Biology and Impacts of Pacific Island Invasive Species. 7. The Domestic Cat (*Felis catus*)[1]

David Cameron Duffy[2,4] *and Paula Capece*[2,3]

Abstract: This article reviews the biology, ecological effects, and management of the domestic cat (*Felis catus*) in the Pacific basin. The cat is one of the most controversial invasive species in the Pacific region because of its complex relations with humans. At one extreme, well-fed domestic house pets are allowed outdoors where they may hunt native animals; at the other, unsocialized feral cats have replaced native predators as apex predators or occupy a new niche on oceanic islands, where they have devastated native faunas. In the middle are stray cats that are still socialized around humans. Feral and stray cats can be reservoirs of diseases that infect free-roaming domestic cats, humans, and wildlife. Given these problems, the best response would be to keep domestic cats indoors, restrict cat breeding, and remove feral populations. However, most Pacific basin societies have failed to reach a consensus on the cat problem, so solutions are ad hoc, often lacking in any scientific basis, and reflect our conflicting views. Compromise management might best fall into three broad classes: (1) eradication of cats should be confined to islands and other areas of high native biodiversity where reintroduction can be prevented; (2) in a landscape of low or moderate biological value, efforts should be made to educate the public to reduce the impact of their cats on remaining wildlife, while excluding cats from "islands" of elevated biodiversity values or human sensitivity; (3) in drastically simplified urban ecosystems, management perhaps should occur only in response to local complaints.

The domestic cat (*Felis catus*) is the consummate commensal associate of humans, serving variously as pet, domestic rodent control, and religious symbol (Serpell 2000, 2002). Distributed by humans around the globe, it has become a formidable predator of small animals, with especially devastating effects on small islands lacking an indigenous terrestrial predator (Fitzgerald 1988). Cats are also responsible for spreading diseases to wildlife and humans (Patronek 1998). These problems have led to control efforts that in turn have caused conflict with those who either value free-ranging cats or dispute the validity of methods used for control.

Cat control elicits strong opinions, based on cultural, socioeconomic, and ethical beliefs. On the one hand, there are those who believe that humans should be responsible for "cleaning up" their effects on native ecosystems. On the other, there are those who argue that most ecosystems have adjusted to cats and it is time to stop "playing God" by intervening in natural systems, in that "native" and "alien" species are equal in value. A discussion of this issue alone could fill a volume and is beyond the scope of this review. However,

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[2] Pacific Cooperative Studies Unit and Department of Botany, University of Hawai‘i at Mānoa, 3190 Maile Way, St. John 410, Honolulu, Hawai‘i 96822.
[3] Current address: Chattahoochee River National Recreation Area, 1978 Island Ford Parkway, Sandy Springs, Georgia 30350.
[4] Corresponding author (phone: 808-956-8218; fax: 808-956-4710; e-mail: dduffy@hawaii.edu).

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throughout the Pacific there is a profound asymmetry between the cat and endangered endemic species: the death of a cat is the loss of an individual of a planet-wide species, but in an endangered species an individual that dies may be irreplaceable.

This review focuses on the ecology, management, and related issues of the feral cat in the Pacific basin and samples the extensive literature, primarily drawn from the region. This is not a complete examination of the "cat problem." There are numerous papers and books that cover cat biology from a wide variety of angles and perspectives in greater detail (e.g., Turner and Bateson 2000, Rochlitz 2005, Denny and Dickman 2010). In our opinion, all cat management must be local, based on the immediate environment, native species, human culture, and techniques available. The best management of cats will occur when those involved make maximum use of all available information, even though political constraints are often present.

NAME

Felis catus Linnaeus, 1758 (Carnivora: Felidae)

Synonyms: *Felis catus domestica* Erxleben, 1777; *F. silvestris catus*

Common names: English: Domestic cat, feral cat, house cat. Pacific region: burrgan (Gamilaraay/Kamilaroi, Australian), cato (Chamorro), gato (Spanish), kattu (Truk), katuu (Palau), kiti (eastern Australia), koyangi (Korean), kuching (Malay), kuri (Rapanui), māo 猫 (Chinese), ngaya (Anangu/Pitjantjatjara, Australia), neko (Japanese), ngeru (Maori), pi'ifare (Tahiti), popoki (Hawaiian), pusa (Philippines), pusi (Papua New Guinea, Samoa, Tonga), putjikata (eastern Australan), vusi (Fiji).

Baldwin (1980) suggested that the word for cat tends to reflect the source of the cats: cultures that received Spanish cats use a derivation of "gato," and cultures that obtained English cats tend to use derivatives of the word "pussy."

DESCRIPTION AND ACCOUNT OF VARIATION

Felis catus (L., 1758) (Figure 1) is a small-bodied felid that typically ranges from 2 to 7 kg as an adult (National Research Council 2006). The combined length of the head and body ranges from 460 to 522 mm, and the tail is typically 280 to 350 mm in length (Whitaker and Hamilton 1998). Females average about 70% or 80% of the mass of males (King 1990). The dental formula for *F. catus* is incisors 3/3, canines 1/1, premolars 3/2, molars 1/1. There is substantial variation in color and coat pattern and body type between domestic cat populations because of various patterns of isolation and human commerce and more recently because of intense selection by humans (Lipinski et al. 2008), but feral cats tend to converge on the "striped tabby" or "mackerel" coloration of *F. silvestris* (the wildcat) (Case 2003). The diploid number of chromosomes is 38 (Case 2003).

Recently, *Felis catus* has been crossed with a variety of wild felids and the offspring marketed as domestic companion animals (Saulny 2005). There is considerable concern in Australia about what would happen if the genes from such hybrids ended up in feral cats (Cooper 2008), and one hybrid form has been banned from Australia (The Age 2008).

ECONOMIC IMPORTANCE AND ENVIRONMENTAL IMPACT

Detrimental Aspects

PREDATION: The domestic cat is a superb predator. If released on an oceanic island without a similar ground predator, when just one generation away from domesticity, or even as a household pet allowed to roam outdoors, it retains its original skills as a predator and may become a replacement apex predator in environments near humans (Bradshaw et al. 1999). Cats hunt even when well fed and continue to kill even when already actively feeding on other prey (George 1974, Adamec 1976). Some argue that cats "may now serve a beneficial role" in particular ecosystems because they have been present so long (Gorman and Levy 2004), but ecological studies reveal a continuing record of damage and extinction (Medina et al. 2011).

DIET: Cats are above all opportunistic, taking available prey (Fitzgerald and Karl 1979). In an overview of diet studies from the

Figure 1. Feral cat at Hilo, Hawai'i (photo by J. Jeffrey).

Northern and Southern Hemispheres, Pearre and Maas (1998) found their main prey to be mammals, with birds secondary, and reptiles and insects more frequent at lower latitudes and during warm seasons (see also Fitzgerald 1988). On islands, mammals were again most important, followed by birds, especially when seabirds are present (Fitzgerald and Turner 2000, Bonnaud et al. 2011). In a review of Australian cat diet studies, Dickman (1996) found that rabbits (*Oryctolagus cuniculus*) and house mice (*Mus domesticus*) were the dominant prey in more arid habitats, but marsupials replaced them in forests and areas closer to humans. On islands he concluded that the prey range was narrower and diet reflected prey availability.

Diet studies from the rest of the Pacific generally reflect those findings (Table 1). This is not surprising because they are a subset of the larger analyses. Rabbits were important in Australia and main-island New Zealand sites, but various species of rats dominated the diets in most areas where they occurred. As reported elsewhere, birds were especially important on smaller islands. To facilitate comparison, most of the diet studies reported in Table 1 are summarized as frequencies of occurrence, tending to bias the data toward small items (Hyslop 1980), which may explain the relative importance of invertebrates. The overall impression is, as elsewhere, that cats will take any available prey that they are physically capable of killing.

species effects: Cats have "contributed to at least 14% of the modern bird, mammal, and reptile extinctions" (Medina et al. 2011:3507). They are believed to have contributed to the extinction of numerous taxa in the Pacific basin, although the evidence is historical and often circumstantial. These extinctions include an endemic subspecies of deer mouse (*Peromyscus guardia*) on Estanque Island, Mexico (Vásquez-Domínguez et al.

TABLE 1

Diets of Feral Cats in the Pacific Region

				Percentage of Diet						
Nation	Location	Habitat	Method[a]	Small Mammals	Rabbits	Waterbirds	Small Birds	Invertebrates	Reptiles/ Amphibians	Reference
Australia	Northern Territory	Arid zone	FO	70 (all mammals)			14	26	18	Partridge et al. (1997)
	New South Wales	Open forest	FO	3/3[b]	82			41	3	Molsher (1999)
	Western	Semiarid	% number	18	37		10	28	7	Risbey et al. (1999): Table 2
Ecuador	Galápagos	Dry coastal	FO	25		14	14	21	14	Konecny (1987*b*)
Japan	Iriomote Island	Subtropical forest	FO	10		3	23	35	3	Watanabe et al. (2003)
Mexico	Socorro Island	Dry coastal	FO	90			23	74	43	Rodriguez-Estrella et al. (1991)
New Zealand	Little Barrier Island	Coastal moist	FO	5–32		4–43	5–18	14–16		Marshall (1961)
	Orongorongo Valley	Forest/river valley	% weight	43/8[b]	23	1–4	4	<5		Fitzgerald and Karl (1979)
	Campbell Island	Scrub, grassland	FO	95		5	35	60		Dilks (1979)
	Herekopare Island	Dense scrub	FO			87	3	47	tr.	Fitzgerald and Vietch (1985)
	Hawke's Bay	Farmland	% weight	39/12[b]	3	1–4	24	2		Langham (1990)
	Stewart Island	Coast and interior	FO	93 (rats)		6–11[c]	44	26	24	Karl and Best (1982)
	Stewart Island	Scrub/ wetland	FO	83 (rats)			27	8	1	Harper (2004)
	Kermadec Islands	Forest[d]	FO	76			35	58		Fitzgerald et al. (1991)
United States	Hawai'i Island	Montane	FO	87			68	17		Snetsinger et al. (1994)
		Montane	FO	48/95[b]			12	46		Amarasekare (1994)
		Montane wet	FO	75/52[b]			68	59		Smucker et al. (2000)
		Subalpine dry	FO	29/76[b]			53	47		Smucker et al. (2000)
		Lowland dry	FO	0/89[b]			21	68[e]		Smucker et al. (2000)

	Coastal to subalpine	FO	89		28	54		Hess et al. (2007)
Maui Island, Hawai'i	Montane wet	FO	85		39	9		Kowalsky et al. (2002)
Various Hawai'i	Various	FO	37/73[b]		37	67	tr.	Mostello (1996)
Jarvis Island	Coral atoll	% volume	2	97		tr.	tr.	Kirkpatrick and Rauzon (1986)

[a] FO, frequency of occurrence or the percentage occurrence in stomach sampled; % number, percentage of items sampled in stomachs sampled; % weight, the average percentage weight in stomachs sampled; %volume, average percentage volume in stomachs sampled. Sample sizes, methods, and definitions of prey types varied between studies so numbers are for relative comparison only.
[b] Rat/mouse frequency of occurrence, because rat and mouse data given separately in original paper.
[c] Penguins (*Eudyptes* spp.) and Sooty Shearwaters (*Puffinus griseus*).
[d] October sample only.
[e] Includes marine invertebrates.

2004); the last population of Stephen Island Wren (*Xenicus lyalli*) of New Zealand (Fuller 2001); and the Socorro Dove (*Zenaida graysoni*) from Socorro Island, Mexico (Jehl and Parkes 1983). Seitre and Seitre (1992) credited cats with the extinction of ground doves (*Gallicolumba* spp.) in French Polynesia.

King (1984) considered cats to have been at least partially responsible for the extinction of six New Zealand endemic species. Endemic rice rats (*Oryzomys* spp.) occur only on Galápagos islands without cats, a possible result of past cat predation (Konecny 1983). Dickman et al. (1993) and Smith and Quin (1996) suggested that cats might have been responsible for the regional extirpation of numerous small Australian native mammals. However, Abbott (2002) cautioned that cats were likely just one among a number of factors involved. Cats contributed to the extinction of 45 bird species in Hawai'i (Berger 1981) and remain a major predator of native Hawaiian birds (Snetsinger et al. 1994, Hu et al. 2001, Kowalsky et al. 2002, Hess et al. 2004).

At the community level, cats at two California sites reduced the diversity and density of native birds and densities of native mammals when present (Hawkins 1998, Crooks and Soulé 1999). In an experimental effort in Australia, Risbey et al. (2000) showed that native small mammals, but not reptiles, decreased where cats became their main predators, following control of foxes, which served as cat competitors or predators. Taylor (1979) suggested that the Macquarie Island parakeet (*Cyanoramphus novaezelandiae erythrotis*) coexisted with feral cats for 60 yr, until rabbits were released on Macquarie in 1879, providing a stable winter food base sufficient for an increased cat population to exterminate the parakeet. Medina et al. (2011:3507) concluded that the presence of such introduced alternative prey "significantly increased the impact of feral cats on birds." Van Heezik et al. (2010) found that predation by free-ranging domestic cats in one New Zealand city was sufficient to make the continued presence of several bird populations possible only through immigration from surrounding areas.

Gastrolobium spp. (Fabaceae), an important food for some Australian native species, produce fluoroacetate, the active ingredient in Compound 1080, used for predator control (Twigg and King 1991). Peacock et al. (2011) reviewed historical records in southwestern Western Australia and documented secondary poisoning of cats that consumed remains of bronzewing pigeons (*Phaps chalcoptera* and *P. elegans*) and marsupials that feed on *Gastrolobium*. The presence of *Gastrolobium* may provide a biochemical defense allowing the persistence of native species in the face of cat predation (Short et al. 2005, Peacock et al. 2011). It would be interesting to examine cat predation in similar ecosystems where native species feed on plants with secondary metabolites potentially lethal to cats and other carnivores.

DISTURBANCE AND BITES: Free-ranging and feral cats dig in gardens, defecate in children's sandboxes and on lawns, make noise, pose a threat to people with asthma, leave a urine stench, and provoke barking by dogs (Proulx 1988, Jarvis 1990, Natoli 1994, Baker 2001). In a California suburban study, approximately 9,000 (2,000 feral) cats produced 14 to 63 kg/ha/yr of feces (28% from feral cats), excluding feces from litter boxes dumped outdoors by their owners (Dabritz et al. 2006).

In the United States, at least 66,000 people are bitten annually by cats, or 21 per 100,000 (O'Neil et al. 2007). In Guam, the incidence was eight per year or 5.5 per 100,000 (derived from Haddock and Cruz [1996]). The difference in incidence may be caused by differences in abundance of cats, ownership, or willingness to seek treatment. In both Australia and the United States, the majority of victims tend to be women (MacBean et al. 2007, O'Neil et al. 2007). Left untreated, up to half of cat bites become infected (Goldstein 1992).

DISEASES TRANSMITTED BY CATS TO HUMANS AND OTHER ORGANISMS: *Diseases of humans:* Cats can transmit a variety of diseases, primarily through their feces, to humans, especially to children and individuals with suppressed immune systems. The full extent of the cost of feral and free-ranging cats to public health is a subject of ongoing study.

Perhaps the most important disease is toxoplasmosis, caused by the protozoan brain parasite *Toxoplasma gondii*, which probably was introduced to the Pacific islands via ships' cats (Lehmann et al. 2006). Cats are the definitive host: the disease occurs only when cats are present. Toxoplasmosis transmission to humans has traditionally been associated with eating uncooked meat or soil, but it can also be acquired by inhalation from dust, soil, or cat litter or even from water contaminated by cat feces (Teutsch et al. 1979, Stagno et al. 1980, Benenson et al. 1982, Dabritz et al. 2006). Toxoplasmosis stimulates sexual arousal pathways in mice confronted with cat urine, suppressing the normal adversion of mice to anything feline and facilitating the transmission of toxoplasmosis to additional cats (House et al. 2011).

Primary infection with toxoplasmosis during human pregnancy produces a higher incidence of miscarriage and stillbirth (Torrey and Yolken 2003). Children who contract congenital toxoplasmosis in the womb can suffer blindness, encephalitis, and developmental retardation (Torrey and Yolken 2003).

In immunocompromised patients such as those with AIDS or being treated for cancer, toxoplasmosis can be fatal, both from initial infection and from reactivation of a latent infection (Montoya and Liesenfeld 2004). In human adults, the presence of antibodies to *T. gondii* has been associated with a number of neurological disorders, including schizophrenia (Torrey et al. 2007), epilepsy (Palmer 2007), altered personality traits (McAllister 2005), "aggregate neuroticism" (Lafferty 2006), autism (Nakamura et al. 2010), brain cancers (Thomas et al. 2011), and increased risk of suicide of women over 60 yr of age (Ling et al. 2011). Although these findings currently remain simply correlations, a physiological explanation exists that may explain some of them. Toxoplasmosis increases the production of dopamine, a neurotransmitter, which promotes reward seeking and risk taking (Arias-Carrión and Pöppel 2007). Dopamine has also been linked with various human diseases such as schizophrenia and attention deficit disorder (Prandovszky et al. 2011). Antidopaminergic drugs used to treat schizophrenia in humans also suppress the effects of toxoplasmosis on rodents (Webster et al. 2006).

Infection rates determined by a variety of methods for feral cats were 4.9% in Western Australia (Adams 2003 in Henderson 2009); 18% in the Philippines (Advincula et al. 2010); 7%–37% in Hawai'i (Wallace 1971, Danner et al. 2007); 8%–29% in South Korea (Kim et al. 2008); 50% in Tasmania (Milstein and Goldsmid 1997); 86% on an atoll in the eastern Carolines (Wallace et al. 1972); and 89% on Kangaroo Island, Australia (O'Callaghan et al. 2005).

Cat-scratch disease, a disease of warmer and more humid areas, is associated with cat bites or scratches and infection by *Bartonella* (*Rochalimaea*) *henselae* and *B. clarridgeiae* via flea feces (Jameson et al. 1995, Kelly et al. 2005). *Bartonella henselae* has been found in the Philippines, Australia, Indonesia, New Zealand, and Hawai'i (Demers et al. 1995, Branley et al. 1997, Chomel et al. 1999, Marston et al. 1999, Kelly et al. 2005) and can be assumed to occur throughout the Pacific region. *Bartonella clarridgeiae* has been found in the Philippines, Indonesia, and New Zealand (Kelly et al. 2004). Cat-scratch disease presents as skin lesions at the site of the scratch or bite, with swelling of the lymph glands following within 2 weeks. The disease usually resolves within 3 months but may progress to pulmonary disease, endocarditis, fever, and coma with "transient blindness" (Regnery and Tappero 1995). In HIV patients, cutaneous and subcutaneous vascular lesions are believed to be caused by *B. henselae*, also associated with household cats and cat fleas (Regnery and Tappero 1995). Feral cats may be a reservoir that passes *Bartonella* to domestic cats allowed to roam free, which may then infect humans (Heller et al. 1997).

Cats are associated with a variety of human gastric diseases. *Cryptosporidium*, a protozoan genus that causes diarrhea in both humans and animals, has traditionally been associated with the species *parvum*, but there is increasing recognition that *C. felis*, usually associated with cats, can infect humans, especially immunocompromised individuals (Matos et al. 2004). In Korea, 91% of feral cats carried *Helicobacter* sp. (Ghil et al. 2009), which has been linked to gastric disease in humans (Heilmann and Borchard 1991). Cats also carry *Campylobacter jejuni* and *C. upsaliensis*, transmitting gastroenteritis to humans through their feces (Deming et al. 1987, Baker et al. 1999), although transmission from food is much more common (Altekruse et al. 1999). Contamination by cat feces can also be a source of yersiniosis (*Yersinia enterocolitica*) and pseudotuberculosis (*Yersinia pseudotuberculosis*) (Yanagawa et al. 1978, Fukushima et al. 1989).

Murine typhus can be transmitted by the cat flea (*Ctenocephalides felis*) from feral cats to free-ranging cats to humans. Hawai'i and New Zealand have occasional outbreaks (Roberts and Ellis-Pegler 2001, Hoskinson et al. 2003). Cat fleas transmit a similar disease called cat-flea rickettsiosis caused by *Rickettsia felis*, which has been reported in New Zealand, Japan, Indonesia, Taiwan, and Australia (Kelly et al. 2004, Pérez-Osorio et al. 2008, Tsai et al. 2009). Plague (*Yersinia pestis*) occurred in Hawai'i and other islands during the 1899 pandemic and persisted with occasional human cases in rural areas of Hawai'i until 1949 (Ikeda 1985). There is some disagreement as to whether plague still occurs in Hawai'i (Tomich et al. 1984, Ikeda 1985). As of 1998, plague was absent from the Pacific (Centers for Disease Control 2005*a*). On the U.S. mainland, cats can spread the disease by bringing infected fleas into the house or by coughing on humans (Centers for Disease Control 2005*b*).

Visceral and ocular larva migrans are caused by human consumption of unwashed vegetables or earth contaminated with cat feces containing *Toxocara cati* (Glickman and Schantz 1981). Ocular larva migrans occasionally results in blindness (Sakai et al. 1998). Playgrounds, especially sandboxes, appear to be especially high-risk areas (Chorazy and Richardson 2005). A children's sandbox and cat feces were also linked to a Florida outbreak of *Ancylostoma* spp. (Centers for Disease Control 2007), responsible for cutaneous larva migrans, a hookworm skin disease contracted following contact with soil in tropical moist areas (Green et al. 2001). *Ancylostoma* is a frequent helminth parasite of cats in Hawai'i (Ash 1962).

Stray cats in Indonesia, where H5N1 influenza has become endemic, are also killed by

H5N1 (Butler 2006). If the disease reaches the Pacific islands, Australia, and New Zealand, feral and free-ranging cats may become a threat to human health (Kuiken et al. 2004).

In the United States, cat bites yield a "complex microbiologic mix" that usually includes *Pasteurella multocida*, capable of producing endocarditis and meningitis in humans (Talan et al. 1999).

Cats appear to be poor reservoirs of leptospirosis (Hathaway and Blackmore 1981), a disease of concern in the Pacific islands (Berlioz-Arthaud et al. 2007), but 34% of Hawaiian cases were reported following exposure to cats (Katz et al. 2002).

Rabies was successfully eradicated from Guam (Glosser and Yarnell 1970) and was absent from the Pacific during 1970–1998, except for the Philippines and Indonesia (RABNET 2011). Rabid cats are more likely than dogs to be the source of exposure for humans on the U.S. mainland (Eng and Fishbein 1990, Craven et al. 1993).

Cats as vectors for diseases of other animals: Toxoplasmosis has been reported in several Hawaiian sea and land birds, including the endangered ʻAlalā (*Corvus hawaiiensis* [Work et al. 2000, 2002]) and the endangered Hawaiian monk seal (*Monachus schauinslandi*) (Honnold et al. 2005, Dawson 2010). The disease has been reported in more than 30 native Australian species (Henderson 2009). Antibodies to toxoplasmosis were found in both Galápagos penguins (*Sphensicus mendiculus*) and flightless cormorants (*Phalacrocorax harrisi*) in the Galápagos Islands (Deem et al. 2010). Cats have been linked to an epizootic of toxoplasmosis in captive kangaroos (*Macropus* spp.), wallabies (*Wallabia eugenii*), and potaroos (*Potorous tridactylus*), with mortality within 4 hr of onset of symptoms (Patton et al. 1986). Toxoplasmosis was also responsible for mortality of southern sea otters (*Enhydra lutris nereis*) off California (Jessup et al. 2007). The full extent of the effect of toxoplasmosis on native species in the Pacific remains unknown, and systematic surveys are urgently needed.

The role of cats in the transmission of bovine tuberculosis (*Mycobacterium bovis*) is of concern. In New Zealand at five sites, 0.4% to 14.2% of feral cats were found to be infected, and feral cats appear to amplify the disease but are unable to sustain tuberculosis in the absence of the brushtail possum (*Trichosurus vulpecula*), the reservoir or maintenance species (Coleman and Cooke 2001). Morris et al. (1994) cautioned that the feral mammal species responsible for the maintenance of bovine tuberculosis may vary by location, depending on ecological conditions. Cattle ranching is found throughout the Pacific, and bovine tuberculosis is present on several islands or has recently been eradicated, as in Australia (Tweddle and Livingstone 1994). The role of feral cats and other wildlife has not been widely examined, despite continuing calls for a better understanding of the role of zoonotic tuberculosis (Cosivi et al. 1998, Schiller et al. 2010).

Feline immunodeficiency virus (see section on Reproduction) is a highly infectious disease of cats that has passed from feral cats to the endangered Tsushima leopard cat, *Prionailurus* (*Felis*) *bengalensis euptilurus*, on Tsushima Island, Japan (Nishimura et al. 1999). A second critically endangered species, the Iriomote cat (*Felis iriomoensis*), has tested positive for several cat virus antibodies (foamy virus, feline calcivirus, coronavirus, and feline syncytium-forming virus); these are not generally regarded as serious pathogens of domestic cats, but the past or current effects on this species confined to a single island are unknown (Mochizuki et al. 1990). Leopard cats from Taiwan have also tested positive for feline parvovirus but not for other diseases that require close contact, suggesting that the two felid species rarely interact (Ikeda et al. 1999).

Extrapolating from table 7 of Dickman (1996), it appears that 38% of 126 pathogens are shared between cats and native vertebrates. Denny and Dickman (2010:22) citing Moodie (1995) found that "at least 30" pathogens "out of more than 100" overlapped. Dickman (1996) cautioned that too little research has been done to understand the consequences of these pathogens for Australian wildlife.

Unfortunately, although there is an extensive field of veterinary medicine directed at owned cats, relatively little attention is paid to feral cats and to wildlife, and even less to their interactions. Finally, we do not know the role of history and changing environments in relation to disease. Current conditions may tell us little; most of the damage, as with diseases and native peoples in the Pacific (e.g., Bushnell 1993), may already have been done.

Beneficial Aspects

Cats owe their wide distribution in the Pacific to their use as rat predators on sailing ships during long voyages (Todd 1977): "On the *Resolution*, a midshipman's cat brought him the rats it caught; he gave the cat the forepart and he ate the back part, cleaned, roasted and prepared" (Beaglehole 1969:135). Cats were sufficiently valuable that when they were stolen from one of Cook's ships during its stay in Tonga in 1777 the culprits were flogged, and an officer reported that cats "can be but ill spared from Ships so overrun with rats as ours" (Beaglehole 1967:133).

Cats traditionally have been used to protect grain and silage (Elton 1953). The maximum weight of a Norway rat (*Rattus norvegicus*) taken by cats is less than 200 g, limiting depredation to juvenile rats, as opposed to 300–400 g adults (Childs 1986). Adult black rats weigh only 140–200 g in Hawai'i (Kramer 1971), suggesting that cats would be effective predators of all ages of that species.

Indoor cats provide substantial quality-of-life benefits, both psychological and physiological, to their owners (Karsh and Turner 1988). Natoli (1994) suggested that in many Italian cities those who care for cats are often old and lonely. Similarly, she noted that cats have become iconographic associations of certain cities and are one of the few accesses to nature for city dwellers.

In the Pacific, cats were a past diet item of Maori, Marquesan, and Fijian peoples (Cruise 1823, Kabris and Terrell 1982, Gibbons 1984), and they remain a food for Australian aboriginal peoples practicing their traditional lifestyles, cats having replaced indigenous species that have become rare (Burbridge et al. 1988, Bird et al. 2005). Cats are still consumed in China and Korea (Podberscek 2009, Macartney 2010) and perhaps elsewhere, including New Guinea (Baldwin 1980).

Regulatory Aspects

Nations tend to have either strong unitary governments that can set policy for feral cats down to the local level, or federated governments, with the regional states maintaining primary control, except over national lands, like national parks, so that policies are more variable. Whatever the structure, there is confusion as to the boundary between feral and owned cats, even if a country has laws and statutes in place to deal with the feral cat issue.

AUSTRALIA: In Australia there are national, state, and local laws concerning feral cats. The National Parks and Wildlife Act of 1972 allows cats to be destroyed if found in a park or designated sanctuary. The Endangered Species Protection Act of 1992 (subsumed in The Environment Protection and Biodiversity Conservation Act of 1999) set in motion a process that culminated in a Threat Abatement Plan for Predation by Feral Cats (1999 and updated in 2008) to assign responsibility for reducing their effect on the Australian biota (Denny and Dickman 2010). Individual states have subsequently developed their own legislation. At the local level, authorities have implemented civic orders requiring various measures such as "no cat zones," curfews, and indoor confinement (e.g., Baker 2001, Buttriss 2001).

CHINA (TAIWAN): In China (Taiwan) the main law of relevance is the Wildlife Conservation Law (1989, amended 2005) to "conserve wildlife, protect species diversity and maintain the balance of natural ecosystems" (Chap. 1, Article 14): "Lost or wild animals which are not endemic to Taiwan may be dealt with by the Authorities if found to be damaging Taiwan's plant or animal habitats" (Republic of China 2009). The Animal Protection Act (1998) requires that cats fed by people also receive medical attention and a safe environment (Agoramoorthy 2009).

JAPAN: In Japan the feral cat seems to fall though the legal cracks for a variety of cultural reasons (Takahashi 2004). The Animal Protection (1973) and Rabies Prevention

(1950) laws apply to domestic but not feral cats. An Alien Species Law (2004) does not apply because feral cats antecede the Meiji period (the 1870s) that was set as an arbitrary cutoff for the arrival of alien species (Takahashi 2004). However, the migratory bird treaty with the United States requires both countries to "control the introduction of live animals . . . that could disturb the ecological balance of unique island ecosystems" (Harrison et al. 1992). Feral cats are designated as game animals under the Wildlife Protection and Hunting Law (1918), but the criteria for distinguishing them from free-roaming house cats remain ambiguous (Takahashi 2004). More recently, management of pest species has devolved to the prefecture level through the voluntary Specific Wildlife Management Planning System (Knight 2006). Local and national coordination was used to trap cats in various islands of the Okinawa and Ogasawara Groups (Izawa 2009). The same local jurisdictions have adopted policies regarding domestic pet management (Takahashi 2004, Izawa 2009).

NEW ZEALAND: Despite the lack of a law for endangered species (Seabrook-Davison et al. 2010), New Zealand has perhaps the strongest laws and policies concerning alien species in the Pacific and has implemented vigorous efforts to reduce their impact (e.g., Veitch and Clout 2002). Under the Animal Welfare Act of 1999 (Section 14, 2), it is an offense to abandon a cat. In 2007, a code of welfare was issued under the act for cats that depend partially or entirely on humans for their food, but not for feral cats, which are independent of humans and as pests may be killed under the Biosecurity Act of 1993 (National Animal Welfare Advisory Committee 2007). Farnsworth et al. (2010) noted that control of feral cats outside preserves or parks is implemented by local councils, using any method that is considered humane.

PHILIPPINES: The Animal Welfare Act of 1998, Section 6, makes it unlawful to kill any animal except when done for the purpose of animal population control. The Wildlife Resources Conservation and Protection Act of 2001 distinguishes between "exotic" and nonnative species. Exotic species that are maintained or bred in captivity fall under its jurisdiction, but feral cats do not appear to be a priority compared with illegal trade and other problems.

UNITED STATES: The State of Hawai'i is representative of jurisdictional issues for feral cats. Federal lands such as national parks, wildlife refuges, and military lands are subject to national laws and regulations that are uniformly hostile to the presence of feral cats (Mattheis 2002). The State of Hawai'i will similarly remove predators deemed harmful to wildlife, and it is illegal to release a cat into the wild, resulting in the "take" (kill) of a migratory, threatened, or endangered bird. It is not clear if this has ever been enforced. The U.S. Endangered Species Act of 1973 has legal consequences for any direct or indirect take of a species listed as endangered or threatened so that a local jurisdiction allowing cat colonies near endangered species appears to be liable for any depredation by cats (Hatley 2003). At the local level, in the City and County of Honolulu, cats may not be legally fed in parks where signs prohibit it; however, the city has allowed the establishment of official Trap-Neuter-Release colonies on city land. The law notwithstanding, both the city and state tolerate unofficial colonies on public land surrounding schools, office buildings, and hospitals.

GEOGRAPHIC DISTRIBUTION

The cat occurs throughout the Pacific (King 1973, Baldwin 1980, Atkinson and Atkinson 2000) (Table 2); however, in many locations it is not clear if the cats are feral or free-ranging domestics. For example, Pernetta and Watling (1978:229) reported cats as widespread throughout the Fijian islands, but "no feral populations of these animals are known at present," but Gibbons (1984:86) reported that in Fiji "feral populations of cats have become established on virtually all inhabited islands." In addition, cats are often absent from smaller islands, particularly those without human activity (Atkinson and Atkinson 2000).

HABITAT

Cats can live in almost any environment where humans are present. Individuals move

TABLE 2

Geographic Distribution of Feral Cats in the Pacific Region

Locality	Present	Absent	No Information	Reference
America Samoa	X			Amerson et al. (1982)
Austral Islands			X	
Australia	X			Abbott (2002)
Baker and Howland	X			Atkinson and Atkinson (2000)
Bonin Islands	X			Obana (1877) in Kawakami and Kujita (2004)
Caroline Islands	X			Wallace et al. (1972)
Isla de Cedros, Mexico	X			Mellink (1993)
Clarion Island, Mexico		X		Everett (1988)
Clipperton Island		X		Pitman et al. (2005)
Cocos Island, Costa Rica	X			Thomas (1960) in Hertlein (1963)
Cook Islands	X			Robertson and Saul (2007)
Easter Island[a]	X			Mann et al. (2008)
Fiji	X			Pernetta and Watling (1978), Gibbons (1984)[b]
French Polynesia	X			Borden (1961), Seitre and Seitre (1992)
Galápagos Islands	X			Konecny (1983)
Gilbert Islands (Kiribati)	X			Amerson (1969)
Gorgona Island, Colombia		X		M. Womack, Princeton University, pers. comm.
Isla Guadalupe, Mexico	X			Pitman et al. (2004)
Guafo Island, Chile	X			Reyes-Arriagada et al. (2007)
Guam	X			Rogers (1995)
Hawaiian Islands	X			Kramer (1971)
Henderson Island, Chile		X		Wragg and Weisler (1994)
Indonesia	X			For small islets, de Korte (1991)
Japan (main islands)	X			Izawa (2009)
Juan Fernández	X			Bourne et al. (1992)
La Plata Island, Ecuador		X		Eradicated (Campbell et al. [2011])
Line Islands (Kiribati)	X			Amerson (1969), Perry (1980)
Lobos Islands, Peru	X			Coker (1919)
Lord Howe Island		X		Eradicated 1980s (Miller and Mullette [1985])
Malpelo Island, Colombia		X		Graham (1975); M. Womack, Princeton University, pers. comm.
Marquesas	X			Hahn (1896); J.-Y. Meyer, pers. comm., 2007
Marshall Islands	X			Borden (1961)
Micronesia, Fed. States	X			Fritts and Rodda (1998)
Nauru	X			Pacific Biodiversity Information Forum (2009)
New Caledonia	X			Gargominy et al. (1996)
New Guinea	X			George (1973)
New Zealand	X			Fitzgerald (1990)
Niue	X			Powlesland et al. (2000)
Norfolk Island	X			Hill (2002)
Northern Mariana Islands	X			Reichel (1991)
Okinawa	X			Izawa (2009)
Palau	X			Wiles and Conry (1990)
Palmyra	X			"Not self sustaining" (B. Flint, pers. comm.)
Papua New Guinea	X			Baldwin (1980), Flannery (1995)
Phoenix Islands (Kiribati)	X			Atkinson and Atkinson (2000)
Philippines	X			Valdez and Recuenco (2003)
Pitcairn Island		X		Eradicated (Bell and Bell [1997])
Sala y Gómez, Chile		X		Vilina and Gazitua (1999)
Samoa	X			Peale (1848)
Socorro Island	X			Jehl and Parkes (1983), Rodriguez-Estrella et al. (1991)
Solomon Islands	X			Atkinson and Atkinson (2000)
Starbuck Island	X			Kirkpatrick and Rauzon (1986)
Taiwan	X			Wu et al. (2009)

TABLE 2 (continued)

Locality	Present	Absent	No Information	Reference
Tokelau Island	X			Kirkpatrick (1966)
Tonga	X			Rinke (1986)
Tuamotu Island	X			Thibault (1988)
Tuvalu	X			Hedley (1896)
Vanuatu	X			Vanuatu Government (2009)
Wake Island		X		Eradicated (Rauzon et al. [2008])
Wallis and Futuna	X			King (1973)

[a] Isla de Pascua or Rapa Nui.
[b] Pernetta and Watling considered the cat domestic only and uncommon, but Gibbons stated that feral populations are well established.

between domestic situations and a feral existence, often with intermediate commensal relationships with humans (Patronek et al. 1997). Feral cats are less likely to become established or persist where similar or larger predators and competitors are already present (see Predators in section on Natural Enemies) and where severe winters limit food without human subsidies (Liberg 1984, Coleman and Temple 1993). In the Pacific region, they are present from subantarctic islands, to tropical rain forests in New Guinea, to deserts in Australia, to numerous oceanic islands, to the tops of Hawaiian volcanoes, to the centers of cities throughout the region.

HISTORY

The domestic cat is sometimes regarded as a distinct subspecies of the wildcat, *F. silvestris*, which diverged from its nearest relative, the Near-Eastern wildcat (*F. s. lybica*), approximately 131,000 yr ago in the Fertile Crescent region of the Middle East (Driscoll et al. 2007). Archaeological evidence from Cyprus suggests that the cat was tamed at least 9,500 yr ago (Vigne et al. 2004) and was fully domesticated 4,000 yr ago in ancient Egypt. It was distributed along trade routes, reaching China just over 2,000 yr ago (Serpell 2000). Later, the cat was spread farther with the expanding Roman Empire, both as an exotic pet and because of its utility in controlling rodents (Zeuner 1963, Serpell 2000). By the 1700s, the cat followed the establishment of European trade and settlements worldwide on ocean-going ships infested with rats. Populations of cats were maintained in these settlements as pets, predators of agricultural pests, and in dockyards for rodent control (Case 2003).

Only anecdotal accounts exist of the history of cat introductions for much of the Pacific region. Given their widespread use on ships, cats likely appeared on islands shortly after first European contact but may not have been reported until long afterward. Cats went ashore with the wreck of the *Nuesta Señora de la Concepción* on Saipan in 1638 and they "soon multiplied" (Rogers 1995:20). Cats were present on Tinian (Northern Mariana Islands) in the mid-1800s and by 1900 were noted in a free-ranging state (Wiles et al. 1990). They were supposedly introduced into Pohnpei between 1832 and 1851 (Jewett 1895).

In 1774, James Cook's voyage left behind 20 cats on Tahiti and several on Ulieta (now Ra'iatea) and Huahine, but the Spanish had already left cats on Tahiti during a previous visit, "several of which are said to have already turn'd wild and retir'd to the mountains" (Beaglehole 1967:973; 1969). Peale (1848:211) reported that on Upolu, Samoa, "a passion arose for cats, and they were obtained by all possible means from the whale ships visiting the islands" and then "the cats have multiplied and become wild." By 1804, cats were already feral in the Marquesas (Hahn 1896). On Erromanga, cats were traded for boatloads of Polynesian sandalwood (*Santalum insulare*) (Turner 1861).

In New Zealand, cats likely arrived with the first explorers in 1769 (Fitzgerald 1990) but remained close to human settlements until about 1870 (Wilson 2004). Ghill (1885, quoted in Atkinson and Atkinson [2000]) stated that cats were introduced to Rarotonga in the southern Cook Islands by early missionaries in the 1820s to help keep down native rats but then turned their attentions to native birds, leading to several extinctions. In Australia, feral cats spread from multiple coastal introductions in the period 1824–1886, so that by 1890 nearly the entire continent had been colonized (Abbott 2002, 2008).

Cats were present in the Galápagos by 1869 (Salvin 1876). In the southern Cook Islands, cats were probably introduced to Mauke by 1825 (Lever 1987) and to Rarotonga by 1828 (Williams 1845). Feral cats are now present on almost all inhabited islands in Fiji, having been introduced in the early 1800s and becoming abundant by the 1870s (Gibbons 1984).

Kramer (1971) suggested that cats were rare or absent in Hawai'i in 1825 because the naturalist on HMS *Blonde* failed to note them during visits to O'ahu and Maui. Brackenridge (1841) reported "wild" cats on the island of Hawai'i in 1840. Spaulding (in Kramer 1971) reported a ship paying for supplies in 1850 with a pair of Manx cats, suggesting that cats were still rare, or at least that Manx had novelty value. However, just a few years later, Mark Twain (1866:1) vividly described the abundance of cats in Honolulu: "companies of cats, regiments of cats, armies of cats, multitudes of cats, millions of cats, and all of them sleek, fat, lazy, and sound asleep."

In the Bonin Islands, cats became feral following their introduction as the islands were settled in 1830 (Obana 1877 in Kawakami and Kujita 2004). On Palmyra Island, cats appear to be occasionally reintroduced by visiting yachts (B. Flint, pers. comm.), and this could be a problem on other previously cat-free islands.

On Jarvis Island, cats were introduced as late as 1885, reintroduced with settlers in 1938 (Rauzon 1985), and then eliminated by 1983 (Kirkpatrick and Rauzon 1986).

PHYSIOLOGY

Body temperature is usually within the range of 38°–39.2°C (Case 2003). The thermoneutral zone is between 35°C and 38°C (National Research Council 2006). The cat maintains its body temperature behaviorally in several ways. Heat is dissipated through increased respiration, by evaporation of saliva applied to the coat during grooming (Case 2003), and by excreting sweat through glands located on the hairless pads of its paws (Lloyd 1963). Between 36° and 40°C, cats begin to show signs of heat stress by panting heavily. Cats become more active below 20°C, presumably to increase heat production, and they begin to shiver below 5°C (Forster and Furguson 1952 in National Research Council 2006). Behaviorally, cats respond to cold by seeking warm areas or by curling up to reduce surface area (Case 2003).

Heartbeat rate varies with age, size, and physiological state but is generally within the range of 120–240 beats per minute (Case 2003). Average respiratory rate is 25 breaths per minute (Case 2003). Metabolic energy use for the cat is recorded variably from 31 to 100 kcal/kg/day at room temperature from different studies, but because the cat's thermoneutral zone is above standard room temperature, cold thermogenesis could have influenced some of these results (National Research Council 2006). Dietary thermogenesis is not recorded but most likely is 10% of the metabolic rate, as in both dogs and humans (National Research Council 2006). Cats require approximately 290–380 kJ/kg/day to maintain body weight (National Research Council 1986). Cats have low amounts of subcutaneous fat and cannot stockpile energy, making continuous hunting necessary for survival (Jones and Coman 1982).

In many areas where there is no source of freshwater, well-fed cats can obtain all their necessary water requirements from their prey (Prentiss et al. 1959) and are capable of surviving on seawater under certain circumstances (Wolf et al. 1959).

Cat eyes are large compared with head size and set forward on the face, giving binocular vision over approximately 120 degrees, plus lateral vision of ~80 degrees on each side, for a total range of vision of 280 degrees, with a protruding curved cornea further enhancing visual range (Case 2003). Cats do not possess extreme visual acuity but are specialized to detect movement very well. Low-light vision is enhanced by the large size of the cornea and the ability to open pupils very wide to illuminate a large portion of the retina. The short distance from pupil to retina results in minimal scattering of light and better illumination of receptor cells. Specialized reflective cells immediately behind the retina reflect unabsorbed light back toward the visual receptors to provide light absorption in dim environments (Case 2003). Cat eyes contain a high proportion of rods (the most sensitive visual receptors) and fewer cones (which respond to bright lights and colors). They have dichromatic color vision, seeing only limited colors (green and some blue but not red), and are slightly myopic, with better vision ~2–7 m away, and poor focus at close range. Cats also have a third eyelid (an extra membrane between eyelid and eyeball) for protection and tear secretion dispersal (Case 2003).

The literature suggests that cats do not exhibit a clear pattern of circadian activity and can be active at any time, although individual cats or populations can show greater activity during certain times (National Research Council 2006). In Hawai'i, Hess et al. (2004) found that cats were most active during 2000–2200 hours, with a lesser peak at 0600–0800 hours.

Cats, like felids in general, require a high protein diet (12–18%), because they cannot synthesize niacin, vitamin A, taurine, or arachidonic acid to produce prostglandins (MacDonald et al. 1984). They also require arginine, large amounts of thiamine, and sulphur-containing amino acids (Bradshaw et al. 1999). MacDonald et al. (1984) argued that retention of hunting skills by domestic cats was necessary to provide nutrients that cats cannot synthesize and that this ability to hunt in turn prevented full domestication, providing the continuing option of reverting to a feral existence.

REPRODUCTION

Cats are highly efficient breeding machines. Female cats are sexually mature as early as 7 months and can produce 1.5–2 litters a year with one to six kittens each (Turner and Bateson 2000, Nutter et al. 2004). They have a short gestation period (63 days) and no delayed implantation. In areas with seasonality, cats become ready to breed as the day length increases in the spring, timing reproduction so that resources are available to support pregnancy and lactation (Turner and Bateson 2000). Kittens wean onto solid food between 4 and 7 weeks of age (Turner and Bateson 2000). Kittens stay with their mothers for roughly 6 months and are sometimes "mothered" communally by more than one female (Turner and Bateson 2000).

Mothers start bringing prey items to their kittens at about 4 weeks of age and take an active role in the development of their kittens' predatory behavior (Leyhausen 1979). However, maternal training is not necessary, because 45% of kittens raised alone killed rats or mice without training, and even kittens raised as vegetarians in the laboratory killed but did not eat rats (Kuo 1930).

POPULATION DYNAMICS

Bernstein (2005) estimated that there were 200 million pet or owned cats in the world. The United States alone may have 90 million owned cats and another 25–100 million unowned cats, based on a range of estimates (Robertson 2008, Lepczyk et al. 2010).

In addition to indoor cats, free-ranging cat populations can be subdivided into three rather fluid subgroups: free-ranging domestic cats that have a home to return to, vagrant and abandoned (unowned) cats that retain some association with humans through local feeding or cat colonies, and feral cats that are independent of and are not intentionally fed by humans (cf. Patronek 1998). Up to 36% of owned cats started as strays before being taken in, and numerous owned cats are in turn abandoned (Patronek et al. 1997, Rochlitz 2000).

Felis silvestris, the ancestor of the domestic cat, is believed to be solitary when adult, but the domestic cat in contrast can vary its sociality, depending on its sex, food, and other environmental factors (Bradshaw 1992, Liberg et al. 2000). Male feral cats typically have larger hunting home ranges and are solitary. Females, when feral, can either be solitary or congregate in groups with other females, many of whom may be related (Turner and Bateson 2000).

Cats can move up to 200 km in a lifetime (Newsome 1991). The only landscape genetics study of feral cats found "High genetic diversity, low structure, and high numbers of migrants per generation" (Hansen et al. 2007:587). Pettigrew (1993) suggested the presence of a large "floater" population, in addition to the resident population. Low degree of structure and a large number of migrants suggest that efforts to control cats must be done at the right scale, which would need to be very large or very intensive if it were to be effective.

Home range size varies greatly depending on the environment, often being greater in what appear to be less-productive environments. Reported measurements also vary by time of day, sex, season, and duration and methodology of the study. On a small Japanese island of 1.25 km^2 where feral cats fed on fish waste at garbage sites, the home range was only 0.01 km^2 (Yamane et al. 1994). In New Zealand farmland, females had a range of 1.88–2.79 km^2, but home ranges in adjacent woodland were smaller (0.37–1.09 km^2); males had larger ranges that cut across habitat types: 2.76–3.00 km^2 (Langham and Charleston 1990). In Hawai'i, home ranges were 5.74 km^2 for males and 2.23 km^2 for females in montane wet forest (Smucker et al. 2000) and 14.18 km^2 for males and 7.72 km^2 for females in semiarid woodland (Goltz et al. 2008). In the Galápagos under arid conditions, home ranges were 3.04 km^2 for males and 0.82 km^2 for females (Konecny 1987*a*). In two semiarid environments in Australia, average ranges were 6.20 and 2.2 km^2 for males (Jones and Coman 1982, Edwards et al. 2001). In the Gibbon Desert, Australia, home ranges varied between 7.00 and 12.00 km^2 (Burrows et al. 2003). At high-latitude, food-poor Stewart Island, New Zealand, the average range was 20.83 km^2 (Harper 2004).

NATURAL ENEMIES

Predators and Competitors

Feral cats do not seem to become well established in areas with "mesopredators" that either compete with or prey upon cats. In New Zealand, Taylor (1984) suggested that stoats (*Mustela erminea*) outcompete feral cats, restricting their presence to larger islands and to areas either with rabbits or close to human habitation. Coyotes (*Canis latrans*) control cats in coastal southern California (Crooks and Soulé 1999). In the northeastern United States, probably representative of continental areas, Kays and DeWan (2004) speculated that coyotes and a small mustelid, the fisher (*Martes pennanti*), limit both feral cat numbers and their use of forested areas. In Hong Kong, cats are most common on Lantau Island, where the rare leopard cat (*Prionailurus bengalensis*) is absent (Pei et al. 2010).

In Australia, Abbott (2002) suggested that feral cats did not successfully colonize the interior until populations of competitors/predators were reduced, including the dingo (*Canis lupus dingo*), tiger quoll (*Dasyurus maculatus*), and the wedge-tailed eagle (*Aquila audax*), as well as the aboriginal peoples. Dingos appear to control cat numbers (Pettigrew 1993, Glen et al. 2007), and cats increased when dingoes and foxes (*Vulpes vulpes*) were "virtually eradicated" from a part of the Gibson Desert of Western Australia (Burrows et al. 2003).

Diseases and Parasites

Cats have a wide range of parasites and diseases. Moodie (1995) reported 15 viruses, 31 genera of bacteria, 17 fungi, and two algae as pathogens of cats and summarized the Australian records, including presence in feral cats.

Among the major diseases of importance to feral populations are feline calicivirus (FCV), feline herpesvirus (FHV), feline panleukopenia or parvovirus virus (FPV), feline leukemia virus (FeLV), and feline immunodeficiency virus (FIV).

Feline calicivirus (FCV) usually only causes low mortality, except in kittens; however, one strain, virulent systemic feline calicivirus (VS-FCV), produces elevated mortality in all age groups (Radford et al. 2007). FCV is more prevalent in crowded conditions, spreads through direct contact with body discharges, and can persist for months in both cats and the environment (Ossiboff et al. 2007, Radford et al. 2007).

Viral rhinotracheitis caused by a feline herpesvirus (FHV) is an upper-respiratory infection associated with high fever and mortality primarily in kittens (Merck 2008). Transmission is primarily by direct contact because the virus survives less than a day in the environment; many cats are latent carriers, resuming shedding of virus following stress (recrudescence), so a crowded environment can be an infectious one (Gaskell et al. 2007). Cohen et al. (2000) showed through models that once an FHV is introduced into a population, it tends to persist because of recrudescence and the turnover of individuals, such that there is a steady availability of newly susceptible cats. Moodie (1995) reported a New South Wales study that showed that 17% of feral cats from a dump site tested positive for antibodies for FHV, but only 9% were positive from a more isolated site.

Feline panleukopenia, parvovirus virus (FPV), also known as feline distemper or infectious enteritis, presents with symptoms of weakness, diarrhea, vomiting, and septic shock and is highly contagious and often fatal, especially in cats less than 5 months old. It is spread through direct contact or through contact with body secretions that can remain infectious in the environment for up to a year (Merck 2008). Cats develop temporary immunity if they survive, so the disease has repeated sporadic outbreaks every time a population of sufficient susceptible individuals accumulates. On small islands, the entire population may be susceptible, so FPV has been used as part of eradication efforts, although it has never proved sufficient by itself (Rauzon 1985, Veitch 1985).

Feline leukemia virus (FeLV) is spread through body fluids and requires close proximity, such as mutual grooming or even sharing a food bowl. Most cats recover, but roughly 30% develop severe depression of the immune system and anemia, eventually succumbing to opportunistic infections (Merck 2008).

Danner et al. (2007) reported a prevalence of 16.2% of FeLV on Mauna Kea Volcano on the island of Hawai'i. This was within the levels capable of significantly depressing feral cat populations in models (Fromont et al. 1997, Courchamp and Sugihara 1999). Lee et al. (2002) and Luria et al. (2004) reported prevalence of only 3.3–3.7% in central Florida and 5.3% in North Carolina. Lin et al. (1995) did not detect FeLV in a sample of 24 "homeless" cats from a shelter in Taiwan.

Feline immunodeficiency virus (FIV) is spread primarily through aggressive interactions, tends to be more prevalent in male and older cats, and like human HIV, leads to a long-term deterioration in the immune system, eventually allowing opportunistic infections (Courchamp and Pontier 1994). Danner et al. (2007) reported 8.8% prevalence on Mauna Kea Volcano on the island of Hawai'i, similar to the 8% reported for South Australia (Winkler et al. 1999) but lower than the 21–25% for Sydney, Australia, feral cats (Norris et al. 2007). Lin et al. (1995) reported a rate of 13% for "homeless" cats in Taiwan. Courchamp and Pontier (1994) reported the global FIV prevalence average for feral cats as 15.7%.

RESPONSE TO MANAGEMENT

The politics of management are almost hopelessly complex because they involve several categories of cats and sharply differing societal views on what constitutes acceptable management of cats, what constitutes "humane" treatment, and whether an individual of an introduced species should have equality with the native species it is often devastating (Meffe 2008).

Acceptable management in a given urban setting might involve doing nothing because of the presence of free-ranging domestic cats. In areas with high wildlife values, however, the presence of cats might be unacceptable. Eradication would be preferred, especially if only feral cats were present, with no source of immigration from an owned population. Eradication is potentially possible on islands or at mainland sites where the rate of removal is greater than population increase, where there is no immigration, where all animals can be removed, and where there are the necessary resources to complete the task (Bomford and O'Brien 1995). However, possible mesopredator release effects (Courchamp et al. 1999), where another predator would replace cats with consequent population increases of prey (Fitzgerald and Karl 1979, Zavaleta et al. 2001), suggest the need for designing eradication programs that take into account such ecosystem effects. At other sites with high biological values, the benefits of eradication may not be worth the social or financial costs, so that localized control targeted at both feral and owned cats would be the default for protecting resources (Bomford and O'Brien 1995).

Methods for Excluding Cats

EXCLUSION ZONES: Local jurisdictions in Australia and New Zealand have declared cat exclusion zones where property owners may not keep cats at all or must keep their cats indoors or confined to their premises (Grayson et al. 2002, Metsers et al. 2010). These are often near natural areas with rare or endangered species (Buttriss 2001). Research by Metsers et al. (2010) suggested that such exclusion zones would need to be more than 2.4 km in breadth in rural areas and 1.2 km in more urban areas. Lilith et al. (2008) suggested that a zone of only 360 m is needed, but they cautioned that local conditions probably determine home range.

In Australia, Moore (2001) and McCarthy (2005) concluded that education is essential for any successful efforts to get the community to keep cats indoors, and Lilith et al. (2006) found moderate public willingness to confine their cats to their properties if needed. However, Moore (2001) concluded that 80% of the free-roaming cats in his community were not owned, so such solutions do not address most of the cat predation problem on wildlife.

FENCING: To keep cats out of areas with sensitive wildlife, a variety of fences have been developed that are resistant to the cat's ability to tolerate electric shock, dig, climb vertical surfaces, and jump at least 1.8 m (Long and Robley 2004). No fence system is impregnable, so backup methods are required within the exclosure to remove cats that breach the fence (Speedy et al. 2007, Department of the Environment, Water, Heritage, and the Arts 2008). Opinions concerning fences are mixed. Some regard them as expensive to set up and maintain, requiring expensive ongoing backup efforts, so that they are best used to protect localized high-value wildlife resources (Coman and McCutchan 1994, Department of the Environment, Water, Heritage, and the Arts 2008). On the other hand, fences can exclude multiple predators and ungulates, as well as cats, and have been used effectively and economically over large areas that were being rehabilitated (Day and MacGibbon 2007).

SONIC DETERRENCE: Mills et al. (2000) found little deterrence produced by an ultrasonic device, but Nelson et al. (2006) found some evidence that such devices reduced the probability of a cat's intrusion into a site and stronger evidence that such intrusions are of shorter duration when devices are present.

ERADICATION: In areas such as islands where the risk of recolonization is low and biodiversity values are high, eradication of cat populations may be the preferred strategy (Wood et al. 2002). This is especially true for offshore or oceanic islands (Veitch 2001). The Pacific region has led the world in such efforts (Veitch 2001, Wood et al. 2002, Nogales et al. 2004, Campbell et al. 2011). Worldwide, cats have been eradicated from fewer than 100 islands, and there remain thousands of islands where cats could be eradicated to reduce their threat to biodiversity (Campbell et al. 2011, Medina et al. 2011).

Use of toxic baits has proved a necessary but not sufficient method for removal of cats in many cases (see Campbell et al. 2011). The ideal toxicant would be specific to cats, or at least to felids/carnivores, humane, fast acting, and inexpensive. Several nonspecific toxicants have sufficient advantages that they have been the primary tactic for eradication (Short et al. 1997).

Many eradication programs have employed sodium monofluoroacetate (1080) in baits as a control method because it is inexpensive and nonpersistent in food chains (McIlroy 1996, Twyford et al. 2000, Algar and Burrows 2003, Rodríguez et al. 2006). Use of this poison is not permitted in the United States. Cats are highly susceptible to 1080 and can be killed "humanely," although this has been questioned (Sherley 2007). Trials are currently being conducted on the effectiveness of para-aminopropriophenone (PAPP), a fast-acting toxicant, which appears to be "humane and effective" for carnivores (Eason et al. 2010*b*), although some bird species may be vulnerable, so the means of presenting the bait must be designed to limit such exposure (Eason et al. 2010*a*).

Cat populations have also been reduced or removed as a result of secondary poisoning. This has occurred following control campaigns undertaken against rodents and opossums (Gillies and Pierce 1999) and lagomorphs (Heyward and Norbury 1999), using 1080 in New Zealand. Secondary poisoning by Brodificoum, a second-generation anticoagulant, targeting rat species, was responsible for eradicating cats on Tuhua Island, New Zealand, and accounted for most cat mortality on Raoul and Motutapu/Rangitoto Islands, New Zealand (D. Williams and E. Murphy, pers. comm. in Parkes [2009]; J. Parkes, pers. comm.). Brodificoum used against rabbits on the Otago Penninsula, New Zealand, resulted in cat deaths (Alterio 1996).

As a general principle, toxicant efficiency depends on bait size, shape, taste, color, strength, and positioning, both to attract cats and to deter incidental take by other species (e.g., Morgan et al. 1996, Wickstrom et al. 1999, Marks et al. 2006, Algar and Brazell 2008).

Trapping is commonly used for eradication, especially in conjunction with other methods (Wood et al. 2002, Nogales et al. 2004). Common live-trap types used include padded leg-hold, gin, and cage/box traps (Wood et al. 2002, Nogales et al. 2004). Leg-hold traps have proved the most effective but require considerable skill (Veitch 2001, Wood et al. 2002). Cage/box traps are generally less effective (Domm and Messersmith 1990, Department of the Environment, Water, Heritage, and the Arts 2008) but may be the method of choice where owned cats are present (e.g., Rauzon et al. 2008). Live trapping is very labor intensive because traps have to be checked at least daily or require a mechanism to signal if a cat is caught (Benevides et al. 2008, Will et al. 2010).

After a variety of attempts with existing traps such as Conibears (Poutu and Warburton 2001), new lethal trap designs have been developed that kill quickly, have reduced risk of bycatch, do not require daily checking, and are humane according to international and New Zealand standards (N. Z. Animal Welfare Act of 1999): "10 of 10 animals to be rendered unconscious within 3 minutes of capture" (Warburton and Poutu 2002, Warburton et al. 2002). These traps appear already to be in wide use throughout the Pacific, although documentation is lacking.

Hunting is also employed frequently in eradication campaigns, either with or without dogs. Prior hunter experience is critical, otherwise the cats that survive become wary (Wood et al. 2002, Rodríguez et al. 2006). Hunting tends to be a preferred technique employed to remove remaining cats at a site (Nogales et al. 2004); however, Bester et al. (2000) concluded that hunting was ineffective at low cat densities.

Biological agents (disease) have been effective as eradication tools when used in conjunction with other methods. One of the major benefits of a biological control can be its self-disseminating nature. Van Rensburg et al. (1987) documented that feline panleukopenia virus (FPV) reduced the cat population size on Marion Island from an estimated 3,409 to 615 individuals in 5 yr (Bester et al. 2002). However, the population stabilized after an initial decline, presumably as resistance developed, suggesting that FPV alone was insufficient (Van Rensburg et al. 1987). Similarly, FPV was used to eradicate cats from Jarvis Island; however, trapping and hunting were needed to finish the effort (Rauzon 1985).

Courchamp and Sugihara (1999) concluded that feline immunodeficiency virus (FIV) and feline leukemia virus (FeLV), both of which remain effective even at low host densities, could serve as effective agents for cat control on islands and have the potential to greatly increase the efficiency of an eradication program, when used in conjunction with other methods. Biological control techniques may not be effective in mainland areas where the diseases and consequent natural immunity are already present (see section on Natural Enemies). Even on islands, there are potential risks associated with these techniques, such as spread of infection to owned cat populations and to closely related species, if either is present.

Methods for Local Control

REDUCING EFFECTIVENESS OF DEPREDATION: A variety of techniques may reduce the efficiency of cats as predators to various degrees, such as neutering, which may reduce wandering/hunting; partial or complete cat curfews (Baker 2001); bells (Ruxton et al. 2002); alarms (Gillies and Cutler 2001, Nelson et al. 2005, Calver and Thomas 2011); and "pounce protectors" (Calver et al. 2007). These, however, do not work for feral cats, or for owned cats if the owners are unwilling to apply them.

HABITAT MANAGEMENT: With the assumption that optimal habitats of some endangered species provide less favorable hunting opportunities for cats, habitat restoration or modification may reduce the impact of cats (Department of the Environment, Water, Heritage, and the Arts 2008). Habitat management was tried for yellow-eyed penguins (*Megadyptes antipodes*) but actually seemed to attract predators, suggesting a need to understand the biology behind potential management (Alterio et al. 1998). In a special case in Australia, restoration of fluoroacetate-producing *Gastrolobium* (Fabaceae) communities could reduce cat populations and predation because their native prey would contain lethal amounts of secondary metabolites (Short et al. 2005, Peacock et al. 2011).

FERTILITY CONTROL: Nonlethal chemical control through fertility management, including effective contraception or abortive agents for feral cats, has yet to be developed (see Moodie [1995] for a general discussion of such contraceptives). Such control could offer an important option for local cat control where public perceptions are important (Fischer et al. 2001). Models of a nonlethal biological control or virus-vectored immunocontraceptive (VVIC) show it would be a more efficient way to disseminate a contraceptive than would a chemical contraceptive deployed in baits (Courchamp and Cornell 2000). However, social acceptance of immunocontraceptives delivered through a live virus might be problematic because of concerns that the virus might jump to other mammals. More pragmatically, in Hawai'i, a bill was recently introduced in the state legislature but failed to pass that called for the "fixing" of all cats sold in pet shops as a means of reducing the release of fertile female cats (Shikina 2011). Such legislation would help remove one source of feral cats.

ENCOURAGING NATURAL COMPETITORS AND PREDATORS: The experimental reintroduction of dingos (*Canus lupus dingo*) or similar mesopredators to control cats and allow recovery of native species has been suggested, but this would face social resistance because of risk to livestock and pets and because changes in the Australian landscape make dingos less acceptable to many Australians (Glen et al. 2007, Department of the Environment, Water, Heritage, and the Arts 2008). Introducing mesopredators to combat cats would, of course, not be an option on islands where terrestrial predators had not naturally occurred, because this would serve to increase the predation burden on the surviving indigenous species.

REDUCING THE PREY BASE: Removing a critical part of the prey base may lead to reductions in cat populations and protection of indigenous prey species. In the Flinders

Ranges, South Australia, rabbit control measures caused a deterioration in female cat body condition and probably reduced subsequent cat populations, relaxing predation on native species (Holden and Mutze 2002). In more urban areas, simple sanitation that reduces rat populations and garbage for scavenging might help reduce feral cat populations, although it is not clear that cats actually control rats in urban areas (Childs 1991, Glass et al. 2009).

MAINTAINING TRAP-NEUTER-RELEASE POPULATIONS: Trap-Neuter-Release (TNR) programs have become increasing common in urban areas and are typically geared toward caring for urban or suburban cat "colonies" of abandoned cats. They use live or box traps to catch cats, which are then neutered, checked for disease, sometimes vaccinated, marked, and returned to a central area where they are usually fed by a caretaker (Slater and Shain 2005). Live trapping in urban areas appears to be more successful than in the wild (Short et al. 2002). A single attempt to use TNR for eradication, on La Plata Island, Ecuador, was unsuccessful (Campbell et al. 2011).

TNR colonies are supposed to eliminate reproduction, because all cats are neutered, so that colonies will eventually become extinct, although this appears to take at least a decade (Slater 2005) and does not appear to have ever happened. In fact, the actual goal often seems to be reduction to a "manageable" colony size with corresponding "decreased complaints" (Neville 1983, Hughes et al. 2002). It has also been claimed that these programs "can allow a sensible number of cats to remain which are often essential for pest control in urban environments" (Robertson 2008:371), although there appears to be no documentation for such a function or for what constitutes "a sensible number."

This methodology has sometimes received uncritical acceptance (e.g., Farnsworth et al. 2010), despite the fact that available evidence clearly shows that essentially all TNR programs fail to eliminate or substantially reduce population sizes of cats (Castillo and Clarke 2003, Winter 2004, Foley et al. 2005). Foley et al. (2005) found that TNR management did not achieve a reduction in cat population growth or in the number of pregnant females. Even when population reduction is possible, it typically occurs over a time frame that is unacceptable in terms of predation on surrounding wildlife (e.g., 66% population decrease over 11 yr [Levy et al. 2003]). Population reductions by TNR programs are usually achieved through adoption (Levy et al. 2003, Longcore et al. 2009), so the more-effective programs might better be called Trap-Neuter-Adopt (cf. Slater 2005).

Population models for cat colonies suggest that trap-euthanasia is more effective than TNR for reducing colony sizes (Andersen et al. 2004), although Schmidt et al. (2009) found that trap-euthanasia did not outperform TNR in the special case of absence of immigration. TNR programs are generally doomed to fail because of immigration from owned cat populations (Patronek 1998, Castillo and Clarke 2003, Natoli et al. 2006). TNR creates an "attractive nuisance" such that people dump unwanted cats in colonies, rather than in shelters (Jessup 2004, Winter 2004). Any reduction in a TNR colony is soon swamped by new arrivals (Schmidt et al. 2009).

There can be social benefits for humans in TNR programs. These programs serve to educate the public, build a constituency for a societal problem, and provide "enhanced feelings of self esteem" for highly dedicated colony caretakers (Zasloff and Hart 1998, Centonze and Levy 2002). TNR colonies can relieve local governments of many of the costs of cat control programs through donation of volunteer time, although this would in turn raise expectations of transparency about reporting on the effectiveness of such programs. TNR also can relieve local humane societies of negative publicity, because cats no longer need to be euthanized. This may be especially true in Asian countries with their religious antipathy toward killing (Takahashi 2004).

However, the politics and ethics of TNR may be complex. People for the Ethical Treatment of Animals (2007) stated: "PETA's experiences with trap-alter-and-release (abandon) programs and 'managed' feral cat colonies have led us to believe that these programs are not usually in cats' best interests" and "we cannot in good conscience advocate trapping, altering, and releasing as a humane way to deal with overpopulation and homelessness."

There are legal questions about TNR programs, because someone has to own the cat to allow it to be operated on, and once owned, it cannot be simply abandoned in many jurisdictions (Jessup 2004). Veterinarians participating in TNR may appear to be on shaky ethical grounds in that they would be operating on a cat that did not belong to the person who brought it in, knowing that it would be abandoned once treated and that it would not be likely to receive further medical attention (Jessup 2004). Similarly, public officials allowing cat colonies on public land are essentially privatizing public space for those who maintain cat colonies, reducing public access to such areas.

If cat colonies present an increased risk of transmission of toxoplasmosis, this appears to violate the U.S. Civil Rights Act and similar statutes of other nations, because the colonies deny certain groups of society safe access to public, common lands (Patronek 1998, Ikeda 2000, Jessup 2004). Municipalities that allow TNR colonies that kill endangered species appear to be in violation of statutes such as the U.S. Endangered Species Act and the U.S. Migratory Bird Treaty Act (Hatley 2003, Jessup 2004), and, on certain Japanese islands, this is in violation of the Japanese–U.S. Migratory Bird Treaty (Harrison et al. 1992).

There are generally no benefits to wildlife derived from TNR programs, because the number of predators is not greatly reduced (Environment Australia 1999). Instead, managed colonies artificially concentrate the hunting impact of colony members (Schmidt et al. 2007), with adverse effects on adjacent wildlife (Smith et al. 2002). Regular movement between colonies (Levy et al. 2003) and between wild and human-populated areas (Guttilla and Stapp 2010) can be common for colony cats, such that their impact extends well beyond the TNR colony area.

Cat colonies may become foci for feline diseases (see section on Natural Enemies). Some of these can be prevented with vaccination; others may require the removal of sick individuals before they infect the rest of the colony. Colonies that do not have adequate and continuing veterinary care have the potential to infect free-ranging domestic cats (Murphy et al. 1999), imposing a financial and emotional burden on adjacent cat owners that either is not usually considered in discussions of cat colonies or is dismissed. On the other hand, Lee et al. (2002) and Luria et al. (2004) have argued that various infectious disease levels do not differ between feral and owned cats, but the more interesting comparison would have been between feral and indoor-owned cats (O'Connor et al. 1991).

CAT SANCTUARIES: Cat sanctuaries maintain feral cats taken from the wild in enclosed areas where they are provided with food, shelter, and veterinary services while removing their impact on wildlife (Winter 2003). This represents what may be the only acceptable compromise between TNR and wildlife advocates (Jessup 2004). Unfortunately, such sanctuaries are expensive and have limited capacity compared with the extent of the problem; however, groups opposed to euthanasia of cats can be given the opportunity within a set time to raise the resources for this option (e.g., Takahashi 2004).

PROGNOSIS

Relations between cats and humans have always been complex. We have worshiped them or feared them, fed them, eaten them, and burned them alive. We have encouraged them to protect our grain supplies and coddled them as companion animals. We have spread them across the world onto isolated islands where they have caused major devastation. Today, in many Pacific nations, we allow our domesticated cats to slip out the front door to continue their predatory habits that take great tolls of wildlife no matter how well fed they are. The high reproductive capacity of cats can have dire consequences for human health and for local wildlife when feral populations are established.

There are three broad settings for cat management in the Pacific: (1) small islands, often uninhabited, with high biodiversity values, where wildlife is the priority; (2) habitats with intermediate to high biodiversity values and human sensitivity within or adjacent to landscapes of low diversity where either wildlife or humans may be the priority; and (3) urban and suburban areas with low biodiversity. However, all cat management is local and is the end result of an interplay of science, politics, local social, ethical, and even religious beliefs.

In the case of small islands with high biodiversity values, the main question is how to remove cats most efficiently, humanely, and with minimum negative effect so as to allow the restoration of the surviving ecosystem. Techniques are steadily improving, as are the sizes of the islands that have been cleared (Veitch 1985, Nogales et al. 2004, Campbell et al. 2011). Removing cats from islands frequently leads to the restoration of bird and other animal populations devastated by cats (e.g., Keitt and Tershy 2003, Ortiz-Catedral et al. 2009). Occasionally the removal of cats may initially have undesirable ecosystem effects, such as increase of rodents or rabbits (e.g., Rayner et al. 2007, Bergstrom et al. 2009), so the order of removal of alien species is important (e.g., Zavaleta et al. 2001).

The second group consists of habitats with intermediate to high biodiversity values and human sensitivity within or adjacent to landscapes of low diversity. Owned and feral cats may coexist, so a variety of strategies is necessary. "Hot spots" such as parks and wildlife reserves may have concentrations of surviving native species that are under intensive management. Free-roaming cats, whether owned or feral, should be aggressively controlled when they venture into such high-value biodiversity "islands," if these cannot be effectively fenced. Owners within the "halo" of expected cat dispersal around these "islands" (e.g., Lilith et al. 2008, Metsers et al. 2010) need to be encouraged through education or statute to keep their cats from wandering into harm's way or warned to expect to lose their cats.

Other sensitive areas include public water supplies, hospitals, and recreation areas such as playgrounds (especially with children's sandboxes) where the presence of cats deprives individuals of the right to use public spaces because of feces or risk of disease (Patronek 1998, Ikeda 2000). In such areas, cats should be controlled by live trapping or fencing. Managed cat colonies should not be located near such human-sensitive areas, and they should certainly never be sanctioned by government in such circumstances.

The third group consists of extensive lowland urban and periurban areas throughout the Pacific where alien species coexist with or have largely replaced the indigenous fauna. In these areas, cats are in the middle of a food chain that includes introduced house sparrows (*Passer domesticus*), black rats (*Rattus rattus*), house mice (*Mus musculus*), and trash and handouts as "prey," with dogs (*Canis lupus familiaris*) and automobiles as "predators." It is not clear either that cats are the dominant pressure on surviving native species in such areas or that management of cats will ameliorate the situation (Lilith et al. 2010). In any event, there are usually not funds to eliminate cat populations over large areas, nor is there likely to be public support. On the other hand, there is no justification for special protection for feral cats as might be given to native species. Although Calver et al. (2011) cogently argue for a precautionary approach to management of free-ranging pet cats in this environment, management will often become a priority only when the resulting combined population is a problem for local property owners or others.

In such situations, TNR colonies may do little harm and have potential to do some good, if only through a management "placebo effect," providing a low-cost alternative to doing nothing, even if it is ineffectual. TNR colony management is only responding to a vacuum that will continue to exist until cat owners understand that indoor cats have longer and healthier lives and do not bring home diseases to their owners (Levy 2002, Jessup 2004). The recent development of "catios" or screened areas that allow owned cats to go outside without being exposed to dogs, traffic, or other problems (Kingson 2010) may represent the future, just as fenced yards have become the norm for domestic dogs.

Ultimately, future medical concerns about toxoplasmosis (McAllister 2005) or other diseases may change public acceptance of free-ranging cats, be they domestic or feral, much as rabies and damage to wildlife changed tolerance for free-ranging dogs (Knight 2006, Jackson and Wunner 2007). At that point, Pacific societies may finally achieve consensus and develop local policies about cats; however, until then cat management will remain as much a matter of controversy and emotion as of science.

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