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## Proceedings of the Vertebrate Pest Conference

### Title

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### Permalink

<https://escholarship.org/uc/item/8x901491>

### Journal

Proceedings of the Vertebrate Pest Conference, 26(26)

### ISSN

0507-6773

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### Publication Date

2014

### DOI

10.5070/V426110364

# Strength of Evidence for the Effects of Feral Cats on Insular Wildlife: The Club Med Syndrome Part II

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**ABSTRACT:** Various types of evidence have been promulgated as proof for the effects of feral cats on wildlife, typically including numerous studies on predation inferred from diet, mortality attributed to pathogens, and photographic or videographic documentation. The strength of these types of evidence is often short of conclusive. For example, studies of predation inferred from diet provide weak evidence for two reasons: 1) they cannot differentiate depredation from scavenging by feral cats, and 2) they cannot address population-level effects on wildlife because it is rarely understood if mortality acts in compensatory or additive manner. Likewise, pathogens may cause mortality of individuals, but population-level effects of pathogens are rarely known. Photographic or videographic documentation provides direct 'smoking gun' evidence that may be useful for positive identification of depredation by cats, or identification of prey designated as threatened or endangered species. However, the most direct and compelling evidence comes from examples where feral cats have been entirely removed from islands. In many cases, several species of seabirds as well as other wildlife have recovered after the complete removal of cats. Where possible, the experimental removal of cats would provide the most conclusive proof of effects on wildlife populations. In other cases where cat removal is not feasible, modeling based on predation rates and life history parameters of species may be the only means of assessing population-level effects on wildlife. Understanding population-level effects of feral cats on wildlife will ultimately be necessary to resolve long-standing wildlife management issues.

**KEY WORDS:** additive mortality, compensatory mortality, evidence, experimental design, *Felis catus*, free-ranging cats

Proc. 26<sup>th</sup> Vertebr. Pest Conf. (R. M. Timm and J. M. O'Brien, Eds.)

Published at Univ. of Calif., Davis. 2014. Pp. 211-216.

## INTRODUCTION

Various types of evidence have been construed as proof for the effects of free-ranging cats (*Felis catus*) on wildlife, typically including numerous studies that infer predation from diet (Hess et al. 2007, Lohr et al. 2013), mortality attributed to pathogens (Work et al. 2000, Work et al. 2002, Honnold et al. 2005), and direct documentation of depredation through photographic or videographic evidence (Laut et al. 2007, Lindsey et al. 2009, Judge et al. 2013). The strength of these types of evidence is often short of conclusive because such studies are not capable of determining causes of population-level change in wildlife. Study design is often the primary limitation in providing reliable evidence supporting predation or disease (McArdle 1996). Although population-level declines of many bird species have been documented, causation cannot be directly attributed to free-ranging cats except where the most rigorous evidence has been obtained.

Approximately half of all neotropical migrant bird species for which there are sufficient data have declined since large-scale monitoring began in 1966; however, the ultimate causes of these declines remain inconclusive (Butcher and Niven 2007). One of the top sources of anthropogenic bird mortality in the United States has recently been identified as predation by free-ranging cats, with losses estimated at 1.4-3.7 billion individuals annually (Loss et al. 2013). Annual mortality of small mammals caused by free-ranging cats is estimated to be even greater (6.9-20.7 billion individuals; Loss et al. 2013). Cats are estimated to kill between 100 and 350 million birds per year in Canada (Blancher 2013). In contrast, wind-energy facilities are estimated to kill

approximately 0.6 million birds and 0.9 million bats each year (Smallwood 2013). Nonetheless, estimated mortality rates alone cannot be used to determine the net effect on populations of each species because it is not known if species' populations respond to these mortalities in an additive or compensatory manner (Burnham and Anderson 1984).

Hess and Danner (2013) reviewed recent evidence and mechanisms by which cats have proliferated and adversely affected insular vertebrate species. Here, I review the various types of data, study designs, and critical evidence for the effects of free-ranging cats on wildlife populations and rank the relative strength of causal evidence for each from weakest to strongest based on examples of each type of study. For each type of study I ask: Is the critical evidence sufficient to determine causality for declines in prey populations?

## RELATIVE STRENGTH OF EVIDENCE: WEAKEST TO STRONGEST

### Dietary Studies

The main shortcoming of all dietary studies of cats (i.e., fecal remains, gut contents) is that they cannot differentiate depredation from scavenging. By their nature, these studies examine which prey cats have consumed after the fact; they are not capable of determining the cause of death of prey. The net effect of scavenging on any prey population is inconsequential because mortality has already been caused by some other factor. Several sources of bias are also possible depending on the design of dietary studies. Dietary studies based on fecal remains may contain inherent biases because soft tissues of animals may be systematically underrepresented (e.g.,

Snetsinger et al. 1994, Smucker et al. 2000). Items such as egg contents, muscle tissues, recently pupated insects, etc., are not likely to be identifiable in fecal samples (Hess et al. 2007). Although dietary studies based on gut contents are less likely to be biased by the absence of soft tissues, species-level prey identification is nonetheless difficult (Hess et al. 2007). The number of prey items is often underestimated because it is based on the number of unique items contained in gut. For example, if two left wings of birds were found, it can be assumed that two individuals were consumed, but if three bird toes were found, it generally cannot be assumed that more than one bird was consumed. Moreover, attempts to estimate overall prey consumption must also account for gut passage rates. It is therefore difficult to extrapolate overall predation rates from dietary studies of cats, and virtually impossible to determine population-level effects on prey in the absence of additional considerations. Rigorously-determined predation rates are nonetheless a necessary component for understanding the effects of cats on wildlife, specifically for modeling predator-prey interactions. It is conceivable that band recoveries in scat or gut contents from individually-marked birds could be used to estimate the proportion of a marked bird population consumed by cats.

### **Disease**

The prevalence of cat-borne diseases such as toxoplasmosis and sarcocystis among hosts or presence of pathogens in the environment may have limited inference for determining population-level effects on wildlife (e.g., Dabritz et al. 2007, Danner et al. 2007, Larkin et al. 2011). Nonetheless, causes of wildlife mortality can often be ascribed to specific pathogens and their sources, but inferences are usually limited to the number of animals found to be killed rather than population-level effects (Migaki et al. 1990, Work et al. 2000, Work et al. 2002, Miller et al. 2002, Honnold et al. 2005). Mortality from diseases is often underestimated because carcasses are not likely to be discovered; therefore the fate of individuals is rarely known, particularly for marine mammals (Dubey et al. 2003). Moreover, the cause of mortality is more likely to be undetermined as the condition of carcasses deteriorate. The best estimates of mortality caused by diseases would likely come from wildlife populations that have been marked and closely monitored for mortality and morbidity, such as endangered species that have been re-released from captivity into the wild (Work et al. 2000, Larkin et al. 2011).

### **Retrospective Assessments of Populations**

Cats are reported to have contributed to a minimum of 14% of all bird, mammal, and reptile extinctions and the decline of at least 8% of critically endangered birds, mammals, and reptiles, most of which have occurred on islands (Medina et al. 2011). However, past vertebrate extinctions were rarely documented in contemporary time; therefore, it is difficult to determine the exact circumstances responsible for these extinctions (Dickman 1996). Quantitative analyses of the role of cats in species' declines would be difficult to parse considering that cats most often arrived coincidentally with a variety

of other anthropogenic agents (e.g., hunting, habitat alteration, diseases, other non-native species introductions; Dickman 1996). Although evidence in each case of extinction is primarily circumstantial, meta-analytical studies could be designed to examine causation if the dates of introduction of cats, dates of extinction, and other confounding anthropogenic factors were definitively known for a large number of cases (Blackburn et al. 2004).

### **Photographic and Videographic Documentation**

Nest cameras provide compelling evidence for depredation, particularly for endangered species, but represent only one stage in the life cycle of prey species, albeit an important and vulnerable stage (Stracy 2011, Ribic et al. 2012, Judge et al. 2013). Although nest surveillance could potentially bias estimates of predation by increasing exposure risk, a meta-analysis of 21 studies of camera effects on nest success found that, on average, the effect of surveillance reduced nest predation rates (Richardson et al. 2009). There are other potentially vulnerable life stages such as the fate of fledglings that must also be taken into account to fully understand the magnitude of effects on prey species. Telemetry may be more appropriate for some other life stages (Balogh et al. 2011), but the size of available telemetry equipment may preclude study of small-bodied prey species and may also affect survival of telemetry subjects.

Animal-borne video cameras (i.e., KittyCams) are potentially capable of providing the least biased estimates of predation rates as well as the extent of scavenging by cats (Loyd et al. 2013), but their effect on cat behavior is unknown. It is possibly that such equipment may subtly handicap cats in their ability to hunt prey, thus resulting in underestimated predation rates. Application of the technique may also be limited in remote landscapes where cats are not habituated to humans.

### **Predation Rates**

Returns to owners of prey items (Lepczyk et al. 2003, van Heezik et al. 2010, Thomas et al. 2012) may be biased by prey killed but not returned, thus potentially underestimating true predation rates. In addition, these studies represent healthy, well-fed cats, for the most part, and may therefore not be applicable to feral or un-owned cats. Continental scale predation rates (Loss et al. 2013) are highly dependent on biases associated with field techniques from which they are extrapolated. Although each study method may contain variable amounts of bias, corrections could be developed by simultaneous cross-applications of dietary studies, returns to owners, and photographic documentation. Corrections would be particularly valuable for determining predation rates in remote areas where cats are difficult to study. Nonetheless, inferences from such studies are limited to the number of prey killed by cats. The ultimate effects of cats on prey populations cannot be determined without accounting for additional processes.

### **Antipredator Responses**

Studies of responses by prey in vigilance, behavior, or physiology to predator presence, simulated or real,

represent protective antipredatory adaptations for avoiding mortality (Caro 2005). Experimental responses to simulated predators have also been shown to affect prey at the population-level by producing fewer offspring (Zanette et al. 2011). Although recruitment may be reduced by loss of eggs, nestlings, or fledglings, adults may avoid predation and thereby improve chances for subsequent breeding opportunities. Such a response is more likely to be compensatory to population change rather than resulting in declines.

### **Predator-Prey Population Modeling**

Modeling to determine the overall effect of predation on prey populations is complex and requires several types of data representing both predators and prey. Such attempts must isolate predation by cats from all other sources of mortality and account for how prey populations respond to the effects of compensatory and additive mortality (Burnham and Anderson 1984). Compensatory mortality is often described as ‘the doomed surplus,’ but is more accurately defined as the “additional risk of death [which] causes a reduction in other forms of mortality so that overall mortality either does not change or is less than it would be if additive” (Ballard et al. 2001). Additive mortality, defined as “additional risk of death [which] does not cause reductions in other forms of mortality, but rather increases overall mortality rate,” and may result in severe long-term population declines if sustained over time, i.e., the number of individuals killed in addition to all sources of compensatory mortality (Ballard et al. 2001).

Individuals that would not have starved, drowned, died of disease, hypothermia, or any other cause other than depredation may contribute to additive mortality. Natural mortality to eggs, nestlings, and fledglings is often high, and therefore more likely to be compensatory. Natural mortality to adults is generally lowest; therefore predation of adults is more likely to have additive effects, particularly for species with low reproductive potential or delayed maturity (Lindsey et al. 2009). Relatively large predators such as cats may consume prey of all life stages whereas small predators such as rodents commonly consume only eggs or chicks (Townsend et al. 2011). Rates of population change are generally more sensitive to changes in adult survival than that of eggs or young (Lavers et al. 2010). Disproportionate mortality of reproductive-age adult females could also become additive, particularly for species with low reproductive potential, long periods of nestling development, or delayed maturity (Lindsey et al. 2009).

Additional data needed to model the effect of cat predation on population change in prey species include estimated survival at each life-history stage (eggs, nestlings, fledglings, juveniles, adults), the sex of individuals killed by cats, the seasonal geographic distribution of prey species relative to cats, and all other significant sources of natural and anthropogenic mortality appropriate to each prey species apart from predation by cats, including: dropout during migration, wind turbine strikes, window strikes, habitat loss, disease, starvation, contaminants, etc. Some long-distance migrant species

may rarely encounter cats on either their breeding ranges in northern boreal forests or neotropical non-breeding ranges. Other species may spend their entire life cycle in exurban areas with high densities of cats.

Another level of complexity which has not been explicitly considered to date is the effect of cats on other mammalian predators. Free-ranging cats are known to kill many species of small mammals which are often predators of birds, primarily at nests (King et al. 1998, Richmond et al. 2011); therefore, free-ranging cats may potentially limit predation by other species of mammals on birds to an unknown extent, although this type of predator-prey interaction has not been studied at a population level.

Although there have been no comprehensive attempts to model the effects of cats on the entire populations of species by accounting for all of the aforementioned complexities, modeling has been used to examine the effects of cats on meta-populations of prey based on predation rates determined by returns to owners (van Heezik et al. 2010). The obvious problem with modeling the effects of predator-prey interactions on prey species is that models need to capture the essential complexity of population processes and must also be driven by unbiased estimates of life-history parameters, few of which are available for prey species. Modeling efforts could become unrealistic if processes are not representative or parameters are biased.

### **Experimental Manipulation of Populations**

The complete removal of cats in an experimental situation such as an island or from other discrete prey population segments provides stronger evidence of causality for the effects of cats on prey populations than other types of studies, and circumvents the uncertainties associated with retrospective analyses or modeling by addressing an essential question: Do wildlife populations recover when depredation by cats has been eliminated? Merits of the experimental approach are: 1) it isolates factor(s) of interest; 2) it controls confounding factors; 3) the response of interest is directly attributable to the manipulation; 4) it is capable of determining and measuring magnitude of cause and effect; and 5) the response of prey populations to the elimination of this specific source of depredation.

Several studies have documented the recovery of birds after the removal of cats, primarily seabirds on islands. Hess and Danner (2013) summarized the effects on 17 species of birds on 10 islands where cats had been removed and a comparative example where 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). An update of these data shows a total of 33 bird populations, 22 of which are unique species, which have increased, recolonized, or recovered following the removal of cats from 12 different islands or parts of islands throughout the world (various authors; Table 1). These data provide the most compelling emerging evidence available that cats have been directly responsible for declines, extirpations, and

**Table 1. Bird populations which have increased, recolonized, or recovered following the removal of free-ranging cats (*Felis catus*) from islands throughout the world.**

Common Name	Scientific Name	Island	Study
Blue Petrel	<i>Halobaena caerula</i>	Marion	Cooper et al. 1995
Great-winged Petrel	<i>Pterodroma macroptera</i>	Marion	Cooper et al. 1995
Common Diving Petrel	<i>Pelecanoides urinatrix</i>	Marion	Nogales et al. 2004
Cassin's Auklet	<i>Ptychoramphus aleuticus</i>	Coronado	Nogales et al. 2004
Black-vented Shearwater	<i>Puffinus opisthomelas</i>	Natividad	Nogales et al. 2005
Sooty Tern	<i>Onychoprion fuscata</i>	Juan de Nova	Peck et al 2008
Great Frigatebird	<i>Fregata minor</i>	Wake	Rauzon et al. 2008
Gray-backed Tern	<i>Onychoprion lunatus</i>	Wake	Rauzon et al. 2008
Wedge-tailed Shearwater	<i>Puffinus pacificus</i>	Wake	Rauzon et al. 2008
Masked Booby	<i>Sula dactylatra</i>	Wake	Rauzon et al. 2008
Brown Booby	<i>Sula leucogaster</i>	Wake	Rauzon et al. 2008
Kermadec Red-crowned Parakeet	<i>Cyanoramphus novaezelandiae cyanurus</i>	Raoul	Ortiz-Catedral et al. 2009
Brown Noddy	<i>Anous stolidus</i>	Ascension	Ratcliffe et al. 2009
Red-billed Tropicbird	<i>Phaethon aethereus</i>	Ascension	Ratcliffe et al. 2009
White-tailed Tropicbird	<i>Phaethon lepturus</i>	Ascension	Ratcliffe et al. 2009
Masked booby	<i>Sula dactylatra</i>	Ascension	Ratcliffe et al. 2009
Brown Booby	<i>Sula leucogaster</i>	Ascension	Ratcliffe et al. 2009
Brown Noddy	<i>Anous stolidus</i>	Howland, Baker	Rauzon et al. 2011
Lesser Frigatebird	<i>Fregata ariel</i>	Howland, Baker	Rauzon et al. 2011
Great Frigatebird	<i>Fregata minor</i>	Howland, Baker	Rauzon et al. 2011
White Tern	<i>Gygis alba</i>	Howland, Baker	Rauzon et al. 2011
Sooty Tern	<i>Onychoprion fuscata</i>	Howland, Baker	Rauzon et al. 2011
Gray-backed Tern	<i>Onychoprion lunatus</i>	Howland, Baker	Rauzon et al. 2011
Red-tailed Tropicbird	<i>Phaethon rubricauda</i>	Howland, Baker	Rauzon et al. 2011
Blue Noddy	<i>Procelsterna cerulea</i>	Howland, Baker	Rauzon et al. 2011
Masked Booby	<i>Sula dactylatra</i>	Howland, Baker	Rauzon et al. 2011
Brown Booby	<i>Sula leucogaster</i>	Howland, Baker	Rauzon et al. 2011
Red-footed Booby	<i>Sula sula</i>	Howland, Baker	Rauzon et al. 2011
Polynesian Storm-petrel	<i>Nesofregatta fuliginosa</i>	Jarvis	Rauzon et al. 2011
Gray-backed Tern	<i>Onychoprion lunatus</i>	Jarvis	Rauzon et al. 2011
Laysan Albatross	<i>Phoebastria immutabilis</i>	O'ahu	Young et al. 2013
Wedge-tailed Shearwater	<i>Puffinus pacificus</i>	O'ahu	Young et al. 2013

extinctions of prey, but also that bird populations are capable of recovery after the removal of cats from islands.

## CONCLUSIONS

The types of evidence which would be most valuable in determining the effects of cats on wildlife populations in order of increasing strength are: 1) estimation of unbiased rates of predation by cats and mortality caused by cat-borne diseases; 2) meta-analytical approaches to retrospective vertebrate extinctions caused by cats; 3) comprehensive modeling to determine the effects of cats on prey populations; and 4) the response of prey populations after the experimental removal of cats. Rigorously-designed experimental removal of cats, where feasible, would provide the strongest causal evidence for assessing effects on wildlife populations. The most compelling available evidence that cats have been directly responsible for declines, extirpations, and extinctions of prey is in the emerging documentation that many extirpated seabird species have recovered or recolonized islands or parts of islands where cats have been removed (Cooper et al. 1995, Nogales et al. 2004, Peck et al. 2008, Rauzon et al. 2008, Ratcliffe et al. 2009, Rauzon et al. 2011, Young et al. 2013). In many cases, natural barriers may allow such experimental approaches to address the effects of cats on resident wildlife even in continental situations. In other cases, however, experimental approaches may not be possible because of the geographic distribution of cats, migratory behavior of their prey, lack of discrete population units, or other logistical limitations.

In these cases, modeling would provide the next-best evidence. Modeling would need to be based on unbiased predation rates and life-history traits of prey to reliably determine the potential for cats to reduce prey population. Although dietary studies of cats, mortality attributed to pathogens, and photographic or videographic documentation of depredation by cats may all provide useful data for modeling the population dynamics of prey, these types of observational studies alone are not sufficient to determine if cats are capable of causing population declines in prey.

The delivery of reliable evidence might identify cases in which the reduction of free-ranging cat abundance could mitigate or reverse declines in wildlife populations. It may also determine if there is a point at which further reduction of free-ranging cat abundance might not result in further mitigation or reversal in wildlife population declines because of greater mortality due to increased abundance and predation by other mammalian species. Such an outcome might indicate that reducing sources of mortality other than predation may be more effective in mitigating or reversing bird population declines. Modeling interactive effects of additive and compensatory mammalian predation on bird populations could assist in resolving disagreements about negative effects of free-ranging cats on bird populations and suggest instances where alternative approaches may be more effective in mitigating or reversing large landscape-scale bird population declines.

## ACKNOWLEDGEMENTS

This work was funded by the Natural Resources Preservation Program, the Invasive Species Program and the Pacific Island Ecosystems Research Center of the U.S. Geological Survey and the National Park Service. We thank reviewers for helpful comments. Any use of product or firm names is for descriptive purposes and does not imply endorsement by the U.S. Government.

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