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ECOLOGY OF AN INVASIVE PREDATOR IN HAWAI`I

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Abstract: Cats (*Felis catus*) brought to Hawai`i in the 1700s now occupy most habitats throughout the islands, including montane and sublapine zones. We studied home range, population genetics, diseases, and diet of feral cats on Hawai`i Island. Feral cats on Mauna Kea live in low densities and exhibit some of the largest reported home ranges. While 95% kernel home range estimates for 4 males ($\bar{x}$ = 1418 ha) were nearly twice as large as 3 female home ranges ($\bar{x}$ = 772 ha), one male maintained a home range of 2050 ha. Population genetics revealed that Mauna Kea may be a source population for feral cats on Mauna Loa and Hawai`i Volcanoes National Park (HAVO). Assignment tests provided strong evidence for male-biased dispersal from Mauna Kea to Mauna Loa. Mauna Kea cats exhibited high seroprevalence for toxoplasmosis (37.3%) and feline leukemia virus (FeLV; 16.2%) distributed among all age and sex classes. Feline immunodeficiency virus (FIV) occurred only in adult males comprising 8.8% of the overall population. We found that cats on Mauna Kea primarily consumed birds, present in 69% of digestive tracts, whereas birds were in only 28% of samples from HAVO. Within HAVO, prey use differed between Kīlauea and Mauna Loa. On Mauna Loa, more feral cats consumed small mammals (89%), primarily rodents, than on Kīlauea Volcano (50%). Mice (*Mus musculus*) were the major component of the feral cat diet on Mauna Loa, whereas Orthoptera were the major component of the diet on Kīlauea. A digestive tract from Mauna Loa contained a mandible set, feathers, and bones of an endangered Hawaiian Petrel (*Pterodroma sandwichensis*). Abundant birds on Mauna Kea may maintain large numbers of feral cats that disperse long distances. Abundant rodents found in Mauna Loa digestive tracts may also support cats that then take advantage of breeding petrels.

Key Words: diet, endangered species, *Felis catus*, feral cat, genetics, Hawai`i, home range, invasive species, predation.

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INTRODUCTION

Ecological studies of invasive predators can be important for at least two major purposes: (1) to determine the extent of predation on native and endangered wildlife, and (2) for developing effective control methods (Veitch 1985, Edwards et al. 2000). For example, disease data may help to understand the risk of transmission to other species, diet studies may yield information about formulating attractive baits, home range size and daily movements may inform trap placement and spacing, and population genetics can provide information about the demography of invasive species useful for developing effective control strategies. Despite the long history of feral cats in Hawai`i, there has been little research on their basic ecology or effects on native wildlife. There are also few published accounts of predation by feral cats on endangered species.

Domestic cats were brought to Hawaii on European ships in the late 1700s (King 1984) and apparently established feral populations by 1840 in remote montane areas of Hawai`i Island (Brackenridge 1841). Feral cats were abundant in forests of Lāna`i and O`ahu by 1892 (Rothschild 1893), and predation of forest birds in the late 1800s was reported by Perkins (1903). Where cats have been abandoned in coastal and lowland areas, high density colonies are maintained by feeding (Winter 2003), which causes mortality to nesting colonial seabirds (Smith et al. 2002). However, in remote montane forests and subalpine areas of Maui (Simons 1983) and Hawai`i Island (Hu et al. 2001) feral cats have lived in comparably solitary,

low density situations for more than a century without human subsidies (Tomich 1986). At higher elevations, feral cats are the most important predators of endangered Hawaiian birds including burrow-nesting seabirds (Natividad-Hodges and Nagata 2001), ground-nesting waterfowl (Banko 1992), and tree-nesting passerines (Hess et al. 2004). Cats are also the definitive host of toxoplasmosis, a disease which has killed both endangered birds and marine mammals in Hawai`i (Work et al. 2000, Work et al. 2002, Honnold et al. 2005).

OBJECTIVES

Our objectives were to determine feline disease prevalence, diet, daily movement rates, home range, and population genetics of feral cats, primarily on Hawai`i Island. We intended to use this information to determine the impacts of feral cats in remote natural areas inhabited by endangered species and to develop a large-scale control strategy. Data presented here came from feral cats that were live-trapped between 1998-2005 on Mauna Kea, and 2000-2005 in Hawaii Volcanoes National Park (HAVO) to reduce predation on endangered Hawaiian birds such as Palila (*Loxioides bailleui*), Nēnē (Hawaiian goose; *Branta sandvicensis*), and `Ua`u (Hawaiian Petrel; *Pterodroma sandwichensis*).

METHODS AND RESULTS

Feline Diseases

We determined prevalence to feline immunodeficiency virus (FIV) antibodies, feline leukemia virus (FeLV) antigen, and *Toxoplasma gondii* antibodies in feral cats captured on Mauna Kea Hawaii from April 2002 to May 2004 (Danner et al. 2007). SnapTM Combo FeLV Antigen/FIV antibody enzyme-linked immunosorbent assays (ELISAs) (IDEXX Laboratories, Inc., Portland, Maine, USA), were used in the field with fresh whole blood according to the manufacturer's instructions. Remaining blood samples were sent to Colorado Veterinary Diagnostic Laboratories (Colorado State University, Fort Collins, Colorado, USA) for analysis of antibodies to *T. gondii*. Six of 68 (8.8%) and 11 of 68 (16.2%) cats were antibody positive to FIV and antigen positive for FeLV, respectively; 25 of 67 (37.3%) cats were seropositive to *T. gondii* (Table 1). About 7.5% of cats had recent or active *T. gondii* infections and may have been capable of transmitting toxoplasmosis to other wildlife through oocysts shed in feces. Antibodies to FeLV and *T. gondii* occurred in all age and sex classes, but FIV occurred only in adult males. The cat population on Mauna Kea may be depressed by feline diseases, but the presence of these diseases suggests they would not make effective biological control agents.

Table 1. Prevalence (percentage) of feline immunodeficiency (FIV) antibodies, feline leukemia (FeLV) antigen, and *Toxoplasma gondii* antibodies indicating exposure or recent infection in feral cats on Mauna Kea, Hawaii, 2002-04.

			T. gondii	
	FIV (n = 68)	FeLV (n = 68)	Exposure (n = 67)	Infection (n = 67)
Adult				
Male	17	17	31	3
Female	0	13	45	18
Juvenile				
Male	0	33	67	0
Female	0	17	29	0
Overall	9	16	37	7

Diet

We analyzed digestive tract contents of 143 feral cats from Mauna Kea, 42 from Hawai`i Volcanoes National Park, and 15 from the island of Kaho`olawe to determine diet. We used consistent methods between each of these locations (Hess et al. 2004, In Press). Entire carcasses were frozen, and then stomachs and intestines were removed and preserved in 70% ethanol. Stomachs were cut open along the concave side and intestines were opened along their entire length. A continuous, gentle stream of water was used in combination with gentle pressure from fingers to rinse and separate food items through soil sieves (US Bureau of Standards size 5 and 10 mesh). Prey items were sorted into respective prey types (e.g., small mammals, invertebrates, birds) and identified to lowest taxonomic level with the help of reference collections. The prey type with the highest frequency of occurrence from Mauna Kea was birds, present in 69% of digestive tracts, whereas birds were in only 28% of samples from HAVO (Figure 1). Approximately 27% of cats on Kaho`olawe contained birds, and < 14% contained small mammals, but > 86% contained invertebrates, including some intertidal marine species.

On Kīlauea and Mauna Loa in Hawai`i Volcanoes National Park, small mammals, invertebrates, and birds were the most common prey types consumed by feral cats (Figure 2). Birds occurred in 27.8–29.2% of digestive tracts. We found a significant difference between Kīlauea and Mauna Loa in the total number of bird, small mammal, and invertebrate prey in the digestive tracts of feral cats ($\chi^2 = 8.39$, DF = 2, $P = 0.015$; Hess et al. 2007). On Mauna Loa, significantly more (89%) feral cats consumed small mammals, primarily rodents, than on Kīlauea Volcano (50%) (2-sample t-test; DF = 29, $t = -3.65$, $P < 0.001$). Mice (*Mus musculus*) were the major component of the feral cat diet on Mauna Loa, whereas Orthoptera were the major component of the diet on Kīlauea. We recovered a mandible set, feathers, and bones of an endangered Hawaiian petrel (*Pterodroma sandwichensis*) from a digestive tract from Mauna Loa. This specimen represents the first well-documented endangered bird to be recovered from the digestive tract of a feral cat in Hawai`i and suggests that feral cats prey on this species.

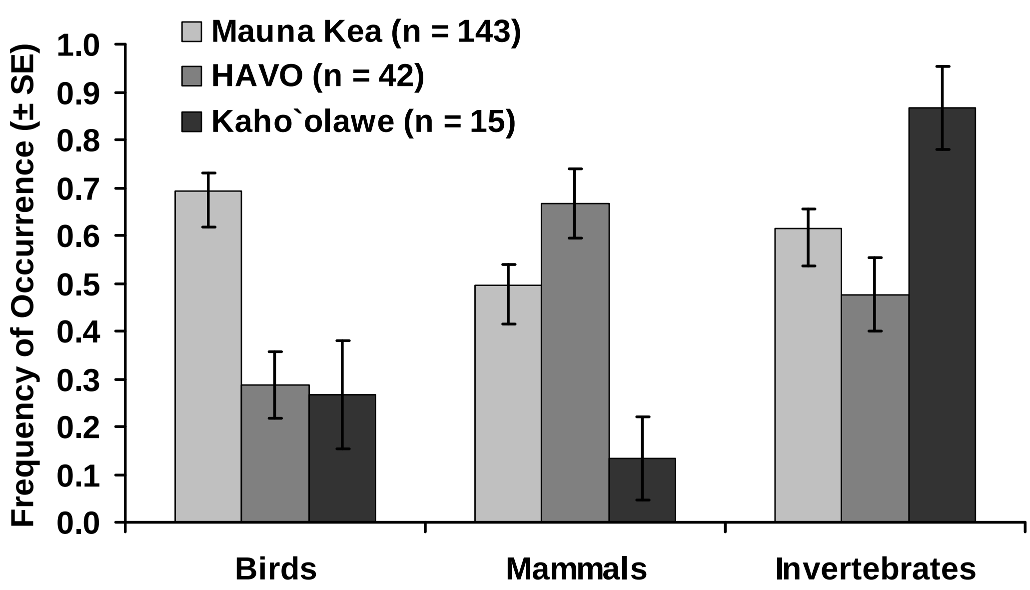

Figure 1. Frequency of occurrence (± SE) of three prey types from digestive tracts of feral cats from Mauna Kea, Hawai`i Volcanoes National Park (HAVO), and the Island of Kaho`olawe, Hawai`i 1998–2005.

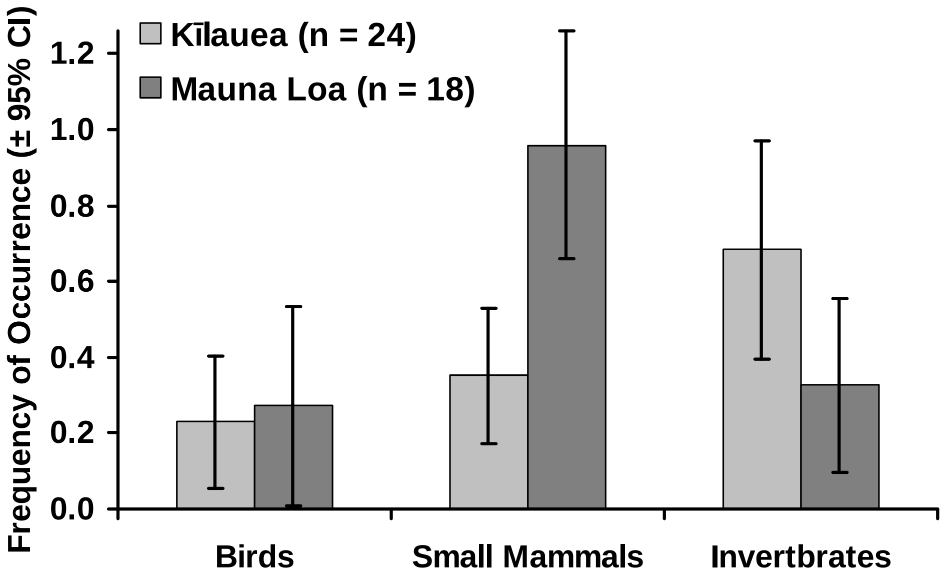

Figure 2. Frequency of occurrence of three prey types (±95% CI) from digestive tracts of feral cats from Kīlauea and Mauna Loa in Hawai`i Volcanoes National Park, 2000–2005.

Daily Movements and Home Range

We studied the daily movement rates and homes ranges of feral cats on Mauna Kea by capturing and fitting 7 males and 3 females with 35-37g Holohil Systems Ltd. model MI-2 radio transmitters, and tracking these animals between 1999 and 2001. To reduce temporal autocorrelation of observations, we calculated t2/r2 statistics for a range of minimum times between observations and determined a minimum separation of 2.85 days was needed to achieve quasi-independent observations (Swihart and Slade 1985, Swihart and Slade 1986). After excluding data points that were taken less than 2.85 days after the previous observation, we calculated 95%, 50%, and 25% fixed kernel home ranges using the animal movement extension (Hooge and Eichenlaub 1997) for Arcview GIS (ESRI 1999). We used least squares cross-validation to estimate a kernel smoothing parameter for each cat, and used the median value (382) for all cats as the final home range estimate as recommended by Seaman and Powell (1996). We then examined the effect of reduced sample size on kernel home range estimates with 1,000 bootstrap minimum convex polygons (MCP) from the remaining locations using the animal movement extension (Hooge and Eichenlaub 1997). We plotted MCP area against sample size to determine if sufficient observations existed to stabilize MCP area; there were sufficient observations to determine reliable home ranges for 4 of the 7 males and all 3 females. Mean daily movement rates between sexes overlapped widely and did not differ (Unequal variance 2-sample t-test; DF = 6, t = -2.08, P > 0.08; Table 2). However, we found that male feral cats on Mauna Kea exhibit some of the largest reported home ranges (Figure 3). While 95% kernel home range estimates for 4 males ($\bar{x}$ = 1418 ha) were nearly twice as large as 3 female home ranges ($\bar{x}$ = 772 ha), one male maintained a home range of 2050 ha (Table 3). Log-transformed 95% (Equal variance 2-sample t-test; DF = 5, t = -3.20, P < 0.03) kernel home ranges for males were significantly larger than those of females, but 25% kernel home ranges for females were larger than those of males (Equal variance 2-sample t-test; DF = 5, t = 3.53, P > 0.02), indicating that males use extensive areas while females make more intensive use of smaller areas. One male's home range was on the West Slope for five months, then shifted 15 km to the South Slope, and never returned.

Population Genetics

We studied seven highly polymorphic microsatellite markers to estimate the genetic structure of three feral cat populations on Hawaii Island. Specific objectives of our genetics research were to (1) evaluate genetic diversity and

Table 2. Mean daily movements of feral cats on Mauna Kea, Hawaii 1998-2001.

Sex	Observations (*n*)	Mean (m/day)	Range (m/day)
Male (*n* = 7)	572	2274	91–6014
Female (*n* = 3)	448	135	109–184
Overall (*n* = 10)	1020	241	91–6014

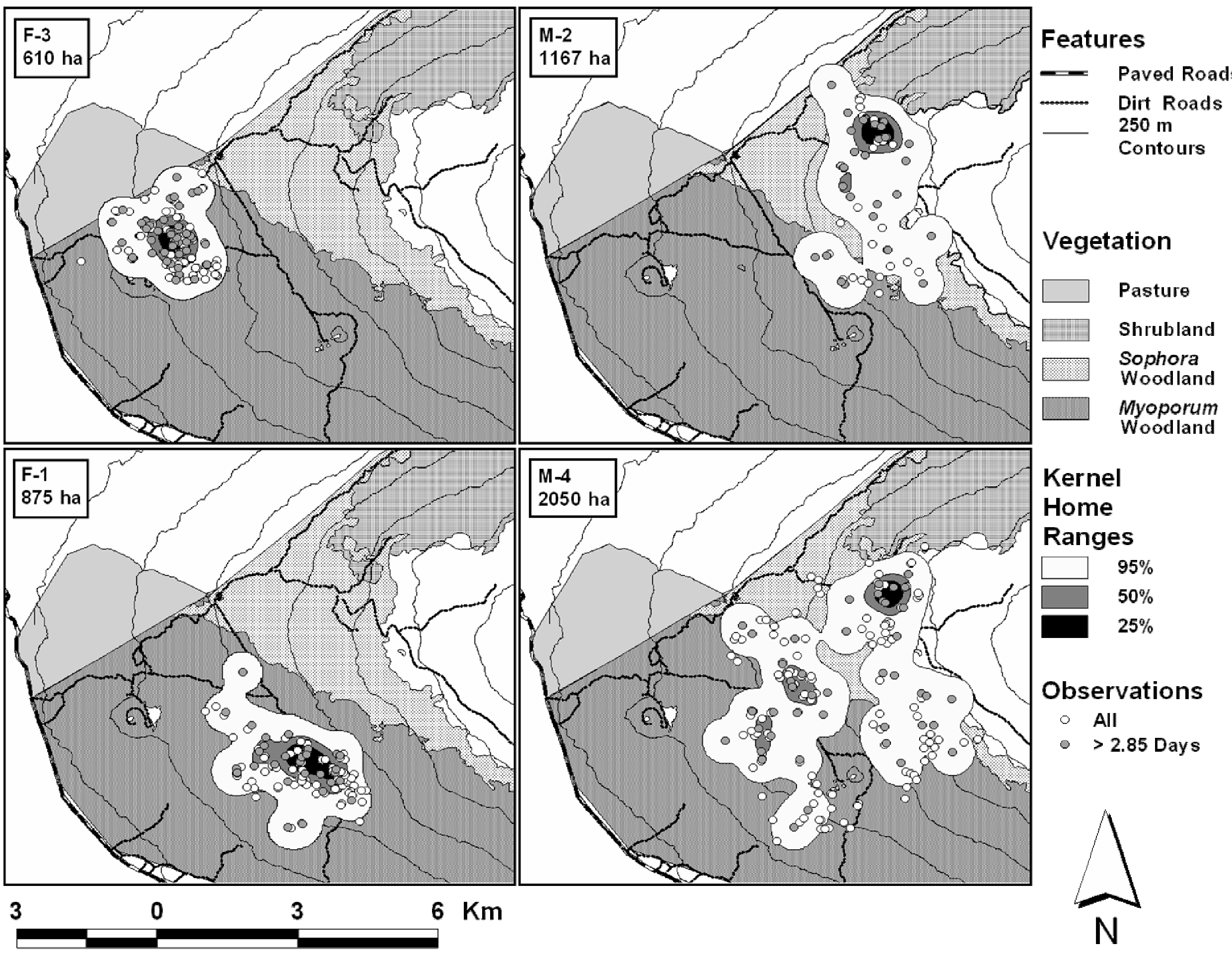

Figure 3. Kernel home range estimates (ha) of feral cats on Mauna Kea, Hawai`i 1998-2001. Non-independent observations were eliminated based on estimated average of 2.85 days to quasi-independence.

Table 3. Kernel home range estimates (ha) of feral cats on Mauna Kea, Hawai`i 1998-2001. Non-independent observations were eliminated based on estimated average of 2.85 days to quasi-independence. Home range was calculated by the median least square cross validation (LSCV) smoothing parameter (H) value of 378. Asterisk indicates significant differences between sexes at $P < 0.03$ based on 2-sample t-test with equal variances.

Sex	25% Kernel* Mean	95% Kernel* Mean	95% Kernel Range
Male (*n* = 4)	32.5 ha	1418.0 ha	1167-2050 ha
Female (*n* = 3)	52.7 ha	772.0 ha	610-875 ha
Overall (*n* = 7)	41.1 ha	1141.1 ha	610-2050 ha

population structure; (2) assess levels of gene flow and connectivity between populations; (3) identify potential source populations; (4) characterize population dynamics; and (5) evaluate evidence for sex-biased dispersal to formulate an island-wide control strategy (Hansen et al. in press). We collected muscle tissue samples from 85 feral cats (49 males, 36 females) and stored samples in lysis buffer at -20°C until extraction. We extracted genomic DNA from the tissue using the QIAGEN® DNeasy™ Tissue Kit (Qiagen, Inc., Valencia, California, US). Technical detail of extraction, PCR amplification, and analysis can be found in Hansen et al. (In Press).

Genetic diversity. High genetic diversity, low structure, and high number of migrants per generation supported high gene flow that was not limited spatially. The mean number of alleles (A) ranged from 7.57 ± 2.99 (mean ± SD) to 9.00 ± 3.83 according to population. After Bonferonni corrections, f values showed a significant departure from Hardy-Weinberg equilibrium in NMK and WMK, suggesting that these populations were inbred (Aspi et al. 2006).

Population structure. Pairwise estimates of population structure (F_{st}), a measure of the genetic variability among populations, were all significant ($P < 0.05$) and calculated (with 95% CI) as 0.038 (HAVO-NMK; 0.008 – 0.071), 0.028 (HAVO-WMK; 0.013 – 0.041) and 0.023 (NMK-WMK; 0.006 – 0.043), indicating gene flow among all populations.

Gene flow and migration rate. Migration rates revealed that most migration occurred out of West Mauna Kea. The estimated number of migrants per generation (Nm) was 6.3 between NMK and HAVO, 8.8 between WMK and HAVO, and 10.6 between NMK and WMK. The mean posterior probabilities of migration rates showed that the majority of individuals were native to their capture locations in all populations with the most originating in WMK (0.708 – 0.927) (Table 4). There was a relatively high degree of migration between populations from WMK to NMK (m = 0.248; 95% CI = 0.032 – 0.325) and HAVO (m = 0.176; 95% CI = 0.034 – 0.312). In contrast, migration rates from both HAVO and NMK into the other populations were very low with the smallest migration rate from HAVO to WMK (m = 0.015; 95% CI = 0.0004 – 0.048).

Sex-biased dispersal. Three measures supported male-biased dispersal and female philopatry (Figure 4). The mean assignment index (mAI_c) is a measurement of the likelihood of an individual's genotype to occur in its sampled location. Negative AI_c values indicate dispersal and positive AI_c values indicate philopatry. Relatedness of males and females differed significantly ($P <$ 0.05) and the mAI_c of males among populations was significantly lower than that of females (mAI_c = -0.900, 1.23, P = 0.007, respectively). The F_{st} value, a measure of genetic variability between males and females, was significantly lower among dispersing males. The higher inbreeding coefficient F_{is} (less inbred) also supported male biased dispersal.

Table 4. Migration rates of feral cats between north Maun Kea (NMK), west Mauna Kea (WMK), and Hawai`i Volcanoes National Park (HAVO) on Hawaii Island. Migration rates (with 95% confidence intervals) were estimated as the proportion of individuals in column populations that originated from populations in rows. Values along the diagonal are the proportions of individuals within a population derived from that population.

	HAVO	**NMK**	**WMK**
HAVO	0.708 (0.667–0.835)	0.116 (0.004–0.277)	0.176 (0.034–0.312)
NMK	0.015 (0.0004–0.048)	0.737 (0.668–0.953)	0.248 (0.032–0.325)
WMK	0.038 (0.001–0.104)	0.035 (0.002–0.127)	0.927 (0.843–0.986)

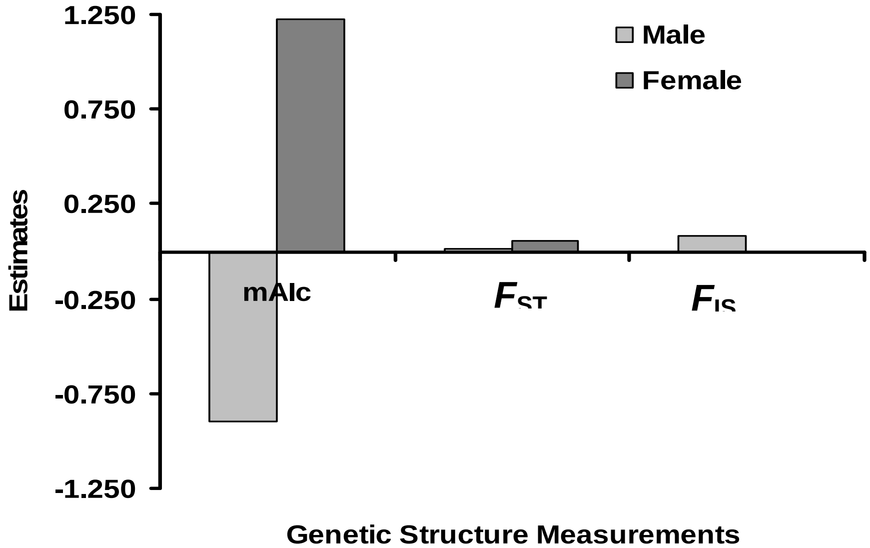

Figure 4. Differences in genetic structure measurements between sexes in feral cats on Hawai`i Island. A negative mean assignment index (mAI_c) indicates dispersal whereas positive mAI_c indicates philopatry. Genetic variability (F_{st}) was significantly lower in males, and the inbreeding coefficient (F_{is}) also indicated male biased dispersal.

DISCUSSION

Our studies of feral cat ecology have yielded a greater understanding of how cats behave and persist and in cool, dry montane and subalpine environments in Hawai`i. Home range and dispersal rates from population genetics show major differences between sexes, and some male cats had high daily movement rates. Male feral cats on Mauna Kea exhibited some of the largest reported home ranges in the literature and population genetics showed great dispersal distances, perhaps to search for mates. Territorial defense in males may also be an important aspect of behavior. One of our 7 collared males, a subadult, abruptly shifted its home range from west Mauna Kea to the south. Other evidence consistent with aggressive behavior comes from FIV prevalence, which was restricted to males, and is transmitted by biting and scratching during fights (Yamamoto et al. 1988).

Diet analyses showed that invertebrates occur frequently in the diet of feral cats in Hawai`i. This agrees with other Pacific region studies. Dickman (1996), found that invertebrates featured much more prominently in the diets of cats from Pacific region islands (n = 12 studies) than from a range of habitats in mainland Australia (n = 22 studies). Orthoptera were among the most common invertebrate prey of feral cats in the Pacific region. On Mauna Kea, birds occurred more frequently than other major prey types, and rats (*Rattus* spp.) were uncommon prey for cats in both of these subalpine environments. Mice were another important food source for cats on Mauna Loa. Abundant small prey may allow feral cats to survive food shortages, maintain populations at higher densities than they would otherwise be able to maintain, and exploit seasonally abundant prey such as nesting birds.

Our hypothetical model of population dynamics on Hawai`i Island is that abundant birds, including nine introduced gamebird species on Mauna Kea, provide plentiful food resources necessary for high reproduction and survival, thereby creating a potential source population. In such prime habitats, male cats may challenge each other for access to mates, and unsuccessful challengers may be forced to disperse to other marginal locations such as Mauna Loa where bird prey is not as abundant (Scott et al. 1986), or to warmer lowland areas such as Kīlauea. Although low compared to estimates of isolated feral cat populations in urban France (f = 0.14; Say et al. 2003) and on a sub-Antarctic island (f > 0.11; Pontier et al. 2005), we found some evidence of inbreeding in the Mauna Kea populations. Inbreeding may be caused by factors

that cause low population density, such as kitten mortality due to feline leukemia virus, feline immunodeficiency virus, and toxoplasmosis, all of which have been documented in feral cats on Mauna Kea (Danner et al. 2007). Apparently, feral cats in Hawaii still exhibit colonizing characteristics. Although we have no definitive evidence to rule out the possibility that domestic house cats were recruited into nearby feral populations, all of the cats we captured lacked diversity in coat coloration and had reverted back to pelage characteristics similar to European wildcats. Mauna Kea may be considered a source population that can be targeted for control. However, recolonization seems likely given the cats' ability to disperse despite barriers such as lava flows.

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