai'i Island. Using microsatellites, Hansen et al. (2007) reported contemporaneous half-siblings on Mauna Kea and Mauna Loa, finding intergenerational movements of >50 km (Figure 3). The west slope of Mauna Kea was a source population of cats for areas such as the Mauna Loa section of HAVO, where Hawaiian petrel depredation by cats occurs. The study also found sex-biased dispersal, with males dispersing farther than females, which was consistent with findings of home range and movements in the Mauna Kea population as well as throughout the Pacific region (Goltz et al. 2008). The implications of such wide-ranging movements suggest it would be difficult to restrict free-ranging cats from any natural areas on smaller islands such as Kaua'i and O'ahu.

Vulnerability and Extinction

Past vertebrate extinctions were rarely documented in contemporary time; therefore, it is difficult to determine the exact circumstances responsible for extinctions, but cats have contributed to a minimum of 14% of all bird, mammal, and reptile extinctions and

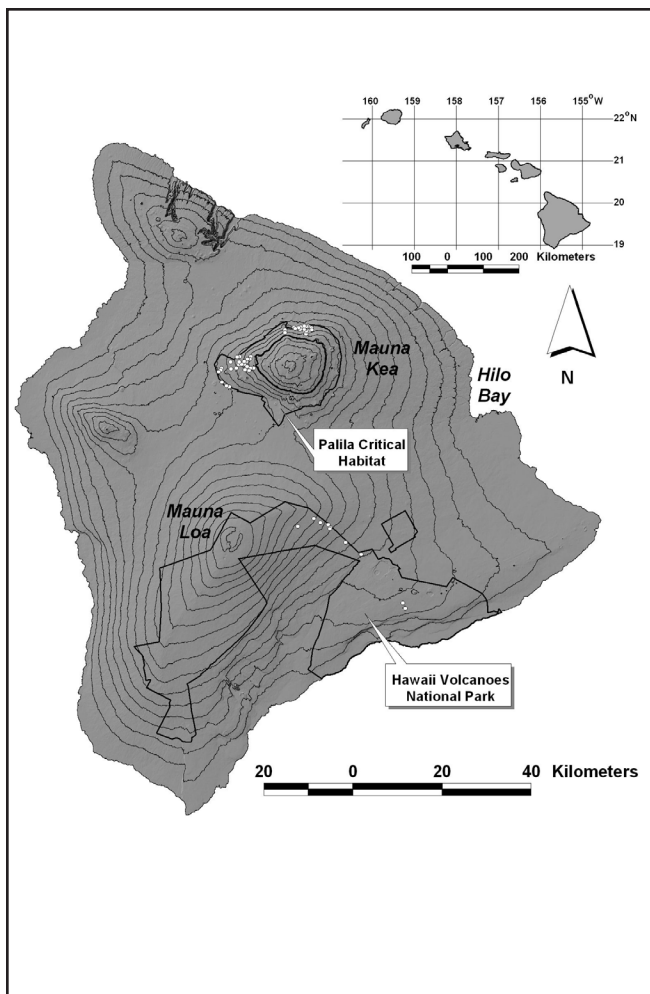


Figure 3. Capture locations of feral cats on Hawai'i Island in studies of population genetics. Genetic analyses found intergenerational movements of >50 km, with contemporaneous half-siblings from Palila Critical Habitat on Mauna Kea and Hawai'i Volcanoes National Park on Mauna Loa. The west slope of Mauna Kea was a source population of cats for Mauna Loa.

the decline of at least 8% of critically endangered birds, mammals, and reptiles, most of which have occurred on islands (Medina et al. 2011). Life history characteristics can predispose insular prey species to extirpation and extinction (Lindsey et al. 2009), and many island bird species exhibit such vulnerabilities: adult predation of species with delayed maturity; low reproductive potential; species that rarely breed again/re-nest within seasons; specialized feeding ecology; long development periods/parental dependence; and altricial young.

Studies of the effects of habitat fragmentation and urbanization demonstrate similarities between avian vulnerability to predation in insular environments and in developed areas where high densities of owned cats range freely. Shrubby vegetation in urban and suburban areas may create situations with habitat that appears to be appropriate for nesting birds, but may in fact be an 'ecological trap' that results in increased mortality through predation (Schlaepfer et al. 2002). Such areas

may function as metapopulation sinks which persist only because of constant immigration from outlying areas. van Heezik et al. (2010) reported that 144 owned domestic cats in Dunedin, New Zealand, brought back a mean of 13.4 prey items/year (median = 4), with cats aged <1 year returning more prey than older cats during a 12-month period. Birds were the most common prey, followed by rodents. Modelling of three bird species indicated low likelihood of population persistence with continued cat predation. Balogh et al. (2011) found that predation accounted for 79% of all gray catbird (*Dumetella carolinensis*) mortalities in a suburban matrix of Maryland, with 47% of known predation events attributable to domestic cats. Stracey (2011) recorded 56 nest predation events in Florida, where cats were the dominant urban predator and Cooper's hawks (*Accipiter cooperii*) were the dominant non-urban predator of northern mockingbirds (*Mimus polyglottos*), recommending that cat owners keep their cats indoors at night because some cats recorded as nest predators in residential neighborhoods were owned cats and all but one cat predation event occurred at night.

Responses of Bird Populations to Feral Cats and Their Removal

It is important to move beyond the phase of documenting the negative effects of feral cats on wildlife to potential solutions. While the effects of cats on comparable insular locations and species provides strong evidence for population declines and extirpations, the inverse situation, where cats are removed from islands, provides even more compelling evidence in many cases. In one such comparative example, wedge-tailed shearwaters (*Puffinus pacificus*) near a cat colony on O'ahu had complete reproductive failure and almost all adults were killed, but 62% of nests produced chicks at a nearby island without cats (Smith et al. 2002). In situations where cats have been removed entirely from islands, dramatic recovery has been documented. For example, five seabird species recolonized remote Pacific Island wildlife refuges of Baker, Howland, and Jarvis after the eradication of cats (Rauzon et al. 2011). Five seabird species also recolonized Ascension Island in the central Atlantic since cats were eradicated, and predation of adult seabirds has ceased (Ratcliffe et al. 2009). On Mexican islands, extirpated Cassin's auklet (*Ptychoramphus aleuticus*) recolonized within 4 years of cat eradication on Coronado, and black-vented shearwaters (*Puffinus opisthomelas*) experienced a ten-fold reduction in predation on Natividad, from >1,000 to <100 per month (Nogales et al. 2004). Both short-term and longer-term recoveries of bird species have been documented after the 1991 eradication of feral cats from subantarctic Marion Island, the largest island from which cats have been eradicated. Great-winged petrels (*Pterodroma macroptera*) and blue petrels (*Halobaena caerulea*) bred more successfully after cat removal (Cooper et al. 1995), and the extirpated common diving petrel (*Pelecanoides urinatrix*) returned to Marion Island (Nogales et al. 2004). Even the removal of small numbers of cats may dramatically reduce depredation. Peck et al. (2008) reported that on Juan de Nova

Island, "...the removal of two cats significantly and immediately reduced the number of dead sooty terns in our plots." In another uncommon example of a forest bird, the control of feral cats on Mauna Kea reduced annual nest predation of endangered palila from 11% to zero (Hess et al. 2004).

CONCLUSION

Cats and the Club Med Syndrome

Hundreds of vertebrate prey species have been found in studies of cat diets throughout islands of the world (Bonnaud et al. 2011), and recent videographic studies have confirmed that cats do not merely scavenge the carcasses of dead birds; they depredate live birds, often endangered species (Laut et al. 2003, Lindsey et al. 2009). Insular prey are particularly vulnerable because of life history characteristics that confer island naïveté; however, habitat fragmentation in continental areas may also confer vulnerability to prey species (van Heezik et al. 2010). Island naïveté may also play a role in the vulnerability of terrestrial insular vertebrates to the feline disease of toxoplasmosis, but the proliferation of cats in coastal areas has even greater potential implications for marine mammals, which are susceptible to either primary or secondary ingestion (e.g., through shellfish consumption) of *Toxoplasma* oocysts as a consequence of freshwater runoff containing cat feces (Miller et al. 2002, Jessup and Miller 2011). Numerous insular vertebrate extinctions have been attributed to cats (Medina et al. 2011).

Feral cats are often the most widespread *de facto* apex predator where no comparably-sized or larger predators exist on islands, having documented home ranges on the order of ≤ 22 km², daily movements of ≤ 6 km, and intergenerational movements of ≤ 50 km (Edwards et al. 2001, Hansen et al. 2007, Goltz et al. 2008). As a consequence, cats are physically able to penetrate the interior of small islands such as Kaua'i or O'ahu within two generations, effectively rendering these islands without any refuge for terrestrial vertebrate wildlife. How do they do this? Cats face few obstacles during their establishment on islands. They face little competition for prey and little mortality from other predators or anthropogenic sources of mortality. Prey are generally naïve and abundant, at least before cat populations reach peak abundance and prey populations have been reduced.

The favorable conditions that have allowed cats to become established and proliferate on many islands throughout the world have mirrored the decline of native vertebrate wildlife on these same islands. Perhaps the most compelling evidence that cats are directly responsible for these declines, extirpations, and extinctions is in the emerging documentation that many extirpated seabird species have recolonized islands where cats have been removed (Cooper et al. 1995, Nogales et al. 2004, Peck et al. 2008, Ratcliffe et al. 2009, Rauzon et al. 2011). We recommend that more thorough monitoring and documentation of vertebrate recoveries be conducted on islands where cats are to be removed, and that similar investigations be conducted in continental situations in cases of experimental

cat removal. Such studies will avoid retrospective uncertainty in determining the cause of past declines and extinctions, and provide more reliable evidence for future wildlife management.

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