The Outdoor Cat:

Science and Policy from a Global Perspective

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Contents

Introduction

This draft white paper has been prepared by the staff of The Humane Society of United States (HSUS) to provide a synopsis of relevant published work aimed at the controversial and complex issue of how the presence of cats outdoors affects wildlife. It was originally intended as background and informational purposes for attendees at the conference, "The Outdoor Cat: Science and Policy from a Global Perspective," in Los Angeles, December 3rd and 4th 2012. This conference was held under the auspices of the Humane Society Institute for Science and Policy (HSISP), Found Animals and the Humane Society Veterinary Medical Association (HSVMA), to engage speakers with wide understanding and many decades of experience with cat issues in the genuine challenges we face in seeking to resolve conflicts involving cats, wildlife and people. It remains incomplete and we offer an apology for any omission or misunderstanding of the information so diligently studied and collected by others. In advancing from its current form we would hope that any necessary corrections would be pointed out so that we might make them right.

We have tried avoiding here, to the extent possible, interpreting the collected information or expressing our organizational or professional opinions regarding these data. That can come later. Our interest in preparing this report, and in holding this conference, was to bring us closer to a reasoned consensus on where and how advocates for wildlife and advocates for cats (as well as advocates for both) can work together to achieve real and tangible benefits. We do not feel this can be achieved in an environment in which polemics dominate. We hold that evidence-based analysis is critical to addressing conflicts with cats and offer this contribution toward that end in the hope that others will augment and improve what we have done here.

Origins and domestication

Cats in the genus *Felis* are currently represented by four, and perhaps five, distinct but interfertile subspecies widely distributed throughout the Old World (Driscoll et al. 2007). Contemporary scholarship shows our domestic cat to have directly descended through multiple matrilines from *Felis silvestris lybica*, the Near East subspecies of the *silvestris* group (Driscoll et al. 2009a). Cats today are variously referred to as *Felis silvestris catus* (e.g. Driscoll et al. 2007), *Felis catus* (e.g. Harris et al. 1995) or, less commonly, *Felis domesticus* (e.g. Duby and Jones 2008). Cats are first associated with humans in a Neolithic burial from Cyprus dated to about 9500 BP (Vigne et al. 2004). They are conspicuous in graves from Predynastic (c. 6000 BP) Egypt (Baldwin 1975, Linseele et al. 2007), but not convincingly demonstrated as domesticates until around 3600 BP, when they appear on Egyptian paintings that show them integrated into human households (Driscoll et al. 2007, 2009b). Egyptians were mummifying cats by the Late Period (c. 2600 BP), as they were many other animals, but genetic evidence differentiating domestic from wild mitotypes suggests domestication was occurring between two to seven thousand years before the practice of mummification began (Kurushima et al. 2012). Genetic evidence further supports a "single protracted domestication episode" (Driscoll et al. 2009a: 9976) from *F. s. lybica* over a broad Near Eastern front, from which cats were most likely moved by human agency into Europe and parts of Asia (Daniels et al. 1998).

Baldwin (1975) presents a sequential model for cat domestication in Egypt that begins with a period of casual contact with early agricultural communities, followed by a period of greater intimacy that acquires important religious components in the worship of two major deities, the fertility goddess *Bast* and the solar god *Re* (later *Amon*). Lastly, cats were brought into a fully domestic condition and widely kept as a household animal. While the Egyptians initially imposed severe restrictions on

exporting cats these were relaxed by Roman times and followed by what Faure and Kitchener (2009) describe as a period of "spectacular globalization" of this one subspecies, whose ready tractability they suggest may have obviated the need for humans to spend any effort in domesticating other forms.

Baldwin (1975) uses "symbiont" as well as "commensal" in describing human-cat relationships from earliest times, both terms characterizing animals who demonstrate a faculty for living in close proximity to humans while retaining largely wild lifestyles. This way of conceptualizing cats is supported elsewhere (e.g. Robinson 1980, Driscoll et al. 2007, Faure and Kitchener 2009). Bradshaw et al. (1999) argue that the obligate, special nutritional requirements cats need could not be provided in human-supplied diets until quite recently, this providing an evolutionary rationale for their having retained hunting skills and motivation. Serpell (2000) takes this further by arguing that cats may have only been domesticated within the last 150 years, although he feels it is probably more accurate to visualize them as drifting in and out of states of domestication and ferality depending on cultural and ecological conditions.

Global Spread

While overland transport would account for cats spreading into Europe and many parts of Asia, it is apparent they also were moved around by sea from early times, as their presence in Cyprus by 9500 BP obviously demonstrates (Vigne et al. 2004). Blaisdell (1993) cites a mandate issued by Edward II (1327-1377) that every English merchant ship have a cat on board as an argument for their being distributed to even remote parts of the globe in the early days of European expansion. Sailing vessels, of course, had to be the principal means of diffusion of cats into the Pacific region, although the records documenting when they arrived are meager (Baldwin 1979). Baldwin (1980) suggested that cats were introduced into Australia from both European sailing vessels as well as into northwestern Australia by local transport of

cats of Indonesian origin, but Abbott (2002) argues that there is no evidence for the presence of cats before Europeans first arrived, with 1798 suggested as the first documented date of entry (Dartnall 1978).

Although domestic cats arrived in North America within historic times, a variety of small felids are known from the southern United States from the Pleistocene until quite recently (Gillette 1976), along with the still extant bobcat (*Lynx rufus*). Domestic cats were introduced into the New World by the time of the second voyage (1493-1495) of Columbus (Baldwin 1979). Mann (2011) notes cats as among the starvation foods described by George Percy in the 1609-1610 struggles of the Jamestown colony, and Rountree (1990) cites a request from the Indian chief Powhatan in 1614 for a cat as part of a truce with the English settlers. Undoubtedly, like elsewhere, cats in the Americas were only loosely attached to human settlements and largely left to fend for themselves. Supplemental feeding and/or confinement of cats was probably rare until the early 20th century, and even then would have conflicted with the utilitarian purpose of rodent control for which cats were commonly valued (Grier 2006). Interestingly, cats do not seem to have played a part in the establishment of the urban rat-catching profession that moved from Europe to the Americas in the 1840's, that role being occupied by the domestic ferret (Snetsinger 1983).

Cats and Wildlife

Although the threat cats pose to wildlife (in particular, birds) was recognized in antiquity (Engels 1999) their value in controlling rodents (Blaisdell 1993) apparently outweighed any such concerns about their predation until quite recently. Not until the mid-19th century were cats in the Americas being widely identified as threats to song and game birds. In 1875, for example, the editor of the children's publication *St. Nicolas Magazine* was advocating the feeding of cats until they became too lazy to hunt

birds, as well as the shooting of "tramp" (i.e. stray) cats (Grier 2006), while by 1908 Elizabeth Reed was raising an alarm in *Bird-Lore* that an "army" of cats was taking upwards of three quarters of all songbirds hatched. Such concerns were amplified with the rise of the twentieth century conservation movement, when naturalists such as William Hornaday (1913) began to focus more strongly on the role played by cats as predators on favored species -- particularly song and game birds.

Edward Howe Forbush (1905a,b, 1907, 1908, 1913, 1916), in his capacity as the Ornithologist for the Massachusetts State Board of Agriculture, was an especially outspoken voice. Although cats do not appear as a concern in his earliest writings about birds (Forbush 1895), he soon was identifying them as significant threats (Forbush 1905a,b), eventually concluding in The Domestic Cat: Bird Killer, Mouser, and Destroyer of Wildlife that the "inutility" of cats had reached an "acute stage," (1916: 3). Speaking for sportsmen, the editor of *Forest and Stream* concurred that cats were a "great and growing evil..." (1916: 904), sentiments embodied earlier in editorial comments published in the ornithological journal *The Auk* (J. A. A. 1904, 1905). Although Forbush claimed that his extensive review of the matter was not intended to demonize cats, many cat advocates thought otherwise and let him know about it. What could have been a more intense clash of interests apparently did not develop further or sustain itself, perhaps becoming lost in the general lack of public interest in environmental issues during the decades of depression, war and recovery (Hannigan 1995). While research into the role cats played as predators continued (e.g. Errington 1936, McMurry & Sperry 1941, Jackson 1951, Elton 1953, Parmalee 1953, Eberhard 1954, Toner 1956,) until the environmental awareness movement of the 1960s, it seemed to do little to stir further controversy.

A publication on cat predation in an English village changed that. Churcher and Lawton (1987) documented the prey brought home by 70 owned cats whose activities they followed over the course of a year. These cats retrieved an average of 14 prey items each from a wide range of species dominated

by wood mice (*Apodemus sylvaticus*) and House sparrows (*Passer domesticus*). May (1988) extrapolated from this finding to estimate that the approximate 6 million cats in Britain were taking in somewhere near 100 million birds and small mammals as prey each year, something he characterized as "feline delinquency.". Proulx (1988) enlarged the dialogue by speculating on the role feral cats might play in disseminating disease to wildlife, owned pets and humans, as well as in causing property damage. Fitzgerald (1990) and Jarvis (1990) joined the debate by raising the concern that prey populations (mice and rats especially) might increase dramatically if cat numbers were depressed, presaging an ongoing debate. Together, these exchanges launched many of the on-going points of discussion (and often conflict) over the issue of cats and wildlife.

In the United States, the debate became heated following a series of publications that focused on farm cats in Wisconsin (Coleman and Temple 1989, 1993, 1994a,b, 1995). These posed the general argument that "…introduced predators such as domestic cats have severely depleted songbird and small mammal populations and have been implicated in local extirpations and extinctions" (1993: 381), raising clearly the issue of cats as potential exterminators of other species. Later, Coleman et al. (1997) concluded that cat predation was a national "conservation dilemma" that called for "an effort to limit in a humane manner the adverse effects free-ranging cats can have on wildlife" (1997: 3). Whether this was warranted and, if so, could actually be accomplished in a humane manner, became the focus of sometimes heated exchanges (e.g. Goldstein et al. 2003, Hatley 2003). Despite not being intended as definitive projections, the Coleman and Temple estimates of wildlife impacts came to be used widely as support of the argument that free-ranging cats killed millions of wild animals, perhaps as many as a billion, annually (e.g. Jessup 2004).

Attention also focused on cats in the 1970's in connection with the protection of threatened and endangered species. Cats had been widely introduced in the past onto many islands where rare and

sensitive species, many of them birds, were especially vulnerable to predation (van Aarde 1978, Apps 1983, Fitzgerald and Veitch 1985). Studies documenting these impacts led to eradication programs (Medina et al. 2011). Such programs were fraught with difficulties, not only in the logistical challenges posed, but by the discovery that other introduced predators, such as rats, and competitors, such as rabbits, responded to cat removal in ways that themselves increased pressure on the native species of concern (Courchamp et al. 1991, 2003). There were also emerging debates about the ethics of eradication and the moral justification of techniques such as poisoning and the introduction of disease (Cowan and Warburton 2011).

Despite their often bitter arguments over how to manage cats outdoors, both cat and wildlife advocates share a common goal of wanting to see those reduced. Responsibility for cat "overpopulation" has long been the provenance of local animal control agencies and humane society organizations, deriving from their traditional role in the control and management of "strays" (Aronsen 2010). Until quite recently, dogs may have disproportionately consumed the attention of the humane movement, but issues involving cats seem almost certainly bound to be a major future focus. By 1980, the issue of managing free-roaming cats had come to the forefront with a national conference in Britain organized by the Universities Federation for Animal Welfare (UFAW 1981). At this conference the concept of Trap-Neuter-Return (TNR) was widely discussed as a possible alternative to the traditional practice of trapping and euthanasia. A number of claims were made in the first publications and discussions of TNR that would later be called into question, but the concept had an immediate appeal to many cat advocates and by the early 1990's had gained popularity in Europe as well as the United States.

TNR, however, came with controversy of its own, largely because it removes and then returns cats to the outdoors --where they can, and do, still act as predators. TNR is criticized as ineffective and

inappropriate (e.g. Hawkins et al. 1999, Clarke and Pacin 2002, Castillo and Clarke 2003, American Bird Conservancy 2004, Hildreth et al. 2010) and claims made in TNR's support have been counter-argued (Longcore et al. 2009). Calls for conservation biologists to be more active in raising public awareness about the impacts of outdoor cats have been growing (e.g. Lepczyk et al. 2010) and estimates of the damage done by cats outdoors revised upward to suggest that significant numbers of wild animals are threatened (Dauphine and Cooper 2009, 2011, Hildreth et al. 2010, Loss et al. 2012). Where Banks (1979) estimated 196 million bird deaths from all anthropogenic causes, cats included, cats alone are now estimated to kill as many as a billion birds (Dauphine & Cooper 2009), with Loss et al. (2012) putting the number most recently at between 1.14 and 4.2 billion. Added to all of the other anthropogenic causes of bird mortality, this forces a critical reevaluation of the issue of cats killing birds, what it means for bird conservation nationally and globally, and what management strategies are needed or even possible in effectively addressing what some believe is a major national conservation dilemma.

Terms Applied to Cats

Of the more than thirty terms used in literature to describe cats, none is universally accepted (Levy & Crawford 2004), but some, such as "feral," "pet," and "house" are broadly understood through wide and repeated use. In addition to what may be called definitional terms, cats are also grouped with other animals under terms such as "nonnative," "exotic," and "invasive" which identify them in specific contexts (Gorman and Levy 2004). Adding to problems from having so many terms in use are those that come from blurring where closely related terms such as "free-roaming" and "free-ranging" or "feral" and "free-living" cat are used. On the one hand, such terminological richness represents the complexity of the lives of cats and the many different contexts in which they are found; on the other, it shows an as

yet unfocused and undisciplined scholarship in which basic agreement about fundamentals has yet to be achieved. It is important that movement toward a better consensus and a setting of preferences takes place, not only to clarify our thinking about cats, but to better define them legally.

Patronek (1998) focused on cats as both biological as well as sociological constructs to identify two principal dimensions relevant to defining cats: where they spend their time and what their ownership status is. He then diagrammed cats along a continuum that moves across lines of ownership and ferality, emphasizing the virtually unlimited statuses they can occupy. Owned, house (e.g. Barratt 1997a), indoor (e.g. Patronek 1998) and pet cats (e.g. Bradshaw et al. 1999, Baker et al. 2010) all are associated with owners, whereas unowned, feral (e.g. Jongman and Karlen 1996, Schmidt et al. 2007a), and pseudo-wild (Bradshaw et al. 1999) cats live in the absence of human care, although they may use human-derived resources such as refuse. Semi-owned (e.g. Todd 1977, Toukhsaki et al. 2007), street (e.g. Gunter and Terkel 2002), stray (e.g. American Bird Conservancy 2004), colony (e.g. Crowell-Davis et al. 2004) and neighborhood (e.g. Patronek 1998) cats all fall into a gray area where some human care and resources are usually provided them, but otherwise they are left on their own. Free-roaming e.g. Mahlow and Slater 2004), inside-outside hunting cats (Kays and DeWan 2004) and roaming (ICAMC 2011) are terms used for cats present in the outdoors and to one extent or another capable of being predators, transmitting disease or causing other conflicts for humans. The terms “house” and “domestic” (e.g. Barratt 1997a) cat are broadly descriptive of all cats irrespective of their lifestyles, identifying the animal itself rather than its condition of ownership or behavior and activity, and distinguishing, for some at least, this group of cats from truly “wild” (e.g. Jongman and Karlen 1996, Bradshow et al. 1999) cats who are genetically and taxonomically distinctive animals. Similarly, the term “pet” (and, more specifically “pedigree,” e.g. Bradshaw et al. 1999) cat would be contrasted with “feral,” which should describe cats who are have minimal or no dependence on humans for any of their needs (Baker et al. 2010). The

term “feral,” however, is itself subject to various definitions and interpretations (e.g. Tabor 1981) and needs to be better clarified. Both “owned” and “feral” cats may be distinguished from what Toukhsati et al. (2007) term “semi-owned” cats, who may be fed but not housed or otherwise cared for by individuals who do not consider themselves “owners.” Other terms describe this condition, such as semi-dependent (Macdonald 1981) and semi-feral (Schmidt et al 2007a, Calver et al. 2011, Baker et al. 2010), allocating the concept a middle ground between full and no lines of responsibility or care.

For purposes of better defining cats operationally, The International Companion Animal Management Coalition (ICAMC) suggests that the best definitions are those that are practical and recognize three categories relative to human-cat relationships: owned, semi-owned and unowned (ICAMC 2011). This seems to strike the needed definitional distinctions required in for management and public policy concerning cats and meet the need for focus on ownership status, lifestyle and degree of socialization found in cats everywhere (Levy and Crawford 2004).

Attitudes and Ownership

How people construct feelings about cats—their attitudes, beliefs and values—helps determine how cats are treated and cared for and how policies concerning their management are supported or rejected. Ownership plays an important role in whether cats are neutered or allowed to roam outdoors, key factors in addressing any conflicts cats may cause. People’s feelings about cats vary considerably as a function of gender, age and socio-economic status and in general are more variable than attitudes towards dogs. Kellert & Berry (1980) found that 17 percent of Americans showed dislike of cats, as opposed to fewer than 3% who felt dislike for dogs. Lord (2008), in a survey of Ohio residents twenty years later, also found 17 percent of those polled not liking cats, with another 21 percent saying they did not care about them. Sixty-two percent of those responding, however, said they liked or loved cats.

Lockwood (2005) enumerated some of the reasons for the dislike of cats, including negative feelings about their promiscuous sexuality, aggressiveness toward mates, social independence, resistance to training, predatory behavior (primarily the perception it is selfish and unnecessarily cruel), nocturnal habits, and annoying vocalizations. Smith (1999) conducted content analysis on the symbolic status of feral cats in Australia and concluded the dingo (the Australian wild dog) represented masculinization and the good for most Australians, while the cat represented feminization and an evil. Cats, he felt, had suffered a "historical inversion" from being praised for control of rabbits to being vilified for predation on native marsupials, bringing home the point that environmental values are intrinsically cultural as well as highly malleable. Perrine and Osbourne (1998) looked at personality differences between people who labeled themselves as either a cat or dog person and found that females were more likely to be cat people and that different personality attributes were associated with whether an individual was considered either a cat or a dog person.

Cats are typically perceived by people as having independent or wild traits that no longer persist in dogs (Clancy et al. 2003), underpinning the public perception (in the United States at least) that it is more humane for unowned cats to be left outdoors cats than it is to euthanize them (Chu & Anderson 2007). In New Zealand differences in attitudes towards cat control vary by ownership status and profession, with support for lethal control more acceptable for feral cats than for strays and welfare considerations overall declining from highest for companion to lowest for feral animals (Farnworth et al. 2011). In Australia, Grayson et al. (2002) examined attitudes with respect to legislative options and found significant age and gender effects, with older people more likely to support restrictive legislation such as licensing or sterilization. Finkler and Terkel (2012) found considerable socio-economic differences in attitudes and behavior towards cats in Jerusalem, with influences related to age, gender education and income level all playing a part in how cats were perceived and treated. In Italy, Natoli et

al. (1999) found that the feelings of cat lovers toward sterilization had changed over a twenty-year period from not being accepted to being almost universally supported.

Many cat owners believe their pets are only happy and satisfied when they have access to the outdoors, a belief that seems to have a strong cultural component. In two areas of southern Chile surveyed by Silva-Rodriguez and Sieving (2011) 100 percent of all cats attached to households were allowed to roam free, as are an estimated 97 percent of owned British cats (Sims et al. 2008). Toukhsati et al. (2012) surveyed cat owners in Victoria, Australia, and found while 80 percent confined their cats at night only 42 percent did so by day. Still, cat owners were aware of the threat to wildlife cats posed, which together with a concern for keeping cats from being injured were principal factors determining confinement. In Jerusalem where more than 50 percent of cat owners have adopted a stray from the streets, only 51 percent of owned cats are allowed outside, with 46 percent being kept indoors only (Finkler and Terkel 2012). Longitudinal data In the United States kept by the American Pet Products Association shows a trend for cats to be kept increasingly indoors, with 52 percent indoors only in 2004, 63 percent in 2006 (a significant increase from 2004) and 64 percent in 2008 and 2010 respectively (APPA 2011). In 2010 only one cat in ten was kept outside by day and 70 percent of cats were kept indoors at night, although in rural areas the number of cats outside is undoubtedly somewhat higher (e.g. Lord 2008). While information on activity when outside is sparse, Kays and DeWan (2004), in a study of suburban cats in New York, found that their 11 subjects spent an average of 8.35 hours/day outside, while Dabritz et al. (2006) found cats averaging 12.8 hours/day outside in three California communities.

Neutering is a second major concern with respect to cat population growth, abandonment and other issues. Fagen (1978a) estimated about 50 percent neutering in two Midwestern cities in the 1970's, while Levy et al. (2003b) estimated this at 90 percent in their survey of Alachua County, Florida.

Chu et al. (2009) estimated that 80 percent of owned cats nationally were being neutered, but the overall rate of neutering among rural residents is likely to be significantly lower (e.g. Lord 2008). Internationally, high neutering rates are reported by Heidenburger (1997) for Germany and Britain, where Bradshaw et al. (1999) report a 97 percent neutering rate for their study area in Southampton. Socio-economic status appears to an important determinant of whether cats are neutered or not (e.g. Chu et al. 2009, Finkler and Terkel 2012).

People's attitudes towards the practice of Trap-Neuter-Return (TNR) in the United States have been a focus of recent attention. Loyd and Miller (2010a,b) found 52 percent of households surveyed in Illinois supportive of lethal control of feral cats while 27 percent supported TNR. Their sample, consisting of 76 percent male respondents, also found higher support for control (67%) among those who had previously experienced problems with feral cats as well as higher rural (71%) support for lethal control than urban (39%). Ash & Adams (2003) questioned employees of a major university to assess attitudes about cat impacts on wildlife on campus and found their sample populations about equally split on whether cat or wildlife welfare was more important. The majority of those queried, however, were apathetic in their attitudes toward the issue of control. Another significant concern for conservationists is the belief that the public holds the protection of wildlife as less important than the welfare of cats (e.g. Grayson et al. 2002). This is especially the case when stakeholder groups supporting cats and birds are compared, as Peterson et al. (2012) did in looking at the differences between cat colony caregivers (CCC's) and bird conservation professionals (BCP's). In relation to what they call "well-founded concerns" of the conservation community over cat colony advocacy, Peterson et al. (2012) found opinions were polarized between the two groups, with opinions differing as a function of age, gender and education as females and older respondents were less likely to support treating cats as pests and females less likely than males to support euthanasia.

The dynamics of cat "semi-ownership" (Todd 1977, Levy et al. 2003a, Toukhsati et al. 2007) will be highly relevant to any eventual control of outdoor cat numbers, as both the attitudes as well as behavior of those engaged in this practice may be highly consequential in determining how many cats are free-roaming and reproductively active. Levy et al. (2003b) reported from a survey in Alachua County, Florida that 12 percent of households fed an average of 3.6 cats that they did not own, and that while 90 percent of owned cats were neutered, only 11 percent of feeders had attempted to do so with cats they did not own. Comparable data on feeding from other surveys shows 10 percent of households in Santa Clara County, California feeding an average of 3.4 cats (Johnson et al. 1994, cited in Levy et al. 2003a), 9% feeding an average of 2.6 cats in San Diego County (Johnson & Lewellen 1995), and 8% feeding average of 3.7 cats in Massachusetts (Manning and Rowan 1992). Dabritz et al. (2006) estimated 8 percent of homeowners fed non-owned cats in three California communities, while Lord (2008) found 26 percent of Ohioans she surveyed were feeding free-roaming cats.

There is some apparent relationship to fundamental variables such as ownership, age, gender and socio-economic status when it comes to people's feelings about cats and how those feelings influence their behavior. The relevant behaviors directed towards cats that might contribute to conflicts or reduce conflicts are neutering, or not neutering, and supplemental feeding of unowned cats in both larger colonies or smaller feeding groups at individual homes and yards. Attention to these variables in management programs, policy formulations or educational outreach and a better understanding of how they factor into resolving conflicts with cats is warranted.

Numbers

Cat populations have been estimated at everything from global to neighborhood scales and through a variety of censusing techniques that vary widely in accuracy and comparability. Some, such as

observational counts (Haspel and Calhoon 1989), mark-recapture (e.g. Konecny 1987a), mark-resight (Schmidt et al. 2007a), distance sampling (Schmidt et al. 2007a), track and spotlight counts (Forsyth et al. 2005) and camera trapping (Heussner et al. 1978, Bengsen et al. 2011) employ techniques common in wildlife field studies, while others such as telephone surveys (e.g. Chu et al. 2009) or summaries from marketing data (e.g. Turner and Bateson 2000) come about because of human ownership of cats. Data are collected for heuristic, scientific and commercial purposes, and vary enough that cross-study comparisons can be challenging. There is a need for critical scrutiny of the ways by which all companion animals including cats are enumerated (Patronek and Rowan 1995), but to date no such review and analysis has been conducted. For free-roaming cats, either feral or owned, the absence of accurate estimates of their numbers impedes management and funding decisions (Finkler and Terkel 2012).

Cat numbers have been estimated across different geographic scales (e.g. global to local), between different types of sites (e.g. farms and cities), across varying habitats (e.g. arid vs. tropical) and as functions of cats influenced or not by humans (e.g. supplemented vs. unfed). Estimates such as the number of feral cats in the United States seem at best to be generalizations or "educated guesses" (e.g. Mahlow and Slater 1996, Lockwood 2005). Once published, however, such numbers may assume lives of their own and acquire unearned credibility simply by being repeated and republished. Statistically reliable estimates accompanied by measures of uncertainty are often lacking. Like so many other things relating to cats, considerable caution should be exercised when speaking about their numbers.

Globally, numbers of cats are a challenge to enumerate, with only owned cats estimated reliably. Turner and Bateson (2000) summarized statistics from the pet food trade to estimate the global population of owned, pet cats at about 142 million in the mid-1990's, while De Silva and Turchini (2008) used similar sources to derive an estimate of 236 million about a decade later. Legay's 1986 (cited in Jarvis 1990) estimate was for more than 400 million owned and unowned cats occurring

worldwide, while Baker et al. (2010) put the number at closer to 600 million. Others (e.g. Jarvis 1990, Levy et al. 2003a, Rowan 2008) speak more conservatively of global populations as simply being in the hundreds of millions while yet others (e.g. Driscoll et al. 2009) suggest the figure for owned as well as unowned is closer to one billion.

Among nations, Australia may be unique in having a population of owned cats in apparent decline. Kendall & Ley (2006) report a drop from 3.2 million in 1988 to 2.4 million in 2006, a finding some had attributed to a high rate of neutering, but which they concluded was more attributable to changing human demographics, in particular the increase in single-person households. In other countries the population of owned cats is likely to be rising, although this trend has not been directly validated. Turner & Bateson (2000) estimated that there were approximately 76 million cats in Europe in the mid-1990's (42.73 million in Western Europe, 32.73 million in Eastern Europe and 1.37 million in other European countries), while De Silva and Turchini (2008) gave an estimate of 63+ million for countries in the European Union. Similarly, Turner and Bateson (2000) estimated 7.24 million cats in Japan at the turn of the millennium, while De Silva and Turchini (2008) gave an estimate of more than 9.5 million less than a decade later. Harris et al. (1995) relate a commonly circulated estimate of 6 million cats in Britain in 1980, of which 1.2 million were said to be feral (Tabor 1981), while they put the number at 7.6 million, with 813,000 feral cats, in 1995. Woods et al. (2003) gave an estimate of 9 million cats in Britain in 2003. By contrast, the number of owned cats in Australia is estimated at around 3 million, while feral cats are estimated at between 10-20 million (Jongman and Karland 1996, Dickman and Denny 2010).

Owned cat numbers in the United States are reported from a variety of sources over a long enough period of time to suggest steady population growth. Several industry and trade organizations conduct surveys of cat owners, including American Pet Products Association (APPA), the American

Veterinary Medical Association (AVMA) and the American Animal Hospital Association (AAHA). The APPA is a frequently cited source (e.g. Lord 2008, Dauphine & Cooper 2009, Hildreth et al. 2010) that publishes estimates biannually, while the AVMA revises its data only once every five years. Turner and Bateson (2000) in their wide-ranging global estimation of cat numbers put the U.S. owned cat population in the mid-1990's at about 56 million animals. Clancy et al. (2003) cite AVMA data for 2002 that estimated approximately 69 million cats living in 32 percent of households. De Silva and Turchini (2008) report a 2006 estimate of 82.2 million from their survey of Euromonitor International data. The AVMA (2007) survey estimated 81.7 million cats, again in 32 percent of American households, while the APPA (2011) gave an estimate of 86.4 million cats in the United States living in 38.9 million households in 2010. Chu et al.'s (2009) report of a random-digit-dial survey of 1205 adults estimated a population of 82.4 million owned cats living in 36.8 million U.S. households. In recent publications a range of 60 to 90 million owned cats in the U.S. is generally given (e.g. Mahlow & Slater 1996, Luoma 1997, Clarke & Pacin 2002, Slater 2002, Dabritz et al. 2006, Lord 2008, Dauphine & Cooper 2009, Baker et al. 2010, Hildreth et al. 2010). On the cautionary side of such estimates Patronek and Rowan (1995) note inconsistencies between sampling approaches that as yet remain to be resolved, and Rowan (2008) cautioned that estimates of the total domestic cat population may be off by as much as 20 percent .

The number of owned cats appears to be consistent based on several survey procedures that appear to be reasonably reliable. Estimated numbers of unowned cats are also reported frequently, but less confidently. This is understandable, since the numbers of cats living outside and surviving must vary greatly from one part of the country to another, with regions having benign climates allowing for higher rates of survival than others. A figure of 60-100 million unowned cats in the U.S. is widely attributable to a number of sources (e.g. Clarke and Pacin 2002, Jessup 2004, ABC 2004, Loyd and Miller 2010, Lebbin et al. 2010, Hildreth et al. 2010, ABC 2012), while more conservative estimates of between 50-75

million have been published elsewhere (Mahlow and Slater 1996, Levy et al. 2003b, Levy and Crawford 2004). How many cats actually are present outdoors is yet another statistic that remains to be better assessed. Dauphine and Cooper (2009) speculate that the total number of cats in the U.S. has tripled over the last forty years for an estimated population of 144-188 million, of which 60-100 million are feral or stray. This leads to an outdoor cat population of between 117 and 157 million cats.

Estimating the total numbers of cat is of interest and potential relevance, but when addressing the conflicts that exist between people, cats and wildlife aggregate numbers may not be as important as relative figures, or cat densities. George and George (1978) conducted an early analysis of predation and cat density, projecting predatory activity in "village" and "rural" populations of different densities as a function of one of three categories of hunting activity. Their study raised the issue of variability in cat densities, something which the rapidly accumulating body of knowledge that followed confirmed. In fact, Liberg and Sandell's (1988) review of the literature showed a mean cat density across studies of 220/km² with a range of from 3/km² to 2300/km². Where Calhoon and Haspell (1989) observed cat densities ranging between 2-5 cats/km² in their Brooklyn, Natoli et al. (1999) report an estimated 14.444 cats km² for a site in Rome, the highest yet recorded. Elsewhere, Page et al. (1992) studied cats at a dockyard site where densities for adults were estimated to be 10-15 km² while Coleman and Temple (1993) estimated statewide density for free-ranging rural Wisconsin cats as 44/km² and Warner (1985) estimated density in Illinois for the rural cat population as 6.3/km². The mean density of cats reported for urban areas of Bristol, England by Baker et al. (2005) was 229 cats/km² while their later survey estimated density at 348/km² Baker et al. (2008).

Variability may be the greatest consistency when it comes to putting numbers to cat populations. But there is no doubt that cats can reach extremely high densities under certain circumstances, and should be recognized along with dogs, as Baker et al. (2010) point out, as the most

numerous and widespread of all urban carnivores. Beyond their sheer numbers lie issues relative to their prowess as predators, the prey they select, the ecological consequences of their predation and the question of when and how the risk of predation to certain valued species can be reduced or eliminated.

Biology and Ecology

The study of cat ecology and behavior draws from both traditional wildlife investigational techniques as well as sociological information involving ownership, caregiving, management and other activities that represent the human dimension of cat issues. With respect to their naturalistic behavior, cats are not as well studied as many "real" wild animals, undoubtedly for the reason that until recently most wildlife scientists just did not relate to them as such. But field research has perforce become a focus, since at least baseline information on natural history is necessary if cat populations are to be managed (Bengsen et al. 2012). Still, there remain many aspects of cat behavior and ecology that are less well known than they should be, particularly when considerable variability has already been documented in such areas as sociality, spatial organization, movements, activity patterns and feeding habits (Liberg et al. 2000, Fitzgerald 1998). The study of cats who are semi-owned or living in colonies particularly could be augmented. An era of controlled design and experimental research on free-ranging cats lies ahead, as there is a commanding need for data that can be used to guide management as an ongoing process.

Activity patterns

Although the ethologist Paul Leyhausen (1965, 1979) began his seminal research on cat behavior and sociality in the 1950s, field research (outside of food habits studies) on cats really only started on a broad front in the 1970's, with studies by Laundre (1977), Macdonald (1981), Dards (1978,1981,1983), and others taking a first look at how cats under different environmental conditions used space and interacted with one another and their environment. Apps (1986) conducted early research using radio

telemetry on Dassen Island, South Africa, one of a number of small islands globally that had become a concern for conservationists because of threats to its endemic fauna from cats and other nonnative species (Apps 1983). He found five adult males and three adult females using home ranges that varied from 11-63 ha. By way of contrast, Bengsen et al. (2012) reported median home ranges of more than 500 ha for 13 cats on Kangaroo Island, South Australia, Goltz et al. (2008) female home ranges of 772 ha and males 1418 ha in the dry subalpine woodland of Mauna Kea, Hawaii and Moseby et al. (2009) home ranges varying from 50 to 13,200 ha in an arid region of South Australia. Other studies looking across a variety of habitats (Genovesi et al. 1995, Brio et al. 2004, Harper 2004, Panaman 1981, Schmidt et al. 2007a) have reported large home ranges in feral cats as well.

Small home ranges have also been frequently documented. In a study of free-roaming cats in Brooklyn, Haspell and Calhoon (1989) reported home ranges in males averaging 2.6 ha and females 1.7 ha, while Mirmovitch (1995) reported home ranges no larger than a third of a hectare for some of the female cats he studied in Jerusalem, while Page et al. (1992) found home ranges averaging between 10 and 15 ha for cats at Avonmouth docks in Bristol. In an early study Liberg (1980) had found that female cats associated with households in rural Sweden had home ranges of between 30 and 40 ha and rarely moved more than 600 m away from the houses to which they were attached. Later, he found that feral females had home ranges approximately four times larger than these household females, which he suggested was needed to meet their basic nutritional requirements (Liberg 1984b).

Meeks (2003) described cats from his study area in an Australian National Park, as belonging to one of two categories – wandering and sedentary – with substantially larger areas used by the cats who wandered. Cats are indeed capable of moving over considerable distances, some apparently related to dispersal, a widespread phenomenon in mammals associated with maturing young leaving their natal

area to seek mates and resources of their own (Caughley and Sinclair 1994). Devillard et al. (2003) followed a colony of 70 cats living in a city park in Lyon, France over an eight year period and used multi-strata capture-recapture modeling to try to disentangle dispersal from mortality data. They found no evidence of male dispersal, while females apparently dispersed between one and two years of age. Dispersal (and immigration) rates were nevertheless low, with only 12% of the population leaving and only five recorded immigrations during the study period. This contrasted with Liberg's (1984b) findings for rural Sweden in which males were the dispersers with females maintaining the fixed home range areas, an observation confirmed for cats elsewhere (e.g. Izawa et al. 1982). Brickner-Braun et al. (2007), in a study of cats in rural areas of Israel, found that most cats did not wander more than 200 m from a food source or cover and that female cats in desert settlements had very small home ranges entirely within settled areas, similar to Liberg's (1980) findings for rural Sweden.

Guttilla and Stapp (2010) trapped and radio-collared cats on Catalina, the third largest of the Channel Islands off the coast of California and found both males and females who had been resident in island TNR colonies being recaptured at an average minimum distance of 10 km (6 miles) or greater from the nearest colony. Moseby & Crisp (2009) found long-range movements in rural Australia of up to 45 km (27 miles) being made by male cats. The movement and activity of cats in rural areas, and especially in connection with preserves and parks, is of special concern to many because of the conservation threats this can imply (e.g. Hess 2011, Palomeres and Deblies 1994). Gillies (2007) radio-tracked a single neutered male cat who lived a little more than a kilometer from a park boundary to determine whether he would be found using the park. In this case the cat was most often found very near to the owner's house or no more than 200 m away in a patch of scrub and was not detected in the park. Palomeres and Deblies (1994) followed a single male cat living in Doiiana National Park in Spain

and found him concentrating his movements around houses (inholdings), being found resting further than 200 m from a house only about 15% of the time.

Ferriera et al. (2011) followed eight cats from Portuguese -Spanish border farm communities and found their activities to be centered around farms, not significantly influenced by season in this Mediterranean climate and most strongly influenced in their model by avoidance of red foxes (*Vulpes vulpes*). They noted that cats used farms as "stepping stones" when making longer movements, as during mating periods. Moseby and Crisp (2009) found cats in South Australia using what they termed "focal points" within their home ranges, remaining to intensively use a small area for as long as two weeks before moving on. Fitzgerald and Karl (1986) found home ranges in cats in the Orongorongo Valley in New Zealand to be highly linear, which they attributed to the valley's topography. Kays and DeWan observed suburban cats near a nature preserve in New York and concluded on average that "cats in our study area rarely entered the forest."(2004: 276). Marks and Duncan (2009), however, in a study conducted at a nature center near Birmingham, Alabama, found a trend for cats to be captured most frequently in the forest interior (defined as >100 m from residences) portion of their study site.

Male home ranges average three times the size of female home ranges (Liberg et al. 2000), although some studies report no difference between the sexes (e.g. Apps 1986, Barratt 1997a, Molsher et al. 2005, Horn et al. 2011, Bengsen et al. 2012). As an example of a study where differences were found, Konecny's (1987a) study of radio-collared cats on the Galapagos Islands reported male home ranges averaging > 300 ha, while females only averaged 82 ha. Guttilla and Stapp (2010) found that sterilization made no difference in either the size or degree of overlap of home ranges compared to intact cats on Catalina Island, with Barratt (1997) as well reporting no differences for desexed suburban cats in calculated nocturnal as well as diurnal home ranges for suburban cats in New Zealand. Females

with kittens, however, are reported to have smaller home ranges than when they are without (Fitzgerald and Karl 1986) and smaller winter than summer ranges are reported for cats of both sexes in rural Wisconsin (Coleman and Temple 1989). This may vary by region, since Konecny (1987a) found that home ranges did not vary from month to month in his study on the Galapagos, and Langham and Porter (1991) report no seasonal change in area used by cats from their 3-year study of cats on New Zealand farmland. They did report, as does Barratt (1997a), that nocturnal home ranges were larger than diurnal ranges in both farm and suburban habitats. Liberg et al. (2000) conclude that female home range is determined by the availability of food resources, while male home range is determined by the availability of female resources.

The extent to which cats occupy and defend defined territories is not clear and an important aspect of their behavior that should be further clarified. Foley et al. (2005) consider cats to be territorial and Driscoll et al. (2009a, b) argue that cats defend exclusive territories "fiercely." Corbett (1978) compared farm cats to cats on the uninhabited Monarch Islands and concluded that the latter were territorial while the former showed tolerance and a form of group organization, apparently as a result of more dependable and abundant food resources. Given adequate resources it is fairly clear that domestic cats can be highly social, especially with respect to groups of related females (e.g. Liberg 1980, Macdonald 1981, Warner 1985, Langham 1992). Liberg (1984b) found female cats in the same kin group sharing a communal home range which he argued was a defended territory from which non-kin females avoided or were aggressively displaced. He attributed "partial territoriality" to males when subordinates lost contests with more dominant cats and thereafter avoided areas frequented by those cats. Mirmovitch (1995) studied cat home ranges in the food-rich environment of Jerusalem and found considerable overlap in both sexes with individuals of the same sex – suggestive of group patterns.

Liberg et al. (2000) also noted that the almost complete lack of transfer observed between female groups and suggested that some force was working to keep female cats from groups apart.

That force may consist in part of communication pathways that advertise occupied (and potentially defended) areas. Feldman (1994) observed captive semi-feral cats for such signaling and while finding no clear evidence that cats used urine or feces in declaring territorial areas, did feel that chin-rubbing and scratching on trees may have served as olfactory and visual markers. She suggested that these behaviors were not so much indicative of territorial defense as intended to mark the presence of individuals within loosely patrolled home ranges. Tabor (1981), however, thought that both scratching and chinning were used to mark territory. Ishida and Shimtzu (1998) noted a disproportionately smaller number of feces being deposited within feral cat core areas, suggesting some form of spatial signaling may have been occurring. The concept of cats holding space and keeping other cats from immigrating into occupied areas undergirds the "vacuum effect" (e.g. Tabor 1981, Neville 1989, Neville and Remfrey 1984, Mahlow & Slater 1996),an aspect of Trap-Neuter-Return programs that has been a focus of particular criticism (e.g. Clarke and Pacin 2002, Longcore et al. 2009).

In addition to the considerable variability observed in their use of space, cats also show variability in their daily activity patterns. Izawa (1983) followed seven cats on the small Japanese island of Ainoshima who had constant, reliable access to two of this fishing village's refuse pits, with peak activity at dusk and dawn. The average resting time for these cats was close to 19 hours/day, attributable no doubt to their having access to reliable and clumped food resources. Liberg (1984b), in a larger study of cats in rural Sweden, reported resting in females as occupying between 46 and 60 percent of their time, while in males it ranged from 35 to 55 percent of the total activity. Bimodal peaks in cats followed by radio-telemetry (e.g. Konecny 1987a) suggest that crepuscular activity is common in

cats unless impeded by other influences. Haspel and Calhoon (1993) suggest one such factor is human activity, finding that free-ranging cats in Brooklyn, New York had a bimodal nocturnal/dawn activity, with peaks at around 0100 and again at sunrise, which they interpreted as avoiding higher levels of human activity at sunset.

Studies of cats associated with farms or suburban residences indicate that cats in these contexts seek and use a variety of habitats, as well as show a demonstrated ability to live in close proximity to humans even when "wild." Langham (1992) reported on the activity patterns of 15 feral cats on New Zealand farmland, differentiating a group of females who denned in a barn from another who denned in an area of swamp and willows. The barn cats moved significantly further between dawn and dusk except during autumn and winter seasons, while the other group was more likely to be active over a 24 hour period. Morgan et al. (2009) used radio-telemetry to follow owned and sterilized cats living near a wetlands preserve in Christchurch, NZ, and found that cat age and home distance to the wetland periphery were highly correlated with cat movement and hunting activity. Younger cats (< 6 years) had greater average movements than older cats, and cats living on the periphery of the wetlands were more likely to have higher activity within this reserve area. Cat movements were not markedly influenced by season or time of day in this study.

Sociality

The degree to which cats can live as solitary or social animals seems, like so much of their lives, to be highly variable. Early researchers (e.g. Barron et al. 1956) inclined toward attributing entirely solitary lives to cats. However, observational studies (e.g. Leyhausen 1965, 1979, Laundre 1977, Fagen 1978) soon detailed enough social or communal organization that the term facultative sociality came into use

to account for groups of cats, such as those seen on farms or sites such as Buddhist wats, that seemed able to go on for generations in the presence of sufficient resources. In circumstances where they are completely divorced from contact with humans, such as some islands, cats seem to live solitary lives, except when breeding or raising kittens (e.g. van Aarde 1978). Cats have a rich repertoire of both affinitive as well as agonistic behavior patterns (Leyhausen 1979, Macdonald 1981, UFAW 1995, Crowell-Davis et al. 2004) which mediate social interactions and undoubtedly help establish relationships that allow for group cohesion. Dards (1983) found social units among dockyard cats that consisted of related females and their offspring, with males attached to the groups in a manner similar to that shown in lion prides. Denny et al. (2002) found evidence of a tightly structured group formation based on female kinship at a waste disposal site in rural Australia, with no evidence of female immigration. In a laboratory setting, Ohkawa & Hidaka (1987) found cats willing to communally nurse kittens, which they attributed to familiarity and the establishment of a "pseudo-kin" group.

Schmidt et al. (2007a) noted that ecological information on free-roaming cats, including needed data on survival and mortality, is lacking. Cats can live fairly long lives if cared for. If not, their lifespans are shortened and vary little from those of other small carnivores. Comfort (1956) reported on an owned male who lived 27 years, and cited a reliable report of a female who was alive at 31 years. Warner (1985) felt that survival past four to five years was rare in Illinois farm cats and that in most instances mortality came before the end of the second year of life. He noted that only one percent of farm cats lived to be seven or more years of age. A variety of causes of mortality were enumerated, with nearly 30 percent simply unknown, but vehicles (26%), disease (17%), and humans and dogs (15%) were identified as important factors. Horn et al. (2011) observed 22 percent annual mortality in unowned cats they followed in Illinois, with two of their 24 subjects being killed by coyotes. Grubbs and

Krausman (2008) followed eight coyotes in Tucson, Arizona for a year and observed them in thirty-six interactions with cats, nineteen of those resulting in coyotes killing cats. Survival of feral kittens is probably quite poor, with perhaps 25 percent survivorship in the first year (e.g. Wallace and Levy 2006). Izawa and Ono (1986) followed the fate of 72 litters on a small Japanese island where dependable food resources were available. They found an average litter size of 3.9 (range 2-5) with a survival rate at ten months of only 9.5 percent.

Food habits

Cats have been termed "nibble feeders" (Bradshaw et al. 1996) for their apparent preference in taking several small meals each day. They have also been called "versatile opportunistic predators" (Pearre and Maass 1998) and "generalist predators" (e.g. Bonnaud et al. 2007) capable of taking a wide range of vertebrate as well as invertebrate prey. They are obligate carnivores, incorporating only small amounts of vegetable material in their diets, much of that incidental (but see Nogales et al. 1996 for a possible exception). Bradshaw (2006) argues there is a "monotony effect" found especially in free-ranging and farm cats, where prey taken commonly in the past is avoided in preference to something new, the advantage being that this aids in achieving a better balanced diet.

Cat feeding habits and preferences have been studied by analysis of stomach contents (e.g. Eberhard 1954, Jones 1977), direct observations (e.g. Forbush 1916, Brickner-Braun et al. 2007), analysis of scats (e.g. Fitzgerald 1980) and prey retrieval tallies (e.g. Churcher and Lawton 1987, Kays and DeWan 2004). Comparing and interpreting information collected using such different methodologies can be a challenge, particularly when trying to determine the importance of different food items in the diet. Liberg (1982) conducted experiments to determine ratios of prey intake to undigested remains in scats so that he could create correction factors for his dietary research – something other studies have

not generally done. Some feeding studies report data by frequency of occurrence of prey items, while others report the relative mass which each prey item represents, making cross-study comparisons more difficult. Liberg (1984a) also points out that the diet of cats will be related to prey abundance, annual production, and availability, but not many feeding habits studies have measured these variables. Prey retrieval studies are subject to question about what a cat might bring home as opposed to consume in the field. Kays and DeWan (2004), for example, estimated that only 30% of prey was being retrieved to homes and preliminary information released from a "KittyCam" study conducted at the University of Georgia suggests that only 23 percent of kills were brought home (ABC 2012). Besides underestimating predation, prey retrieval studies may be influenced by seasonal factors and the failure of research conducted at a local level to be representative of predation throughout a wider population (Barratt 1998).

The majority of studies on cats' food habits indicate a strong preference for mammalian prey (e.g. Parmalee 1953, Eberhard 1954, Coman and Brunner 1972, Jones 1977, Apps 1983, Liberg 1984a, Konecny 1987b, Coleman et al. 1997, Paltridge et al. 1997, Hall et al. 2000, Kays and DeWan 2004, Langham 1990, Morgan et al. 2009, and see Fitzgerald 1988 for a review). Besides small rodents, lagomorphs (rabbits and hares) may be freely and even preferentially taken at times. Liberg (1984a), for example, found wild rabbits (*Oryctolagus cuniculus*) were predominant prey items in his study in rural Sweden, consistent with some earlier studies (Apps 1983, Coman and Bruner 1972, Jones 1977). Fitzgerald et al. (1991) found cats on Raoul Island subsisting almost exclusively on Kiore (*R. exulans*), a much smaller (60-80 g) species than Norway rats (Rattus norvegicus) at 300-500 g or the black rat (*Rattus rattus*) at 100-350 g. Harper (2004, 2005) did find, however, that all three species on new Zealand's Stewart Island (Raikura) comprised the bulk of prey both by frequency of occurrence and

preponderance and that cats did not apparently prey-switch to birds when numbers were low, either starving or leaving their home range areas when rat abundance seasonally declined.

Birds typically rank second in feeding studies but can be the most commonly taken prey in mammal-free or mammal-depauperate environments (e.g. Fitzgerald and Veitch 1985, Harper 2010). Under some circumstances, diets may emphasize insects (e.g. Gillies and Clout 2003, Medina and Garcia 2007). Campos et al. (2007) examined scats in both suburban and rural areas of southeastern Brazil and found that invertebrates were the most commonly consumed food item (63%) by cats in both areas, followed by mammals (20%). In his summary of diet studies, Fitzgerald (1988: 129) observed that on continents, mammals comprised 68 percent of prey, while birds were found at an average frequency of 21 percent. There may be an evolutionary basis for the hunting of small mammals evident in the specifics of how cats hunt as well as when they are likely to be most active (Leyhausen 1979, Fitzgerald 1988).

In early studies of cat predation there was much interest on impacts on game species, something which appears to be of less concern now. Errington (1936) did not feel that cats were a significant predator of the bob-white quail (*Colinus virginianus*), at least with respect to healthy birds in winter, a finding confirmed by Parmalee (1953) for the Post Oak Region of east-central Texas. Other reports looked at unusual and unexpected findings that represent perhaps the generalist as well as sometimes idiosyncratic nature of cat predation. Nadar and Martin (1962), for example, reported on a male cat whose stomach contained the remains of eight shrews (*Blarina brevicauda*). Gaughran (1950) noted that cats frequently killed and ate weasels (*Mustela erminea murica)*, and other studies seem to confirm this (Frank and Loss-Frank 1989, Flux 2007). Gill (1975) observed cats preying on varying hares (*Lepus americanus*) and Seabrook (1989) reports them as important predators of sea turtle (*Chlonia mydas*) hatchlings.

Despite concerns for how completely they represent the actual numbers of prey taken, retrieval studies have illuminated many details of cat feeding habits. Churcher & Lawton (1987) reported a total of twenty-two species of birds and fifteen species of mammals taken in their year-long retrieval study in the English village of Felmersham. Wood mice (*Apodemus sylvaticus*) and House sparrows (*Passer domesticus*) made up the bulk of prey items at 17 and 16 percent of the total, respectively. Barratt (1997b, 1998) recorded prey brought to owners by cats in Canberra, Australia over a 12 month period, finding as had other studies that mammals comprised the bulk (65%) of prey. He notes, however, that the 17% of the prey represented by birds did consist of a wide range (47) of species, with the majority of these (41) native species.

Jackson (1951) addressed the specific role of cats as predators of commensal rodents in his study of food habits in Baltimore, identifying sites where collections of cat feces could be found ("scatoria") determining that remains of Norway rats were found only in seven percent of scats and at 30 percent of sites. Evidence of mouse predation was much lower. His findings suggested refuse was a major component of the diet of feral urban cats, a conclusion reached as well by Childs (1986) in his later Baltimore-based study. Haspell and Calhoon (1989) also found refuse an important part of the diet in their work on cats in Brooklyn, as well as feeding by individual people (Haspell and Calhoon 1990). Brickner-Braun et al. (2007) reported on predation of wildlife by domestic cats from rural settlements in Israel, recording the stomach contents of killed cats and taking direct observations of owned cats. A total of 12 mammal, 26 bird, 18 reptile and one amphibian species were consumed. Cats were also recorded eating refuse, with the proportion of manufactured food and refuse in the diet decreasing from 70% volume in rural settlements to 44% among cats in open areas. Mammals made up 75% of volume of wild animals in stomachs, while amphibians comprised 10%, birds 9% and reptiles 6%.

Fitzgerald (1980) found black rats (*R. rattus*) to be the most important prey of cats in New Zealand's Orongorongo Valley, as Langham and Porter (1991) did in their three-year study of feral cats on New Zealand farmland.

The diet of cats on islands is of special concern to conservationists, given that endemic island species may be highly rare, unique and vulnerable to mammalian predation. Bonnaud et al. (2011) reviewed 72 studies of insular cat diets from 40 islands and concluded that introduced mammals were the most frequently taken prey. For example, Jones (1977) found rabbit remains in 82 percent of scats and 71 percent of gut samples from cats on Macquarie Island, Karl and Best (1982) identified rats from all three introduced species on Stewart Island in 93 percent of scats and Bonnaud et al. (2007) documented black rats (*Rattus rattus*) in 89-94 percent of scats examined from Port-Cros, a small Mediterranean island. These finding, however, do not mean that cats are not having a negative impact on native birds, since island species such as the Yelkouan Shearwater (*Puffinus yelkouan*) on Port-Cros and kakapo (*Strigops habroptilus*) on Stewart are in urgent need of protection from any predation pressure. Bonnaud et al. (2009) suggest that Port-Cros Island is in fact a sink where Shearwater have repeatedly immigrated but not been able to expand and grow as a population due to impacts from predators.

Impacts

Although occasional reference is made in antiquity to cats harming bird populations (Engels 1999), until quite recently it would be more likely to hear their virtues extolled as "useful allies" (Mivart 1891) in the war against rodents. Some question this benefit (e.g. Elton 1953, Driscoll et al. 2007), but it makes common sense to conclude that cats are at least locally helpful around homes and farmsteads in

suppressing the smaller rodents that appear to be their preferred prey. In addition to performing utilitarian services, cats have been widely appreciated as human companions, even if vilified at certain times in the past (Tabor 1983). The growth of the global cat population in concert with an increase in other anthropogenic impacts, has led to contemporary concerns for the effect cats may have on natural ecosystems. At the same time, the consequences of ferality, abandonment and neglect on cats themselves continue to raise welfare concerns and humane interests as has been the case for more than 100 years (Serpell 2000).

Early conservationists focused predominantly on cats killing game and song birds (e.g. Forbush 1916, Errington 1936). Today, interests have broadened to other concerns, such as the transmission of disease to wildlife (e.g. Jessup 2004), or humans (e.g. Gerhold and Dabritz 2012), threats to the wildcat (*Felis silvestris silvestris*) gene pool (e.g. Brickner 2003) and even economic impacts (De Silva and Turchini 2008). Cats released on islands are a special focus of concern for many conservationists (Medina and Nogales 2009) as are cats introduced into ecosystems where native animals may be especially vulnerable to predation (e.g. Dickman 2009). Cat predation is arguably most problematic when rare, threatened or endangered species are at risk, but it is appropriate to speak of it in the broader context of "subsidized" predation as well (e.g. Jessup 2004). Some may argue that feeding reduces predatory drive, but Biben (1979) demonstrated that hunger was not a necessary condition for killing, although the probability of a kill increased as hunger did.

Because they are often provided supplementary food or have access to dependable human waste, cats can avoid the consequences that other predators face if they limit the availability of their prey (e.g. Sims et al. 2008 -- but see Harper 2005 for an apparent exception). Cats can reach densities in some habitats, such as the urban, well in excess of what wild predators could ever achieve unless they too had access to supplemental food (e.g. Baker et al. 2010). Woods et al. (2003), for example,

speculate that the estimated 9 million cats in Britain represent a twenty-fold greater density than is naturally achieved by pre-breeding populations of native predators such as stoats (*Mustela ermenia*)and weasels (*Mustela nivalis*) and a 38 times greater density than the pre-breeding population of foxes (*Vulpes vulpes*).

Predation

Pearre and Maass (1998) summarized more than thirty studies of cat predation and concluded that cats most commonly took prey that was about 1% of their body weight, which is much less than is typical for other carnivores. Kutt and Kitchener (2012) examined stomach contents collected from cats in north-eastern Australia and found on average stomachs relatively full (~200 g/cat) of prey that was selectively small in each of three groups: mammals (<10 g, range 50-100 g), reptiles (10-50 g) and birds (50-100 g). Brio et al. (2005) reported that prey of <50 g made up at least 80 percent of the totals for both free-roaming domestic (*F. s. catus*) and wild (*F.s. silvestris*) cats as well their hybrids in Hungary. This preference may account for the apparent scarcity of Norway rats (*Rattus norvegicus*) in their diet (Jackson 1951, Elton 1953, Childs 1989, Glass et al. 2009), since adults of that species weigh between 300 and 500 g typically.

Despite their inherent methodological problems (e.g. Barratt 1998, Baker et al. 2005) cat feeding studies have generated a wealth of information on activities in different habitats, numbers and type of prey killed, effects on rare, threatened and endangered species, and the impact of cat predation on wildlife relative to other forms of mortality. Predation studies have also opened new lines of thinking and research in respect to cats as ecological competitors (e.g. George 1974), the concept of sublethal effects (e.g. Stone et al. 2004), the role of cats in mesopredator release (e.g. Gambino et al. 2007) and the amplification of predatory impact through "hyperpredation" (e.g. Courchamp et al. 2003). Many

questions about cat predation remain to be answered, chief among which may be whether it is compensatory or additive (e.g. Baker et al. 2005). As yet relatively few studies have looked at individual variation in hunting skills or the effect of aging on hunting activity and more information about these points would be helpful. Add to this the many social aspects of the human-cat relationship that remain to be elucidated, and the need to continue active research on cats appears clear.

Cat predation can be ephemeral, unpredictable and spatially dispersed (Cooper et al. 2012), which is almost surely why so few studies have relied on direct observations to document this behavior. Calhoon and Haspell (1989), for example, noted only one instance of predation in more than 180 hours of observations of cats in their study in Brooklyn, despite noting that birds and small mammals were plentiful and potential prey. Kays and DeWan (2004) documented 31 attempted hunts in 181 hours of observation of suburban cats in their New York study, with small mammals the objects of the hunt in 52 percent and birds in 23 percent of observations. The overall success or kill rate was 13 percent. Dunn and Tessaglia (1994) used volunteers in the Project FeederWatch program coordinated by the Cornell Laboratory of Ornithology to record predation at back yard bird feeders, finding that 51 percent of all predation could be attributed to two species of hawk (sharp-shinned, *Accipiter striatus* and Cooper's, *A. cooperi*), with cats causing 29 percent of deaths from predation. Cooper et al. (2012) advocate for the use of volunteers, homeowners and neighborhood residents , especially in suburban and urban environments, as part of a "citizen science" to better understand the role cats may be playing.

Baker and co-authors (2003, 2005, 2008) examined the role cats play as predators in a series of studies in Bristol, England. Baker et al. (2003) documented the abundance and distribution of small mammals in residential gardens and concluded that predation pressure from cats combined with the fragmentation of good habitats exerted a negative effect on the distribution of the wood mouse

(*Apodemus sylvaticus*), the only species commonly found around residences. The wood mouse was also found to be the urban cat's most common prey in a later study (Baker et al. 2005), comprising more than half the total 21 prey items taken annually by cats (five mammal, ten bird and one amphibian species). Baker et al. (2005) calculated minimum and intermediate predation rates, based on identification of positive as opposed to uncertain remains (spring juveniles, for example) and found that for House sparrow (*Passer domesticus*), Dunnock (*Prunella modularis*) and robin (*Erithacus rubecula*) the minimum rates were moderately high: equivalent to 45% of the combined total of pre-breeding density and annual productivity. Baker et al (2008) went on to estimate the number of birds killed annually at five sites within the city and compared this with breeding density and productivity. Even though 60% of the cats studied for a period of one year never returned prey home, the authors' estimate of the number of birds killed was large relative to breeding density and productivity at some sites, leading them to conclude that cats could have been a major source of mortality for some species of birds. The minimum predation rate (prey per cat per year) based on all study areas ranged from slightly more than 1 to less than 6, while maximum rates varied between 1.5 to about 12. Seventeen species of birds were classifiable as prey, with House sparrows, robins and Dunnocks representing about half of the identifiable total. Wood mice (*Apodemus sylvaticus*) were by far the most common mammal taken and mammals represented 62 percent of identifiable prey returned. Later, Baker et al. (2010) concluded that under some circumstances cats could be limiting local prey species, but that it remained to be determined whether this mortality was additive or compensatory.

Barratt (1997b, 1998) conducted a study of 214 cats (210 neutered) from 143 households in Canberra, Australia from which he was able to document prey brought home. The majority of cats (≈82%) caught fewer than 5 prey species (X=2.8), with more than half (56%) of all prey caught being

House mice (*Mus musculus*). Overall, 65% of all prey items were mammals, with birds making up 17% (with a total of 47 species of which 41 were native). Barratt (1997b) concluded that prey was taken by the cats he studied in proportion to its relative abundance. Most cats were observed to catch fewer than 10 prey/year (range 0-72) and among the significant interaction terms that could be identified, proximity to suburb edge and adjoining habitat seemed most relevant. Most of the variation in prey capture and competence between cats was unexplained.

Balough et al. (2011) documented both nest and post-fledgling survival in gray catbirds (*Dumetella carolinensis*) in three suburban neighborhoods and found that predation accounted for 79 percent of all mortality, with cats responsible for 47 percent of that. Nest predation and adult predation are, as Shocat (2004) points out, different things. The literature on nest predation in urban environments remains inconclusive in respect to whether it is even greater there than in other habitats. Undoubtedly, however, cats, birds (such as crows and jays) and predators like raccoons are important factors whose roles remain to be more completely elucidated (Lahti 2009, Thorington and Bowman 2003).

Birds are at times important components of cat diets. Hess et al. (2004) found them present in 82 percent of stomachs examined from cats collected on Mauna Kea, while closer to 30 percent at Kilauea and Mauna Loa (Hess et al. 2007). Fitzgerald and Veitch (1985) found a small population of cats on Herekopare Island subsisting largely on petrels, land birds and insects, and Harper (2010) reports about 20 percent more bird than mammal remains in stomachs and scats from Auckland Island. Mead (1982) analyzed returns from ringed birds and summarized the extent of cat predation on 18 species. He found close to a third of all reported causes of mortality attributable to cats for the two top ranked species, Dunnock (*Prunella modularis*) and robin (*Erithacus rubecula*). This declined to about 6 percent in

swallows (*Hirundo rustica*) because of their typically aerial habits. The top six species taken by cats were all characterized as ground or low vegetation feeders. Van Heezik et al. (2010) found slightly higher percentages of birds (37%) than mammals (34%) in their study of cat predation in Dunedin, New Zealand, and suggested that the mortality to birds was additive. Hawkins et al. (1999) presented findings of a study of two parks near San Francisco, California, where cat and no-cat areas had been established. They found that more native mice were trapped in no-cat areas and more introduced House mice in the cat areas. They also reported native birds such as the California quail (*Callipepla californica*) and brown thrasher (*Toxostoma rufum*) present in the no-cat areas, but not in places where there were cats. Jessup (2004) suggests that this occurs because European species have had time to adjust to cat predation, whereas native species have not.

The diversity of bird species taken by cats may exceed that of mammals, even when the latter predominate in the diet. Brickner-Braun et al. (2007), for example, found that although mammals made up 75 percent by volume of the prey in cats from rural areas of Israel and birds only nine, there were 12 mammal species taken as opposed to 26 species of birds. Calver et al. (2007), in their study in Perth, Australia, found cats again preying predominantly on five species of mammals, with 13 species of birds taken and 11 species of amphibians and reptiles.

Cats are known to exhibit considerable variation in hunting skills (Tschanz et al. 2011) and there is much that remains to be learned about the role of experience as kittens in respect to competency, and prey preference (Caro 1980, Turner and Meister 1988). Little is known about how individual variation in skills or motivation to hunt affects predation success, but some studies suggest it is enough of a factor to warrant closer examination. Churcher and Lawton (1987) report that some cats in the Felmersham study caught no prey at all, while others caught many animals. Van Heezik et al. (2010)

reported 25% of the cats in their study of cat predation in Dunedin did not bring home prey. Baker et al. (2008) found only 40 percent of the cats they followed for a year returning prey home, something they thought could either be due to cats consuming prey in the field or simply not engaging in successful hunts. Barratt (1998) also reported substantial variation in the amount of prey captured by individual cats in his study near Canberra, the majority of which he notes as unexplained. Barratt (1997, 1998) observed a range of from zero to 72 items/cat/year brought home in his studies in Canberra, Australia, with most (70%) of the 214 cats bringing home fewer than 10 prey items/year, and a large majority (81.9%) catching fewer than 5 species (mean=2.8). Some cats are apparently very successful and accomplished hunters, as the three documented by Morgan et al. (2009) who brought home more than 100 prey items per year.

Churcher and Lawton (1987) also attributed variability in prey taken in part to the age of cats studied. Although ageing is commonly linked to a higher risk of becoming a victim of predation it also can affect the competence of predators (MacNulty et al. 2009). Flux (2007) documented predation by a single neutered female cat over a 17 year period in his 0.5 ha suburban New Zealand garden. The cat, who was fed ad libitum, caught a gradually increasing number of prey until reaching a plateau of about 60 items/year between ages 3-7. Over the entire period of observation the cat's prey consisted of about 58% mammals and 40% birds, with amphibians and reptiles making up the remainder. From ages 8-12 the number of prey caught declined to 15 items/year and from ages 13 to 17 to around 5 prey items/year. The exception was rabbits, whose numbers went up during ages 9-16. Monitoring of local bird populations at the same time showed significant declines for some species, none of which were attributable to the cat. Frank and Loos-Frank (1989) also documented a long-term record of predation by a single female cat from a German village when she was between five and fifteen years of age. During this time she brought home 52 birds and 430 mammals, with 44 percent of the birds she caught

being house sparrows. Among mammals, common voles (*Microtus arvalis*) were her most common, at 21 percent of all captures.

Overall, predation rates estimated from retrieval studies show wide variation. Baker et al. (2003), for example, estimated 21/prey/cat/annum, while Churcher & Lawton (1987) estimated 14, (Howes 2002) 28.9, (Ruxton et al 2002) 71.7 (based on average of 5.5/cat over 28 days) and Woods et al. (2003) 27. Kays and DeWan (2004) average predation rate estimated to be 0.53-1.8 prey/ha/summer month; or 1.7 kills/cat/summer month. Numbers of prey caught have been used to extrapolate to regional or even national impact assessments. Forbush (1908, 1913, 1916) engaged more than two hundred correspondents to report on cat predation, leading to his estimate that a mature cat on "good hunting grounds" in Massachusetts killed about fifty birds a year. From this he extrapolated to an annual estimate of approximately two million birds killed in the state, less than estimates produced by colleagues for Illinois and New York (1916:44-45). May (1988) projected on the estimated predation reported by Churcher and Lawton (1987) to predict 100 million bird deaths/annum in Britain and Coleman and Temple (1993, 1994) and Coleman et al. (1997) estimated that between 8 and 219 million birds were killed in Wisconsin each year, exclusive of predation by cats in urban areas. This was derived from an estimate of 1.4-2.0 million free-ranging cats, some 23% of their kills being birds (Coleman and Temple 1994). Mitchell and Beck (1992) estimated that the range of songbirds killed by urban and rural cats in Virginia was 3.1-26.2 million/year, using observations from four urban and one rural cat who retrieved prey. Lepczyk et al. (2003) estimated that cats in southeastern Michigan killed between 0.7-1.4 birds/week across a rural to urban landscape, with a minimum depredation rate of approximately 1 bird/km/day. Truly broad projections such as May's for Britain have been made for the continental United States as well. Jessup (2004), examining the data presented by Coleman and Temple (1995) and Coleman et al. (1997) suggested that cats killed, on a national scale, annually, hundreds of millions and

perhaps as many as a billion small animals. That estimate has recently been updated by Dauphine and Cooper (2009), who place the number of bird mortalities alone at about one billion, while more recently Loss et al. (2012) suggested mortality estimates ranging from 250 million-1.5 billion birds from free-roaming house cats and 890 million-2.7 billion from feral or semi-feral cats, totaling from 1.14-4.2 billion in all.

Cats are said to have been involved in the extinction of more than thirty species of birds on islands (Courchamp et al. 2003, Dauphine and Cooper 2009, ABC 2004), arguably the most serious claim that can be put against them. In some cases cats are believed to be at least partially responsible for extinctions where no systematic records or studies were conducted (e.g. Kawakami and Higuchi 2002). Perhaps the most famous case of a cat-driven extinction is that of the Stephen's Island wren (*Traversia lyalli*). On that New Zealand island, a single cat belonging to the lighthouse keeper was said to have been responsible for driving this flightless bird to its end. Although the loss of this species through predation by cats is not disputed, the event was probably not as rapid as often claimed and may have involved more than a single cat (Galbreath and Brown 2004). To date, cats seem to be implicated in only one continental bird extinction, the Paradise Parrot (*Psephotus pulcherrimus*) of Australia, and then only in context with a larger set of threats. However, the Florida scrub jay (*Apelocoma coerulescens*) is deemed to be threatened in part by cat predations (Webster 2009). While birds greatly outnumber the mammals cats are said to threaten, Vazquez-Dominguez et al. (2004) attribute the extinction of the Angel de la Guarda deer mouse (*Peromyscus guardia*) to predation from a single cat that took place between 1995 and 1999. LaFever et al. (2008) modeled the impact of cats on the threatened marsh rabbits (*Sylvaligus palustris heffneri*) and suggested that extinction of this race could be expected in ten years if no action were taken. Mitchell et al. (2002) attribute the eradication of cats on Long Cay in the Turks and Cacos Islands to the restoration of an endangered iguana (*Cyclura carinata*).

George (1974) first raised a question as to whether cats might have an indirect impact on wildlife through ecological competition, raising concerns that cats might be indirectly limiting raptor species who depended upon the prairie vole (*Microtus ochragaster*). Liberg (1984a) later suggested support for such a theory of ecological competition, and it continues to be raised in situations where cat impacts are discussed (e.g. Loyd & Miller 2010a). Courchamp et al. (2003) cite an example involving birds on the Kerguelan Islands where predation by cats on petrels may deprive skuas of their prey and curtail their ability to reproduce. Brio et al. (2005) studied the diets of domestic, wild and hybrid domestic-wild cats in Hungary for the possibility of competition and Phillips et al. (2010) examined the possibility of competition between feral cats and island foxes (*Urocyon littoralis clementae*) on San Clemente Island, concluding that despite overlap in diets the two species seemed to be able to partition preferred prey in a way that avoided impacts. A special case of competition is raised by De Silva & Turchini (2008) with respect to the forage fish harvested to make cat food. They estimate yearly consumption of such fish at 13.71 kg/cat, making up a substantial part of the 13.5% of the total 39.0 million tons of wild caught forage fish that is used for purposes other than human food production and which represents in their opinion a limited biological resource perhaps better employed elsewhere.

The issue of "mesopredator release" was first raised by Crooks and Soule (1999) who demonstrated that the removal of apical predators (e.g. coyotes) from some ecosystems could results in the "release" of other species (e.g. cats) who had in part been controlled by the larger predator. Rayner et al. (2007) demonstrated from a 35 year dataset that the eradication of cats from New Zealand's Little Barrier Island led to a decrease in the breeding success of a burrowing seabird, Cook's petrel (*Pterodrama cooki*), because of population increases in rats (*R. exulans*) who consumed eggs and nestlings. Le Corre (2008), in summarizing this and other known causes of decline in petrels worldwide, cites cats as involved in at least five documented declines, but always with other predators or known

mortality factors such as bycatch in longline fisheries implicated as well. Where both cats and rats could prey on vulnerable birds, Le Corre (2008) notes, it is important to understand life history factors and the differential vulnerability to predation young and adults might have. Jones and Ryan (2010) report evidence for increased mouse (*Mus musculus*) predation on albatross (*Diomedea dabbenena*)and several burrowing petrels at Gough Island following eradication and caution that monitoring should be a part of any cat removal programs.

It is unclear whether cats may be at times "surplus killers" in the sense observed in species such as red fox (Kruuk 1972), but it is known that they will take prey even when sated (e.g. George 1978, Coleman and Temple 1993). Thus, the well fed pet cat allowed to roam outdoors is said to have a significant impact on wildlife, especially in urban environments (Balough et al. 2011). Peck et al. (2008) noted that 22 percent of the terns killed by cats in their study on Juan de Nova Island were not consumed, suggestive of surplus killing, while Short et al. (2002) did not identify surplus killing in cats in Australia, as they did in foxes and dingoes (*Canis lupus dingo*).

Hyperpredation can be defined as a process where one prey species exerts an indirect effect on another by causing an increase in the abundance of a common and shared predator (Baker et al. 2005). Taylor (1979) speculated that the introduction of rabbits to Macquarie Island helped lead to the decline and eventual extinction of the endemic parakeet (*Cyanoramphus noveezelandiae erythrotis*) because rabbits provided cats with a dependable prey base during times when the parakeets were not abundant. Courchamp et al. (1999, 2000, 2003) expanded on this idea for island systems and modeled its consequences, suggesting that control of both the introduced predators as well as introduced prey species was needed. Baker et al. (2005) visualized hyperpredation in urban cat populations through human provisioning of food which created a situation analogous to that which others have described for insular populations. Dauphine and Cooper (2009) also argued that island habitats – by which they

meant to include natural areas surrounded by development as well as physical islands – were especially susceptible to hyperpredation effects.

More specific impacts attributed to domestic cats involve their interbreeding or competing with wild species. Macdonald and Burnham (2010) identified two principal threats -- interbreeding and the transmission of disease—from domestic cats (*F. s. catus*) to wild stock (*F. s. silvestris*) in Scotland. They note that the issue of conserving the remaining wild cat population is "beset by complex scientific, legal and ethical issues alongside daunting practical ones." (2010:22). Among the practical issues remains that of simply being able to distinguish reliably between wild cats and their domestic counterparts (Kitchener et al. 2005) while among the ethical concerns is the defining of mammalian species in the face of introgression (Daniels and Corbett 2003).

Growing attention has also been focused recently on the nature of sub-lethal effects of cat predation. Stone et al. (1994) addressed the issue of behavioral diversity in a study of lava lizards (*Tropidurus spp.*) on the Galapagos Islands by examining the novel concept of cat impacts on a rare behavior – wariness. They suggested that one result of cat predation on islands where they and lava lizards were found together was a loss of tameness that was characteristic of the lava lizard on more pristine islands. Beckerman et al. (2007) suggested the theoretical possibility that the simple presence of cats in the environment might affect the reproductive performance of prey, a theory Zanette et al. (2011) tested on song sparrows (*Melospiza melodia*) by actively eliminating direct predation and using playback calls and sounds to manipulate perceived risk. Obviously, much more needs to be known about the possibility that perceived risk (fear) can reduce reproductive performance, but the theoretical possibility has been raised.

Predation on islands is of special concern to conservationists because of the rarity and vulnerability of many island species (Courchamp et al. 2003, Medina et al. 2011, Bonnaud et al. 2011).

Bonnaud et al. (2011) reviewed 72 studies of cats conducted on 40 islands worldwide and found a total of 248 species consumed: 27 mammals, 113 birds, 34 reptiles, three amphibians, two fish and 69 invertebrates. Of these species, three mammals, 29 birds and three reptiles were listed as threatened by the IUCN. Overall, however, Bonnaud et al. (2011) note that a few species of introduced mammals were the most frequent prey of cats on islands. In the Canary Islands Medina and Nogales (2009) identified five mammals, 16 birds, 15 reptiles and 32 invertebrates as being preyed upon by cats, with four threatened and on the IUCN Red List. The authors noted as well that cats were significant predators on other introduced mammals and that it would be important to take into account the problems associated with hyperpredation and mesopredator release as management programs were planned.

Some island studies have demonstrated a complex interplay between cats and rats, such that the removal of cats resulted in unanticipated changes in rats and other predators that threaten to undo any gains sought by the removal of cats. Hughes et al. (2008) report on seventeen years of monitoring of terns (*Onychrprion fuscatus*) on Ascension Island. The terns were monitored from 1990 to 2007, with cats removed between 2001 and 2004. Adult tern predation stopped with the removal of cats, but mynahs (*Acriodotheres tristis*) and rats (*R. rattus*) were taking eggs, and rats shifted behaviorally to taking tern chicks as well. The tern population seems to be increasing seasonally and through improved incubation successes, but the extended breeding period for these birds requires additional years of observation before the full effects of cat removal can be determined. Elsewhere, studies following removal of cats focus on recovery of specific species, which in some cases at least is significantly demonstrated (e.g. Keitt and Tershy 2003).

It is hard to draw specific conclusions and find definite trends involving the impact of cat predation on their prey populations from existing studies. Mead (1982), for example, concluded that

cats were a significant source of mortality for a number of avian species for which returns were available, but that there was no clear evidence of overall harm to the populations of these birds. Jarvis (1990) argued that cats were simply substitutes for other predators in the urban environment, but others (e.g. Woods et al. 2010) have argued that the densities reached by cats in cities greatly exceed anything native predators would ever achieve (but see Hadidian et al. 2010 for high densities in urban raccoons). Baker et al. (2005) concluded that localized looses they observed were likely to be non-trivial, but that even though occurring at very high densities predation overall "…appeared unlikely to affect population size for the majority of prey species (2005: 310)." This they suggested was a result of selection in urban areas for species that had successfully adapted already to cat predation. Barratt (1997b, 1998) felt that cat predation on prey populations remained equivocal, as did Sims et al. (2008) who noted that the "intense debate" surrounding the impacts of cats on wildlife was hampered by a "quite basic lack of information," but that as yet no conclusive evidence had demonstrated a markedly adverse impact in areas other than on certain islands. Flux (2007) cautioned against removal or exclusion of cats from this type of habitat in New Zealand without a better understanding of what such action might do to release non-native rodent populations. Others have raised truly broad and far-reaching contentions concerning the impact of cat predation, with Dauphine and Cooper (2009) suggesting it might supersede habitat loss , and Loyd and Miller (2010a,b) raising concern that cat predation could even have a general and pervasive negative effect on ecosystem health.

Disease

Cats have been identified as causing a number of concerns with respect to the transmission of diseases harmful to humans, (e.g. Nichol et al. 1981, Proulx 1990, Aquirre et al. 2007, Alfonso et al. 2007, Gerhold and Dabritz 2012,), livestock (Langham and Porter 1991), and to others cats, including wild species

(Brown et al. 2008). Gerhold and Dabritz (2012) review the current status of rabies in cats, noting that cats are responsible for more human exposures now than are dogs and expressing concern for exposures not being consistently reported to health boards. The Centers for Disease Control in Atlanta (CDC) generate statistics on rabies nationally, noting that about ninety percent of the animals reported each year with confirmed rabies are wildlife. In 2008 and 2009 approximately 300 cases of rabies in cats were reported as opposed to 80 in dogs per annum, which is attributed in part at least to the tendency for people to take dogs for veterinary care and vaccinations more than cats (CDC 2012a).

Cats are the definitive host for *Toxoplasma gondii*, the parasitic organism responsible for the disease Toxoplasmosis, a leading cause of death attributable to foodborne illness in the United States (CDC 2012b). Cats can shed oocysts for 3-5 days after initial infection and shed many millions of oocysts over a median period of eight days as a one-time event in their lives (Dabritz and Conrad 2010). Nichol et al. (1981) found that more than 50 percent of urban cats tested in England were infested with *Toxocara*, and Henriquez and Roberts (2009) found that 30 percent of people in the United Kingdom were infected and harboring dormant *Toxoplasma gondii* cysts in their brains. Wild animals may be equally susceptible to infection as well, and two endangered species, the sea otter (*Enhydra lutris*) and Hawaiian monk seal (*Monachus schauinslandi*) are known to have been fatally infected (Dabritz et al. 2006, Honnaud et al. 2005). Dabritz et al. (2006) looked at outdoor fecal deposition by cats in three California communities and calculated that 76.4 tons of fecal matter was deposited outdoors annually, along with another 29.5 tons discarded as part of indoor litter. Litter improperly disposed of by flushing into toilets is also implicated in the environmental threat *Toxoplasma gondii* poses, especially to animals such as seals and otters (Dabritz and Conrad 2010).

Cats can also transmit the Feline Leukemia Virus (FeLV) and Feline Immunodeficiency Virus (FIV) to other cats and to wildlife. Guttilla and Stapp (2010) found slightly less than 30 percent of the free-

roaming cats they trapped on Santa Catalina Island to be infective for FeLV and/or FIV. It is believed that FeLV virus from a single domestic cat led to the death of five Florida panthers (*Puma concolor coryi*), an endangered species (Brown et al. 2008). This comprised a population threat significant enough to prompt a vaccination program aimed at the puma population (Cunningham et al. 2008).

Other impacts on birds

The U.S. Fish and Wildlife Service (2002) makes an "educated guess" that a minimum of 10 billion birds breed in the United States and that fall populations may be on the order of 20 billion. These populations are at risk for a wide variety of mortality factors into which the impact cats have must be placed. Banks (1979) reviewed data for major sources of bird mortality for the U.S. Fish and Wildlife Service, mentioning that domestic pets probably took a large number of birds, especially ground nesters, without attributing specific numbers to them. He attributed the greatest cause of direct mortality of the then estimated 196 million birds killed as a result of human activity to be hunting, largely restricted to birds in three orders (Anseriformes, Galliformes, and Columbiformes). Of hunted species the mourning dove (*Zenaida macroura*), is most likely to be preyed upon by free-roaming cats. While Banks (1979) estimated that hunting accounted for 60 percent of the mortality in the three orders on which it was concentrated, he also argued that the most intensely harvested species were "essentially unaffected by the human activities discussed" (1979:13).

Bird (2004) summarized annual human-related mortality of birds in the United States, placing cats third on a list of six major causes. Both recreational hunting (estimated 120 million deaths/year) and collisions of birds with human structures (164 million–1.3 billion estimated deaths/year) exceeded estimates of deaths to birds from cat predation (estimated 118 million/year). The only other significant cause of mortality estimated by Bird (2004) is pesticide poisoning, which is

estimated at approximately 72 million deaths/year. Cherkassky (2011) reviewed causes of mortality to birds and identified habitat loss as the single greatest threat, but noted that secondary anthropogenic causes of bird mortality have resulted in a cumulative effect that is responsible for overall declines in numbers. Using estimates of 80 million pet cats and 60-100 million free roaming cats she agreed that the number of one billion birds (Dauphine and Cooper 2009) was a conservative estimate. Cherkassky accepted a similar estimate for Klem's (2009) upper limit for fatalities from collisions with glass, and listed eight other principal sources of anthropogenic mortality to account for an upper limit of approximately 500 million bird deaths. Impacts are disproportionately spread across groups, with, for example, 23 of 64 seabird populations affected by long line fishing listed as in danger of extinction, (Cherkassky 2012). In all cases, the impact of predation (or others sources of mortality) is largely a function of how abundant different groups affected are. Erickson et al. (2005) estimated 100 million bird deaths from cats as a conservative figure and put cats as third in the cumulative mortality chart that saw buildings (550 million) and power lines (130 million) as the only greater sources, although they do not account for mortality from hunting.

Other anthropogenic causes of bird mortality for which better estimates are needed include habitat destruction, fragmentation, and conversion; various agricultural and home landscaping activities which destroy nests and nestlings or expose birds to herbicides or pesticides; oil spills; entanglement in discarded fishing line, nets or other materials ; lead poisoning; electrocution on fences and power lines; and direct destruction of nests and nestling during development at certain times of the year. Environmental causes, such as storm events, and facilitated nest predation and parasitism because of fragmentation and urbanization, also can be mentioned as yet unmeasured impacts. Bird diseases have not yet been subject to the sort of meta-analysis that could produce reliable estimates, nor has the

impact of boys with BB guns, or the facilitation of avian and other natural predators through habitat alterations and human cultural practices (e.g. bird feeding). The effect of any one of these anthropogenic sources of mortality, as well as their cumulative impacts, have yet to be determined precisely, but Arnold and Zink (2011) modeled collision mortality using records for 188 species of eastern North American land birds and concluded that mortality from that source had no discernible effect on bird populations as a whole.

Management

Managing conflicts with outdoor cats is complex and fraught with technical difficulties and social controversy that, despite over a century of effort to address solutions, remains an ongoing challenge. The argument that we need to "do something" about cats falls on two sides of the issue – protecting wildlife and advancing the welfare of cats. Advocates for cats and advocates for birds take strong stands on how and when to impose controls while the general public may be disinterested or even apathetic (Ash and Adams 2003). Cats have not arrived yet as a socially significant issue for many people, and until they do real progress may be hard to achieve.

Managing conflicts with cats can be visualized as occurring at one of two levels – the strategic or the tactical. Strategies involve the plans that frame management actions. Tactics are the actual practices used to accomplish management strategies. Cat management can be the interest and responsibility of many different entities, ranging from animal care and control agencies, local humane societies, national non-profit organizations, universities, local, state and federal government agencies and special interest groups, among others. Management must take into account factors such as cat ownership and legal status along with understanding the habitats and environmental conditions for the particular cats in question. Importantly, planning must consider closely whether lethal or non-lethal controls are

preferred or warranted and the implications of using either. Tactics such as public education are likely to be relatively non-controversial, while others such as poisoning or the introduction of disease will be much more controversial and could generate strong opposition.

Managing feral cats requires a better understanding of how cats use space and budget their activities (Moseby and Crisp 2009, Bengsen et al. 2010) than is the case with owned cats, although a strong argument can be made for better information concerning the activity of owned cats when they are outdoors as well. Changing human behavior is more relevant to owned than to feral cats, or those cats who are "semi-owned." Control of feral cat populations occurs typically by lethal means, often applied unevenly without efforts to monitor effectiveness (Dickman and Denny 2010). For their part, nonlethal policies aimed at cats are often haphazard and lacking in agreed-upon guidelines (Longcore et al. 2009). People's feelings and attitudes about cats and their management is critical, but often not well enough understood to be used effectively towards management (Slater 2004, Dickman and Denny 2010). Collaboration of broad coalitions of groups and individuals and multi-disciplinary partnerships are crucial to sound management approaches (e.g. Jessup 2004, Van Heezik 2010), but hard to create and harder to sustain.

A broad range of management and control measures exist and have been applied for both feral as well as owned cats. Proulx (1990) suggests leash laws, registration of all cats, reduction of licensing fees for sterilized cats and improved control patrols as possible ways to control owned cats, to which Lilith et al. (2006) add keeping cats indoors at night, confining them to the owner's property, sterilizing them, restricting the maximum number cats that can be owned, banning ownership in environmentally sensitive areas and impounding or destroying cats found in nature preserves as management options. The American Bird Conservancy recommends educating the public to spay/neuter owned cats, not to

feed feral cats, promote legislation prohibiting abandonment and feeding, encourage greater involvement of stakeholders, advocate humane removal, and support of cat sanctuaries (ABC 2004).

Among the recommended options for feral cats are sterilization, culling by various methods, re-homing, relocation, and placement in shelters (Jongman and Karlen 1996). Warner (1985) lists three criteria for control of feral or free-ranging cats: determine numbers accurately, determine impacts accurately and determine acceptable means of control. Approaches like Warner's focus on the need for management to be based on sound data, justifiable techniques that can achieve demonstrable benefits, and monitoring of results to ensure program efficacy (Kogan 1998, Hadidian 2010, ICAMC 2011). Evaluation of management actions is essential given that retrospective analysis shows that effectiveness cannot be demonstrated even with some long-term programs (Hone 1996, Walsh et al. 2012).

Legal issues

Cats are covered by various legal protections and may be subject to restrictions or control under other enactments. The vagueness with which cats are defined in given contexts and at different times can impede the consistent application of legal sanctions (Farnworth et al. 2010, 2011). Gorman and Levy (2004) and Hatley (2003) address some of the issues associated with the legal status of cats in the United States and identify a variety of federal and state laws as potentially applicable to cats, but do not find clearly established consensus about when, where and how these may be applied. Legally, cats in the United States are widely accepted as domestic, not wild, animals even when in a wild or feral state, whereas in Great Britain, for example, feral cats are legally regarded as reverted from domestic to being wild animals (Neville and Remfrey 1984). The issue of how to classify feral cats has not been conclusively decided by law in the United States (Baker et al. 2011). The authority to manage cats, domestic and feral, is not well codified in many instances and may be discretionary with different land

managers and local authorities. Cats viewed as "pests" may be subject to trapping and destruction by wildlife control businesses that may freely trap and kill cats believed to be feral without any onus (e.g. Kruise 1995).

Federal laws such as the Endangered Species Act (ESA) and Migratory Bird Treaty Act (MBTA) may be invoked with respect to the killing of protected wildlife by cats. Conceptually, it might be argued that caregivers for cats in Trap-Neuter-Return (TNR) programs could be enjoined under the ESA, because the cats are likely to live longer lives and be at risk to kill protected wildlife (e.g. Jessup 2004). Similarly, the "take" of wildlife by cats remains to be addressed by the courts, with both strict and liberal interpretations of the MBTA by different courts likely to be invoked in any legal challenge (Baker et al. 2011). A third federal law, the Marine Mammal Protection Act (MMPA), could similarly be invoked with respect to "taking" if the court were to rule that the spread of disease from cats to protected marine mammals constituted a "taking." However, the apparent narrow construction of MMPA does not suggest that such a challenge would prevail (Baker et al. 2011).

State laws with respect to cats, including feral cats, are decidedly more complex than federal law and deserve more serious study. However, only thirteen states and the District of Columbia have any laws that mention feral cats (Baker et al. 2011).

The idea of preemptive management has been raised for cats under some scenarios in which a "precautionary principle" is invoked to act to prevent damage even before harm has been demonstrated (Clergeau et al. 2004, Lilith et al 2006, Morgan et al. 2009, Baker et al. 2010, Calver et al. 2011). One intention in employing this approach is to mount early, fast responses to threats imposed by nonnative species when a reasonable certainty exists that harm will be forthcoming. With respect to cats, it is argued that current studies document wildlife mortality sufficiently to trigger use of the principle pending definitive studies of risks. The precautionary principle also might be considered relevant from

an animal welfare perspective if a persuasive demonstration could be made that populations would eventually grow to a point where lethal action would be compelled. Although such determinations would be far from simple to reach, the welfare principle of affecting fewer rather than more animals would be invoked in such a case (Kirkwood et al. 1994).

Ethics

As both a domestic companion and a free-roaming feral animal, the cat presents numerous ethical challenges and dilemmas. One context within which the human-cat relationship can be placed is that of obligations that people have, or should have, toward cats as animals subjected to domesticity, moved throughout the globe and treated in ways that range from nurture as companions to eradication as "pests." Burgess-Jackson (1998) argues that there has been relatively little discussion of human responsibility to companion animals, with a tendency to regard them as an "undifferentiated mass." Palmer (2003), addressing urban environmental ethics, argues that humans have a causal responsibility and duty to provide care for the animals we regard as pets. She raises the point that "Since the animals had no choice in the matter [of being there], it seems that negative judgments, if appropriate at all, must rest on the human responsible for their presence, not on the animals."(2003:69). For all the controversy their publications raised over cats, Coleman et al. did explicitly note that people had "a responsibility to both the cats and the wild animals they may affect" (1997:1), and that the effort to limit any adverse effects free-ranging cats might have on wildlife must be conducted in a humane manner.

Ethical considerations arise among professionals engaged in both veterinary care and research as well. Anderson et al. (2004) and Barrows (2004) discuss the particular challenges free-roaming and feral cats present to veterinary professionals, noting the risks such animals cause as reservoirs of

infection for owned cats, as potential public health hazards through the transmission of rabies and zoonotic disease agents, and, of course, for their impacts on wildlife. Barrows (2004) argues that TNR is in practice an act of "reabandonment" that causes more harm than good to both cats and the environment. Errington (1936), in collecting data from cats he shot in Wisconsin, expressed no concerns about taking owned animals, noting that seven of the animals he shot were "obvious" pets. Ratcliffe et al. (2009), describing the removal of cats from Ascension Island, note that 38 percent of owned cats on the island were victims of the eradication process, something they describe as causing "public consternation." Cats are increasingly being trapped and killed or taken to municipal shelters by private wildlife control businesses (Kruise 1995). Frazier (2007) describes an elaborate ruse at one large commercial business where cats were being fed and cared for that involved convincing caregivers that skunks were transmitting disease to and killing cats. This allowed her to trap for cats without the vandalism and sabotage that occurred when other companies earlier tried directly to take cats, because in this instance the caregivers thought she was trapping for skunks. Nearly 200 cats were removed from the property along with skunks and raccoons caught incidentally.

Full-scale eradication efforts seem to invoke the most controversy and ethical challenge when it comes to the control of feral cats. Such population management of cats currently occurs largely on smaller islands where complete eradication is a more realistic possibility (Medina et al. 2011). However, lethal control is also employed on a larger scale in efforts to limit if not eliminate local populations (e.g. Morgan et al. 1996, Moseby and Hill 2011, Moseby et al. 2011) and "removal" is advocated for parks and other habitat "islands" embedded within larger, heterogeneous landscapes (e.g. Clarke and Pacin 2002). Justification usually rests in such cases on the idea that as an introduced and nonnative species

the cat can have a deleterious impact on native species and even become a determining force in their extirpation or at times, extinction (e.g. Taylor 1979, Steadman 1989).

The management challenges under these different scenarios, however, can be quite different. Duffy and Caprece (2012) suggest contextualizing conflicts with cats in a scheme of "compromise management," where: 1) eradications are confined to islands and other areas of high native biodiversity where reintroductions can be prevented, 2) public education is the focus of efforts to reduce cat impacts in areas of moderate biological value and 3) management occurs only as a response to local complaints in drastically altered urban ecosystems. Cowan and Warburton (2011) focus on the ethics of eradication and call for greater attention to the welfare consequences of programs dedicated to such efforts. For animal damage professionals welfare concerns are increasingly recognized as important components of any programs – a "first order" concern, as initially termed by Schmidt (1989).

Cats as "pests"

Feral cats are often regarded as "pests" and subject to the practices used by wildlife damage managers to control animals deemed injurious to human interests. Although justifying wildlife damage abatement programs has long been a concern (e.g., McCabe and Kocizky 1972), a general set of management principles consonant with both ethical and pragmatic constructs has only recently begun to take form (e.g. Fisher and Marks 1996, Marks 1999, Littin et al. 2004, Hadidian 2012). The International Companion Animal Management Coalition (ICAMC) has called for an IPM (Integrated Pest Management) approach to managing feral cats. IPM, although not having an agreed upon and universal definition (Kogan 1998), has become a dominant model for responsible control of both invertebrate as well vertebrate "pests" since the 1970's. IPM encompasses a set of major principles, including "integration" (meaning the harmonious use of multiple methods), "management" (as a set of decision rules based on

ecological, economic and social considerations) and "economic injury level" (as a trigger for management action) in a traditional stepwise decision-making process (Hadidian 2010). The ICAMC cat management approach consists of five steps: a) initial data collection and assessment, b) identification of influential factors in cat population management, c) development of components for a comprehensive cat population program, d) design of the intervention, and e) implementation, monitoring and evaluation (ICAMC 2011).

Consistent with IPM concepts, Hadidian et al. (in press) propose a "Preferred Management Approach" to cats that that includes meeting the following criteria:

The need to act should be clear (justification)

Any benefits sought must be realistic (achievability)

The methods to be employed must be able to achieve benefits (effectiveness)

The approach must be targeted to the problem-causing individuals (specificity)

The methods used must be the most humane available (welfare priority)

The consequences of actions must be amenable to evaluation (monitoring)

Nonlethal Management

Nonlethal conflict management for cats involves a variety of tactics used separately or in combination with the intent of not causing mortality, but which may nonetheless have welfare consequences for the animals targeted (Sharp and Saunders 2005a,c). Nonlethal tactics typically target individuals or smaller groups rather than populations. In wildlife damage management, nonlethal approaches might include efforts aimed at physically preventing or excluding animals from places where conflicts occur, deterring or repelling them from places or resources to which access must be denied, or teaching or aversively conditioning individuals to dissuade them from using specific areas or being drawn to attractions (such

as dumpsters). Such approaches are widely used to address conflicts with wild animals and described in detail elsewhere (e.g. Decker et al. 2002, Hadidian et al. 2007).

Cats can frequently be excluded from access to places where they are not wanted by fencing. Because they are fairly adept climbers, it is sometimes difficult to fence them out of areas, but with a proper design and adequate placement this can be achieved. Moseby and Read (2006), for example, tested a 180 cm high wire fence with a foot apron (to prevent animals from digging under the fence) and a "floppy" overhang which successfully deterred feral cats. The costs of effectively fencing large areas (for example, seabird colonies) can be great, but where the species or resource being protected is significant, still cost-effective (Miller et al. 2010).

The concept of large exclusion zones that keep cats from accessing valued resources through habitat management has been suggested. Alterio et al. (1998), for example, tested what they dubbed the "Grass Wall hypothesis," in which grasslands on New Zealand's South Island were retired from grazing to see if the taller grasses that sprang up would inhibit the movement of predators, cats included. They found this had the opposite effect, but concluded that work such as theirs highlighted the need for research on biological controls before widely advocating or implementing them. Mesters et al. (2010) in another test of exclusion zones followed 38 radio-collared cats at two urban fringe sites and one rural site in New Zealand to further examine how large exclusion zones would need to be to protect an endangered skink. Where Lilith et al. (2008) had proposed a 360 m buffer as sufficient to keep cats out of preserves, Mesters et al. (2010) suggested that exclusion zones would have to be at least 2.4 km wide in rural areas and only slightly less on the urban fringe.

Deterrents are devices that work to prevent cats from being successful hunters. These may include bells, collars, bibs or other devices that make it difficult for cats to surprise prey or thwart their

ability to pounce and grab prey successfully. Belling cats has often been recommended, although studies of efficacy have come to mixed conclusions about this technique. Morgan et al. (2009) in a study of radio-collared cat in Christchurch, NZ did not find rates of predation significantly affected by whether cats were wearing a bell, as was also reported by Barratt (1998) in his study of cats in New Zealand. Gordon et al. (2010), however, found reductions of 50 percent for bird and 61 percent for rodent predation in belled cats subject to a six week on, six week off split trial. Calver et al. (2007) conducted a similar split trial of the CatBib™, a device intended to interfere with a cat's ability to pounce, and found that alone or with bells the bib stopped 81% of cats from catching birds, 33% from catching reptiles and amphibians, and 43% from catching mammals. Adding bells did not change the rates of predation. Nelson et al. (2005) investigated the use of sonic devices as well as bells and found that cats with bells returned 34% fewer mammals and 41% fewer birds, while cats with sonic devices returned 38% fewer mammals and 51% fewer birds compared with cats wearing a plain collar.

The backyard remedy for a trespassing cat has often been to turn a hose on him, a technique which if applied often and persistently might eventually have a desired effect in causing the cat to avoid the area entirely. Many other ways of aversively conditioning cats can be imagined; some are humane, others are not. All are fairly labor intensive unless automated, as are devices such as oscillating sprinklers combined with detectors motion-triggered by nearby auditory devices that produce sounds that cats find unpleasant at sonic and possibly ultrasonic ranges. Mills et al. (2000) found only a mild demonstration of effect, such as ear-flicking, in cats exposed to a commercial device intended to repel them, but Nelson et al. (2006) evaluated a device called Catwatch (apparently only distributed in Britain) and concluded that it had promising deterrent effects that became more effective over time. A similar device called CatStop™ is distributed in North America by Contech. The chemical repellent

methyl nonyl ketone is registered by the U.S. EPA as a cat and dog repellent and available commercially in nearly fifty different commercial products as granular or liquid formulations (Hadidian et al. 2007).

Other means of management, such as confinement, that would not traditionally apply to wild animals are available for cats when they are owned. Patronek (1998) called for identifying and overcoming the attitudinal barriers to confining cats indoors or otherwise, to prevent them from being able to kill prey. A survey of 550 cat owners in Germany suggested that slightly more than half reported behavioral problems in confining their cats, including anxiety, scratching furniture, feeding problems, aggression, inappropriate urination and spraying and defecation in the house (Heidenberger 1997). Jongman (2007) noted that while most people may feel their cats need to roam, roaming carries welfare risks toward which owners may or may not be attentive. She suggested that most behavior problems associated with confined cats might not be abnormal behaviors per se, but simply behaviors that needed to be redirected to natural substrates. Toukhsati et al. (2012) surveyed residents in Victoria, Australia and found that beliefs about cat confinement were related to concerns about both the protection of cats as well as wildlife. They suggest broad consensus exists among both owners and non-owners of cats for confinement.

Public education and the teaching of responsible pet ownership have long been considered key components to any lasting solution to cat overpopulation problems, and continue to be advocated as necessary steps in holistic solutions (e.g. Proulx 1988, Hildreth et al. 2010). Education provides the basis for attitude and value formation about cats and can support such needed efforts as confinement and neutering. It can also, perhaps, aid in building support for programs such as licensing and identification of pet cats, which as Patronek (1998) notes, remain controversial.

Perhaps the most promising approach to feral cat control from both a practical as well as humane perspective involves the development and application of an effective contraceptive, one that can be administered orally. Robertson (2008) noted that widespread non-surgical contraception was a realistic goal for the future, but that other approaches to managing cat populations were needed until effective compounds for that purpose were found. Munson (2006) reviewed the available contraceptive agents, noting that the progestin contraceptives (megestrol acetate, melengesterol acetate, medroxyprogesterone acetate, and levonorgestrol) administered orally, in implants, or as depot injections are effective in preventing pregnancy, but that long-term exposure is associated with hyperplasia and cancers which put them at a disadvantage. Gonadotropin-releasing hormone (GnRH) analogs are effective in both males and female cats (Levy et al. 2004, Munson 2006) whereas Porcine Zona Pellucida (PZP) apparently is not (Munson 2006, Levy 2011). Further research and development is obviously needed in the area of contraception, with an orally effective compound and delivery system imperative to the development of effective programs at the scale required.

Lethal Management

The lethal control of cats has always been controversial and represents perhaps the greatest challenge in managing the conflicts humans have with these animals. Lethal control occurs at scales ranging from the practices of individuals who seek to eliminate cats they regard as nuisances, the activities of business professionals contracted to eliminate cats as "pests," the municipal animal care and control programs conducted by agencies and nonprofit organizations, and sanctioned full-blown eradication programs aimed at removing cats entirely from designated landscapes. Eradication programs have

primarily been conducted on islands and have employed a variety of techniques aimed at completely eliminating populations of cats that will have, in some cases, been self-sustaining for centuries.

The intent in island removals is to return often fragile and unique ecosystems to their former state, allow for recolonization of sensitive species, and prevent species deemed injurious to those systems. Nogales et al. (2004) summarized removals from islands globally, noting that cats have been eradicated from 48 islands, the majority of which were small (< 5 km^2), among the methods used for removal were hunting and trapping, poisoning (directly or secondary through poisoning of rodents), and the introduction of viral disease (feline panleukopenia), with methods often combined. Courchamp et al. (2003: 368) note that the "history of island restoration has been dominated by catastrophic failures." Sometimes, removals can be compromised by immigration or restocking of controlled populations, as for example the case on Ascension Island (Ratcliffe et al. 2009), where owned cats remain present after the removal of ferals and are a risk to create a new generation of cats who become free-ranging. Wood et al. (2002) argue that removing cats is an effective way to protect biodiversity but that they are difficult to eradicate. This raises the issue of repeated management rather than complete eradication, where the only follow-up required would be to prevent re-colonization. Hilton and Cuthbert (2010) summarize cat eradication programs from islands, with 21 islands under the jurisdiction of five countries representing successful cat removals at the time of publication.

Shooting

Shooting has its proponents as a means of population control, although a proposed change to Wisconsin hunting laws aimed at establishing any cat seen outdoors as an unprotected species that could legally be shot at any time was quickly retired following an uproar which the governor characterized as making the state a "laughingstock" (Imrie 2005). This was not the case in Poland, where the Animal Protection act

of 2002 made it legal to shoot both free-ranging cats and dogs (Wierzbowska et al. 2012). Moreover, there is no doubt that many cats are shot when spotted afield by hunters, their legacy and reputation as killers of game birds remembered. Hildreth et al. (2010) argue that gunshot is approved as a euthanasia technique by the American Veterinary Medical Association (AVMA), noting further that in some states, such as Nebraska, rural residents are allowed to trap and shoot feral cats on their property year-round.

Disease

Diseases such as Feline Panleucopenia Virus (FPLV) have been introduced on islands in attempts to control free-ranging cat populations (van Aarde and Skinner 1981, van Rensenburg et al. 1987, Bertheir et al. 2000). This virus works either by direct transmission from one cat to another or by persistence in the environment and subsequent acquisition, allowing for infection to continue even after the cat population has been reduced to a low density (Berthier et al. 2000). However, while achieving a quick and dramatic reduction, disease has not been shown to eliminate island cat populations by itself and has necessarily had to be accompanied by other lethal efforts (van Rensenberg et al. 1987).

Poisons

The use of poisons to kill feral cats has been mostly confined to island eradication efforts. Research on the use of toxicants involves not only an examination of the efficacy of available compounds (Eason and Frampton 1991) but also of delivery systems and non-target uptake (Risbey 1996, Marks et al. 2006), secondary poisoning (Alterio 1996) and potential for exposure, and economic and logistical concerns (Veitch 1985, Algar and Burrows 2004, Johnston et al. 2007). Morgan et al. (1996) assessed the use of rodenticides (brodiafacoum and alphachloralose) to kill cats in Australia, while others have focused on the use of the toxicant Sodium fluoroacetate or compound 1080 (e.g. Eason and Frampton 1991, Risbey

et al. 1997, Altiero 2000, Algar et al. 2002). Moseby and Hill (2011) conducted large conducted a large scale baiting trial with 1080 on foxes and cats and fouond a significant decline in cat activity after only one of eight baiting events. Eason et al. (2010) investigated the use of para-aminopropiophenone (PAPP), a toxin being developed as an alternative to others in current use; its action in causing methemoglobinemnia is argued to work to provide gradual loss of consciousness and death without the pain or suffering that other compounds cause.

Trapping and removal

Although trapping and removal of cats has long been a longstanding management practice, surprisingly little seems to be known about its actual effectiveness. Slater (2004) remarked that to the best of her knowledge no location had ever achieved long-term control through this method, and in situations where cats are targeted for removal and the subsequent effort takes only some animals, such programs are known to fail (e.g. Zaunbrecher and Smith 1993). Cats are fairly easily trapped (Hall and Pelton 1979, Sharp and Saunders 2005b,c) and the use of cage traps is standard in municipal control as well as TNR programs. Hess et al. (2009) suggest trapping of cats at or near their sources of dispersal as a potentially more way to effectively control their presence in more rugged natural landscapes. A live-trapping and removal program using specially modified leg-hold traps was conducted successfully on San Nicolas Island in California (Hanson et al. 2010, Will et al. 2010, Ramsey et al. 2011), but with a relatively small population (57) of cats subsequently placed in a sanctuary environment that would be impractical for cost reasons to apply at a large scale. Short et al. (1997) evaluated several control methods for feral cats in western Australia, including spotlight shooting, trapping, and poisoning, and found that trapping was the most successful (based on kill rates for radio-collared animals), but also the most labor intensive.

Trap, Neuter and Return (TNR)

Trap-Neuter-Return (TNR) and its variants such as Trap-Test-Vaccinate-Neuter-Return, Trap-Neuter-Return-Manage and Trap Test, Vaccinate, Alter, Return (Hughes et al. 2002, Ash and Adams 2003) are experiments in feral cat management that first began in England and Europe in the 1950's as an alternative to the traditional management practice of trapping and killing unowned cats (Hammond 1981, Remfry 1981, Kristensen 1981, Neville and Remfrey 1984, Tabor 1981, 1989, Berkeley 2004). TNR has come to be hotly debated even as it has expanded to wider use in many parts of the world. This debate involves first and foremost TNR's effectiveness in controlling cat populations, with opposing claims that it works (e.g. Remfry 1981, Neville and Remfrey 1984, Zaunbrecher and Smith 1993, Mahlow and Slater 1996, Centonze and Levy 2002, Slater 2002, Levy et al. 2003a, Mendes-de-Almeida et al. 2012) or does not work (Clarke and Pacin 2002, Castillo and Clarke 2003, Winter 2004, Jessup 2004, 2010, Guttilla and Stapp 2009, Lebbin et al. 2011). These positions essentially frame what can be called preservationist and conservationist interests in the matter. Attention has only recently turned to trying to better understand such stakeholders from a human dimensions perspective (e.g. Lord 2008, Peterson et al. 2012).

As TNR was first being proposed, some observers expressed concerns about how neutering would affect cat health and behavior (Rees 1981, Remfrey 1982), and the welfare consequences of TNR remain an important concern to proponents (Levy and Crawford 2004). For those who oppose the practice, the adverse health and behavior consequences of colony living has been emphasized (e.g. Jessup 2004, ABC 2004). Rees (1981) observed a cat colony living on a hospital grounds for a two year period and noted that cats remained in "good" health. Gibson et al. (2002) screened 185 feral cats and

kittens trapped on Prince Edward Island as part of a TNR program and found 12 percent were positive for FeLV, FIV or both. Fischer et al. (2007) conducted a prospective study to determine if vaccination at the time of neutering for various cat diseases would be effective and observed what they considered an "excellent" immune response. Levy and Crawford (2004) found about a four percent incidence in cats surveyed in Alachua County, Florida for FeLV, FIV and feline coronavirus, which was not substantially different from the infection rate observed in owned cats kept as pets. Guttilla and Stapp (2009), working with free-roaming cats on Santa Catalina Island, report 28.9% of cats trapped and tested proved positive for FIV, FeLV or both. Scott et al. (2002) examined 5,323 cats trapped in Alachua County, Florida for sterilization as part of a TNR program and euthanized twenty (0.4%) for various reasons, including health-related issues. Wallace and Levy (2006) looked at data from over 100,000 cats admitted nationally to TNR programs between 1993 and 2004 and also report that an average 0.4 percent of those handled were euthanized because of debilitating conditions.

A principal claim made by TNR advocates and challenged by those opposed to the practice is that TNR colonies will shrink through attrition over time. This is based largely on the assumption that neutered cats will die or occasionally emigrate (Neville and Remfrey 1984, Mahlow and Slater 1996). However, it faces counterclaims that colonies actually attract immigrants or encourage the dumping of unwanted pets (e.g. Clarke and Pacin 2002, Castillo and Clarke 2003). The term "vacuum effect" has been used to describe the process whereby colony cats hold sites against immigrants through aggressive behavior or territorial (such as scent-marking) activities (e.g. Tabor 1981, Alley Cat Allies 2102), but field studies have not confirmed that this effect is consistent or universal. Gunther et al. (2011) followed four urban feeding groups in Tel Aviv over a period of a year and found that the number of cats in two neutered groups increased significantly while those in the two intact control groups decreased, also significantly. They conclude that the cause of increase in the neutered groups was attributable to higher

immigration as well as lower emigration rates, and recommend that neutering be persistent in TNR colonies. Finkler et al. (2011) conducted a companion study of behavior in these same groups and found that the frequency of agonistic behavior was lower in the neutered groups and primarily attributable to interactions involving intact males who had moved into them. Guttilla and Stapp (2009) likewise set up field research to test the hypothesis that cats living in colonies would show less tendency to roam than intact cats. They found 13 percent of their captures in a trapping effort to be cats from established colonies on the island who were captured an average of 10 km from the colony they had previously been trapped in, leading the authors to conclude that TNR would be ineffective on an island-wide basis.

Rees (1981) conducted what is apparently the first and only national survey of TNR, locating 704 colonies throughout Great Britain in 1977. He conducted field observations on a colony located on a hospital grounds that originally consisted of 34 cats and reported relative stability at that number over a two year period, with only one female immigrant. Zaunbrecher and Smith (1993) documented an early TNR effort at a medical facility in Louisiana that had previously trapped and removed cats on an ad hoc basis, with a TNR effort beginning after the prior approach became controversial. Starting with 40 cats in three social groups, at the end of 36 months five had died and another five had disappeared without any kittens born into the now neutered population. Six replacement cats had joined the colonies, presumably immigrating from a village which was located about two miles away. Centonze and Levy (2002) surveyed caregivers for 132 cat colonies in north central Florida in which the overall population was found to decline by 26 percent over a median period of 18 months. Levy et al. (2003) conducted studies of the cat colonies on the University of Central Florida Orlando campus between 1991 and 2002, although no census was conducted before 1996. At that time 68 cats were recorded in residence, a number which six years later was estimated to be 23. Three of the eleven cat colonies on campus were

eventually depleted of cats. Menedes-de-Almedia et al. (2012) reported on a feral cat colony at the Zoological Park in Rio de Janeiro where a hysterectomy program conducted annually from 2004 to 2008 and then biannually thereafter saw an initial population of 40 cats in 2004 reduced to 26 in 2006 and 17 in 2008. Natoli et al. (2006) reported on a large-scale and long term TNR effort in Italy involving 103 colonies that showed a significant overall decrease in cat numbers after neutering with 55 colonies showing fewer cats, 20 remaining stable and 28 increasing in numbers. Stoskopf and Nutter (2004) worked with cat colonies in rural North Carolina and found numbers in six of the colonies where cats had been surgically sterilized to decline by a mean of 36 percent over two years, while in three control colonies there was a 47 percent increase in cat numbers, with considerable site to site variability in population shifts observed.

TNR is claimed to have a number of benefits beyond the potential to reduce cat numbers. Among these are that it improves the health of feral cats (Hughes & Slater 2002, Foley et al. 2005), reduces public health risks (Hughes & Slater 2002), avoids euthanasia as a control method (Gibson et al. 2002, Foley et al. 2005), reduces risks to free-roaming cats (Hughes & Slater 2002), reduces threats of feline and zoonotic diseases (Foley et al. 2005), improves quality of life for homeless cats (Foley et al. (2005), makes cats less likely to roam, spray and fight (Mahlow & Slater 1996, Hughes & Slater 2002), decreases nuisance complaints (Hughes & Slater 2002), and is more humane (Hughes & Slater 2002).

Alternatively, TNR is claimed to have negative impacts beyond not reducing cat numbers. Among these are that it helps spreads zoonotic disease (Mahlow & Slater 1996), affects ecosystem health (Loyd and Miller 2010b), competitively impacts native predators (George 1974), has hidden economic costs in surgeries (Mahlow & Slater 1996), leads to a questionable quality of life after release (Lepczyk et al. 2010), creates risks to public health and safety (Hildreth et al 2010), leads to the deaths of

native wildlife (Hildreth et al 2010, Crooks & Sole 1999, Pimental et al. 2000, Lepczyk et al. 2003, 2004, 2011, Jessup 2004, Kays & DeWan 2004) and has no clear ecological benefit (Guttilla and Stapp 2009).

A number of modeling exercises have been conducted to determine the efficacy of TNR as opposed to other methods of management, principally the traditional approach of Trap-Remove-Euthanize (TRE). Anderson et al. (2004) used published data in a matrix population model to parameterize low to high intrinsic growth rate scenarios. They concluded that a spay rate of 88% would be needed to stabilize the population growth if all fertile females were free to breed. Budtke and Slater (2009) reached a similar finding under a slightly different scenario in which sterilization was modeled on 10, 20 and 30% of intact adults and juveniles with seven combinations of parameters assessed under different levels of survival and fertility. In their model, population growth stabilizes (assuming a 3-year life span for feral cats) when 71% of females (81% of adult females) are sterilized. Without juvenile sterilization this would equate to 91% of adult females needing to be sterilized. Under this modeling scenario altering survival was of more immediately consequence than reducing fecundity, as appears true under other modeling scenarios as well (e.g. Schmidt et al. 2009). Foley et al. (2005) used data from TNR programs in San Diego, California and Alachua County, Florida to estimate costs of TNR as opposed to TRE programs, concluding that TNR was approximately twice as expensive to implement as TRE, even when volunteers are used in TNR efforts. They conclude that TNR is only effective when the total number of colony cats in an area is below 1000, and that reducing the rate of abandonment appears to be a more effective strategy for reducing feral cat numbers. Jones and Downs (2011) studied cats in colonies in five South African university sites and concluded that at 55 percent sterilization the populations were stabilized, but that a 90 percent neutering was preferred to bring population numbers down and garner public support for the program.

Loyd and DeVore (2010) also concluded that TNR would be optimal for small local populations of less than fifty cats while TRE would be the optimal management strategy for populations greater than 50 cats. Lohr et al. (2012) modeled effectiveness and costs of TRE and TNR approaches and concluded that even modest immigration of cats in TNR colonies would affect their ability to be reduced to extirpation. Schmidt et al. (2009) examined 11 different combinations of TRE and TNR at three different levels of immigration (0, 25 and 50%), and concluded that lethal control was more effective than non-lethal for populations in which immigration was occurring. Their results differed from those of Anderson et al. (2004) in that euthanasia did not outperform TNR for demographically closed populations. Immigration, which is reported to be as high as 21 percent in some populations (Natoli et al. 2006) is a significant issue relating to the attributed failure of TNR to succeed in reducing cat numbers (Castillo and Clarke 2002, Clarke and Pacin 2003). Passanisi and Macdonald (1990) reviewed the state of knowledge about cat colonies in Great Britain in a series of interviews and case histories and noted that it was "virtually impossible" to give an objective assessment of TNR based on a paucity of real data.

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