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Using population genetic tools to develop a control strategy for feral cats (*Felis catus*) in Hawai'i

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Abstract. Population genetics can provide information about the demographics and dynamics of invasive species that is beneficial for developing effective control strategies. We studied the population genetics of feral cats on Hawai'i Island by microsatellite analysis to evaluate genetic diversity and population structure, assess gene flow and connectivity among three populations, identify potential source populations, characterise population dynamics, and evaluate sex-biased dispersal. High genetic diversity, low structure, and high number of migrants per generation supported high gene flow that was not limited spatially. Migration rates revealed that most migration occurred out of West Mauna Kea. Effective population size estimates indicated increasing cat populations despite control efforts. Despite high gene flow, relatedness estimates declined significantly with increased geographic distance and Bayesian assignment tests revealed the presence of three population clusters. Genetic structure and relatedness estimates indicated male-biased dispersal, primarily from Mauna Kea, suggesting that this population should be targeted for control. However, recolonisation seems likely, given the great dispersal ability that may not be inhibited by barriers such as lava flows. Genetic monitoring will be necessary to assess the effectiveness of future control efforts. Management of other invasive species may benefit by employing these population genetic tools.

Introduction

Population genetic tools have proven beneficial for the management and conservation of rare and endangered wildlife (Paetkau *et al*. 1997; Spong *et al*. 2000). Only recently have these tools been applied in invasive species management (Robertson and Gemmell 2004; Abdelkrim *et al*. 2005; Rollins *et al*. 2006). Invasive species are the main cause of species extinctions in island ecosystems (Courchamp *et al*. 1999) and the second main cause of biodiversity loss after habitat destruction (Vitousek *et al*. 1997). Successful management of invasive species requires identifying a target population of manageable size that has a low recolonisation risk (Robertson and Gemmell 2004). Attempts to control only a fraction of the population or a sink population could result in rapid recolonisation (Robertson and Gemmell 2004; Abdelkrim *et al*. 2005). Identifying routes of potential migration is difficult using direct observations, but vital for controlling invasive species (Robertson and Gemmell 2004; Abdelkrim *et al*. 2005; Rollins *et al*. 2006). Population genetics can provide valuable information about the demographic status and dynamics of invasive species and may provide an alternative approach for developing control strategies (Robertson and Gemmell 2004; Abdelkrim *et al*. 2005; Pontier *et al*. 2005).

Feral cats (*Felis catus*) are currently listed as one of the '100 world's worst invasive alien species' (Lowe *et al*. 2000). Domestic cats were brought to Hawai'i on European ships in the late 1700s (King 1984) and feral animals were reported by 1840 in remote montane areas of Hawai'i Island (Brackenridge 1841). Currently, feral cats occur in low densities in montane forests and subalpine areas of Maui (Simons 1983) and Hawai'i Island (Hu *et al*. 2001) and are frequent predators of endangered Hawai'ian birds including colonial seabirds (Smith *et al*. 2002), ground-nesting waterfowl (Banko 1992), and tree-nesting passerines (Hess *et al*. 2004). Cats also carry *Toxoplasma gondii*, which has caused fatal toxoplasmosis in endangered Hawai'ian birds (Work *et al*. 2000, 2002) and Hawai'ian monk seals (*Monachus schauinslandi*) (Honnold *et al*. 2005).

The behaviour of feral cats in remote subalpine and alpine environments of Hawai'i makes traditional methods to understand population dynamics problematic; they are solitary, elusive, hard to capture, and inhabit areas that are difficult to survey (Hess *et al*. 2004). Their dispersal patterns and the inaccessibility of remote locations also make them logistically difficult to manage. Research on the genetic structure of feral cats in island ecosystems is rare (Pontier *et al*. 2005), but can provide

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valuable information for formulating control strategies and determining the scale and location of control efforts (Rollins *et al*. 2006). Here, we describe the use of seven highly polymorphic microsatellite markers to estimate the genetic structure of three feral cat populations on Hawai'i Island. The objectives of our research were to (1) evaluate genetic diversity and population structure, (2) assess levels of gene flow and connectivity between populations, (3) identify potential source populations, (4) characterise population dynamics and (5) evaluate evidence for sex-biased dispersal. We present results that can be used to formulate an island-wide control strategy.

Study areas

Study areas were located on Hawai'i Island in Hawai'i Volcanoes National Park (HAVO), and on North Mauna Kea (NMK), and West Mauna Kea (WMK) in designated critical habitat for palila (*Loxioides bailleui*) (Fig. 1). NMK and WMK were characterised as dry subalpine woodlands from 1701 to 2835 m elevation. HAVO extended from 800 to 2700 m elevation and consisted of montane wet forest grading into drier 'ōhi'a (*Metrosideros polymorpha*) scrub and subalpine shrubland. Substrates in HAVO were geologically young and interspersed with recent lava flows. HAVO and Mauna Kea were separated by extensive recent lava flows. The linear distances separating WMK from NMK, WMK from HAVO, and NMK from HAVO were 18 km, 50.2 km, and 53.5 km, respectively, and greater than the average home ranges reported for feral cats on Mauna Kea (1418 ha and 770 ha, respectively: D. Goltz, unpubl. data). The approximate areas from which cats were captured varied from 8 km^2 at NMK and 32 km^2 at WMK, to 87 km^2 at HAVO. Traps were arranged on transects perpendicular to elevation contours on NMK and WMK, and parallel to contours in HAVO. The population density of cats was unknown.

Methods

Population sampling and microsatellite analysis

Feral cats were trapped during 2000–05 to reduce predation on endangered species such as nēnē (Hawai'ian goose, *Branta sandvicensis*) and 'Ua'u (Hawai'ian petrel, *Pterodroma sandwichensis*) in HAVO, and palila on NMK and WMK. Traps were checked daily and cats were euthanised according to University of Hawai'i IACUC Protocol 97-063. We collected muscle tissue samples from 85 feral cats (49 males, 36 females) and stored samples in lysis buffer (0.1 M Tris–HCl pH 8.0, 0.1 M sodium EDTA, 2% SDS) at –20°C until extraction. We

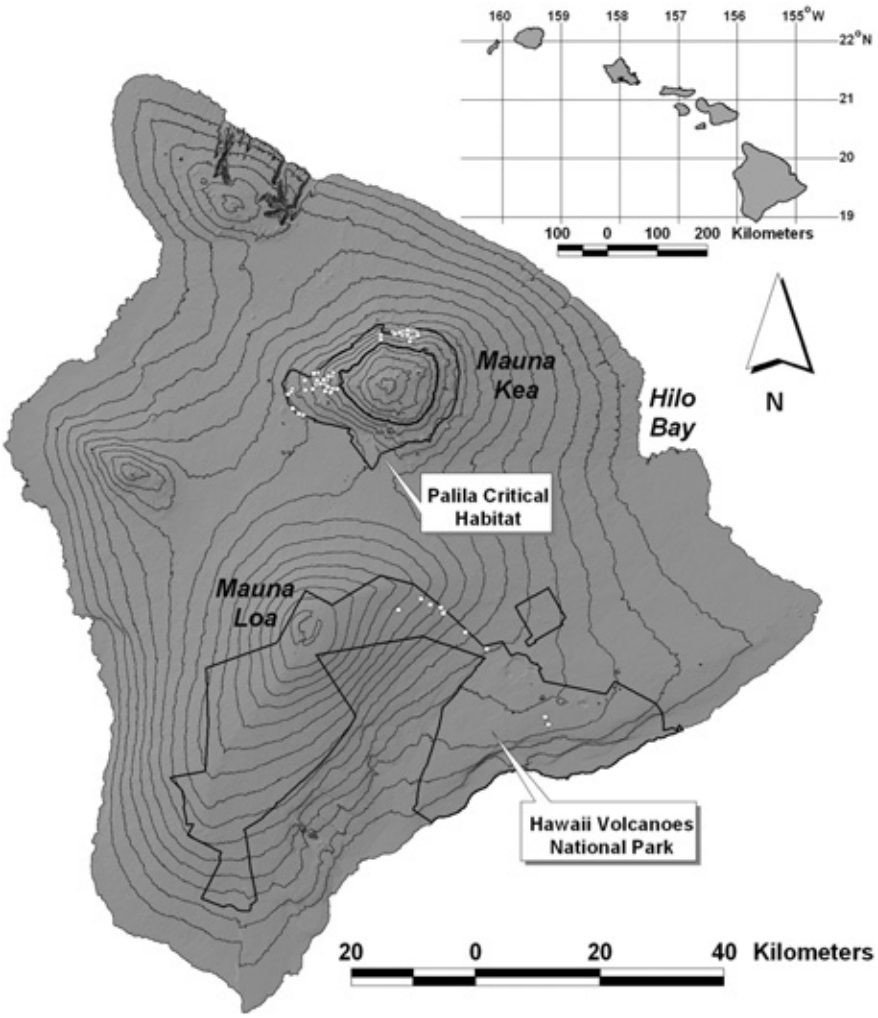

Fig. 1. Capture locations of feral cats sampled for genetic analyses (white dots) on Mauna Loa within Hawai'i Volcanoes National Park (19°26′N, 155°19′W) and on the north (19°54′N, 155°27′W) and west (19°49′N, 155°36′W) slopes of Mauna Kea within the critical habitat of palila (*Loxioides bailleui*). Elevation contour intervals are at 250 m.

extracted genomic DNA from the tissue using the QIAGEN® DNeasy™ Tissue Kit (Qiagen, Inc., Valencia, CA, USA).

We generated complete genotypes for all feral cat samples using seven polymorphic short-tandem repeat (STR) microsatellite markers previously developed and optimised for multiplexing of domestic cats (Menotti-Raymond *et al*. 2005) and included a gender-identifying sequence tagged site (STS) from the domestic cat Y-chromosome SRY gene. The markers were labelled with D2, D3 and D4 WellRED fluorescent dyes (Beckman Coulter, Fullerton, CA, USA) at the five-prime end of either the forward or reverse primers. This allowed multiplexing of all eight marker loci in one sequence run by distinguishing loci and associated alleles that overlapped in size.

A single PCR (polymerase chain reaction) was performed for each sample in a 20.0-μL volume containing 1 × PCR Gold buffer (Applied Biosystems, Fullerton, CA, USA), with final reaction concentrations (adapted from Menotti-Raymond *et al*. 2005) as follows: 1.5 mM $MgCl_2$, 0.8 mM dNTPs, 1 unit *Amplitaq* gold DNA polymerase (Applied Biosystems), 0.16 mg mL^{-1} bovine serum albumin, 8 μL microsatellite primer mix (see final concentrations in Table 1), and ~20 ng genomic DNA. PCRs were performed with a MJ Research PTC-200 DNA thermocycler, using conditions optimised by Menotti-Raymond *et al*. (2005). The eight-primer pair multiplexes were then visualised on a Beckman Coulter CEqn 8000 automated capillary sequencer, one lane for each DNA sample (Core Genetics Facility, University of Hawai'i at Hilo). Allele sizes were estimated using CEQN 8000 version 7.0 and then visually inspected, taking into consideration the expected allele size in base pairs for each of the eight loci and the original DNA clones from which the microsatellite loci were developed (Menotti-Raymond *et al*. 2005).

Genetic diversity

Genetic diversity for each population was summarised as the average number of alleles per locus (A) and average observed (H_O) and expected (H_E) heterozygosities (Nei 1978) with FSTAT 2.9.3 (Goudet 2001). We calculated the unbiased inbreeding coefficient f (similar to F_{IS}: Weir and Cockerham 1984) for each population–locus combination and tested for deviations from Hardy–Weinberg equilibrium with GENEPOP 3.4 (Raymond and Rousset 1995). Departure from Hardy–Weinberg expectations was assessed by exact tests with unbiased P-values based on a Markov chain simulation (with 1000 as dememorisation number, 500 batches and 1000 iterations per batch: Guo and Thompson 1992). Loci were combined by Fisher's method (Raymond and Rousset 1995) to examine departure from equilibrium for each population. A Bonferonni correction was used to adjust significance levels across multiple tests (Goudet 2001). All loci occurred on different chromosomes or different linkage groups on the same chromosome (Menotti-Raymond *et al*. 2005) and were considered independent markers.

Population structure

We investigated population structure among the three populations by using several methods with analyses for all feral cats, and separate analyses for males and females. We calculated the unbiased estimator θ (analogous to F_{ST}: Weir and Cockerham 1984) for all population pairs with FSTAT (Goudet 2001). In addition to θ, ρ (analogous to R_{ST}: Slatkin 1995) was estimated with R_{ST} CALC 2.2 (Goodman 1997) after standardisation of allele sizes in R_{ST} STANDARDISE 2.2 (Goodman 1997). We tested for correlation between the values of θ and ρ by using a Mantel test (Pearsons correlation, with 10000 iterations: Manly 1991) conducted in MANTEL 2.0 (Liedloff 1999). We tested the significance levels of θ and ρ for each population pair by calculating P-values and 95% confidence intervals (CI) by a bootstrap procedure. We compared pairwise θ estimates with log-transformed geographic distances (ln(km)) to assess whether dispersal is limited spatially for feral cats. Significance of the relationships was tested by a Mantel test (Pearsons correlation, with 10000 iterations: Manly 1991) conducted in MANTEL 2.0 (Liedloff 1999). Geographical distances between individuals were calculated with ARCVIEW GIS 3.2 (ESRI 1999).

Table 1. Multiplexed primer sequences and final concentrations of seven short-tandem repeat (STR) microsatellite markers and a gender-identifying sequence tagged site from domestic cat Y-chromosome (SRY) used for population genetics analysis of 85 feral cats on Hawai'i Island

STR marker	Final concentration (μM)		Primer sequence (5′ – 3′)	Size range (bp)
FCA441	0.5	F:	GTGTCTTGATCGGTAGGTAGGTAGATATAG	113–137
		R:	D3-ATATGGCATAAGCCTTGAAGCAAA	
FCA723	0.8	F:	D2-TGAAGGCTAAGGCACGATAGATAGTC	243–317
		R:	GCCACCCAGGTGTCCTGCTTC	
FCA731	1.8	F:	D2-ATCCATCTGTCCATCCATCTATT	337–401
		R:	GGTCAGCATCTCCACTTGAGG	
FCA733	0.8	F:	GATCCATCAATAGGTAAATGGATAAAGAAGATG	128–226
		R:	D2-TGGCTGAGTAATATTCCACTGTCTCTC	
FCA740	1.1	F:	D4-CCAAGGAGCTCTGTGATGCAAA	308–336
		R:	GTTCCCACAGGTAAACATCAACCAA	
FCA742	1.4	F:	D4-AAATTTCAATGTCTTGACAACGCATAAG	122–175
		R:	GCCAGGAACACCATGTTGGGCTA	
F124	1.1	F:	D3-TGTGCTGGGTATGAAGCCTACTG	255–367
		R:	GTGTCTTCCATGCCCATAAAGGCTCTGA	
SRY	0.04	F:	D3-TGCGAACTTTGCACGGAGAG	96–97
		R:	GCGTTCATGGGTCGTTTGACG	

We used a Bayesian Markov chain Monte Carlo (MCMC) approach to cluster individual genotypes from all cats ($n = 85$), male cats ($n = 49$) and female cats ($n = 36$) into respective populations and determine the most likely number of populations (K) as implemented in the program STRUCTURE 2.0 (Pritchard *et al*. 2000). Posterior probability values for K (log-likelihood; ln(L)) were estimated for preassigned number of clusters ($K = 1$–6 for all cats, $K = 1$–3 for males and females) using the mixed ancestry (admixture) model, a burn-in of 30000 iterations (checking that parameters α and likelihood had converged), and 100000 MCMC repetitions for 3–4 independent runs. We used only genetic information and excluded geographic location from analyses. The K value where the likelihood reached an asymptote was chosen as the number of populations (Pritchard *et al*. 2000).

We then conducted individual-based assignment tests that assign an individual to the population in which its genotype is most likely to occur to identify possible migrants (Aspi *et al*. 2006). First, we assigned samples into respective populations based on the highest proportion of membership (q) from results obtained in STRUCTURE. Second, we used the Rannala and Mountain (1997) Bayesian individual assignment method to estimate the likelihood that a cat originated from a given population as implemented in GENECLASS2 (Piry *et al*. 2004). The probability of an individual being a resident was compared with randomly generated genotypes (10000 replicates) and an individual was rejected from the population if the value was below $P < 0.01$

Effective population size

To estimate the current number of successfully breeding individuals per population, we used the method of linkage disequilibrium described by Bartley *et al*. (1992) to estimate the effective population size ($Ne(D)$) and 95% CI for each population as implemented in NEESTIMATOR (Peel *et al*. 2004). To investigate short-term trends of $Ne(D)$, we identified temporal sampling periods that corresponded to trapping intervals in HAVO and NMK and estimated the $Ne(D)$ and 95% CI for each sampling period by Hill's (1981) one-sample method. Owing to the small numbers of cats caught each year in HAVO, the first and second temporal sampling periods occurred from 2000 to 2002 ($n = 6$) and 2003 to 2005 ($n = 9$), respectively, with samples pooled to increase sample sizes. The first and second sampling periods for NMK occurred in 2004 ($n = 18$) and 2005 ($n = 21$), respectively. This analysis was not available for WMK as there was only one sampling period, in 2003 ($n = 31$).

Gene flow and migration rate

To obtain indirect measures of gene flow between populations, we estimated the number of migrants per generation (N_m), where N is the effective population size, m is the proportion of migrants per generation, and

$$N_m = (1/F_{ST} - 1)/4$$

(Slatkin 1995). N_m estimates are based on historical rates of gene flow and include only individuals that successfully reproduce (Pearse and Crandall 2004).

To determine possible source populations that could be targeted for control (Rollins *et al*. 2006), we estimated recent migration rates among populations by the Bayesian approach as implemented in BAYESASS+ 1.3 (Wilson and Rannala 2003) and approximated 95% CI. The program was run with a MCMC length of 3000000 iterations, a burn-in period of 100000 (checking that the chains had converged and the log-likelihood values had peaked), and the input parameters (ΔP = allele frequency, Δm = migration, Δf) set at 0.15, 0.10, and 0.20, respectively. This analysis included all migrants regardless of success at reproduction (Rollins *et al*. 2006).

Sex-biased dispersal

To assess sex-biased dispersal, we examined potential differences between sexes in genetic structure and relatedness. We performed an assignment t-test in FSTAT as described by Goudet *et al*. (2002) and calculated mean assignment indices (mAI_c), θ estimates and f estimates for females and males among the populations (Favre *et al*. 1997). We used program IDENTIX 4.03 (Belkhir *et al*. 2002) to estimate pairwise relatedness (r_{xy}) of males and females by applying the method of Lynch and Ritland (1999) and approximated 95% CI. We compared the relatedness between female and male cats within individual populations and relatedness of females among all populations. To investigate potential differences in relatedness between populations, we examined r_{xy} estimates and geographic distances between individuals by the Mantel test (Pearsons correlation, with 10000 iterations: Manly 1991) conducted in MANTEL 2.0 (Liedloff 1999).

Results

Genetic diversity

The mean number of alleles (A) ranged from 7.57 ± 2.99 (mean ± s.d.) to 9.00 ± 3.83 according to population (Table 2). Mean H_O ranged from 0.30 to 0.95 according to locus, and ranged from 0.63 ± 0.03 (WMK) to 0.76 ± 0.04 (HAVO) according to population. Mean H_E and H_O were not significantly different in any population but mean H_E was larger than H_O (0.72 ± 0.07) in WMK. Except for F124 and FCA731 ($P < 0.002$) in NMK and WMK, the single-locus f values did not differ from zero ($P > 0.05$). Multilocus f values ranged from –0.01 ($P = 0.16$) in HAVO to 0.09 ($P < 0.0007$) in WMK with an overall value of 0.03 ($P = 0.0001$) between all loci and populations. After Bonferonni corrections, f values showed a significant departure from Hardy–Weinberg equilibrium in NMK and WMK, suggesting that either (1) inbreeding may have increased, we unintentionally sampled parent–offspring pairs, or (2) null alleles are present in these populations (Kyle and Strobeck 2001; Schwartz *et al*. 2003; Aspi *et al*. 2006).

Population structure

Overall estimates of ρ (0.023; $P = 0.008$) showed results similar to those of θ (0.028; $P = 0.0001$). Pairwise θ estimates 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). Pairwise ρ-values (with 95% CI) were significant ($P < 0.05$) for HAVO–WMK and NMK–WMK (0.047, 0.017–0.135; and 0.025, 0.008–0.083, respectively) but not for HAVO–NMK (0.004, $P = 0.274$, –0.009–0.084). Pairwise values of ρ and θ were not correlated (Mantel test $r = –0.649$, $P = 0.853$) and pairwise ρ-values had extremely large 95% CI (almost twice as large as θ estimates). When populations are weakly structured with high rates of gene flow, θ provides a more accurate estima-

Table 2. Measurements of genetic diversity for feral cats on Hawai'i Island

Expected (H_E) and observed (H_O) heterozygosities, average number of alleles per locus (A) and the unbiased inbreeding coefficient, f, were estimated using seven microsatellite loci in the three feral cat populations sampled in Hawai'i Volcanoes National Park (HAVO), North Mauna Kea (NMK) and West Mauna Kea (WMK). The values with asterisks indicate a significant ($P < 0.002$) deviation from Hardy–Weinberg equilibrium after Bonferroni corrections

Locus	HAVO (n = 15)				NMK (n = 39)				WMK (n = 31)			
	H_E	H_O	A	f	H_E	H_O	A	f	H_E	H_O	A	f
FCA441	0.550	0.600	4	–0.091	0.489	0.564	5	–0.154	0.446	0.516	4	–0.158
FCA723	0.890	0.867	10	0.027	0.769	0.744	14	0.032	0.829	0.806	15	0.027
FCA731	0.879	0.800	9	0.089	0.862	0.757	11	0.122*	0.829	0.296	11	0.643*
FCA733	0.883	0.867	8	0.019	0.833	0.949	9	–0.139	0.850	0.806	8	0.051
FCA740	0.507	0.533	3	–0.052	0.610	0.513	5	0.159	0.454	0.452	6	0.005
FCA742	0.698	0.800	8	–0.147	0.786	0.744	9	0.054	0.778	0.774	7	0.006
F124	0.888	0.800	11	0.099	0.800	0.795	9	0.007*	0.826	0.774	12	0.063*
Mean	0.756	0.752	7.57	–0.008	0.736	0.723	8.86	0.012	0.716	0.632	9.00	0.091

tor than ρ (Balloux and Goudet 2002). Therefore, ρ-values were not used in further analyses. Genetic differentiation between population pairs was not significantly correlated with distance (ln(km)) (Mantel test $r = 0.789$, $P = 0.167$).

Bayesian clustering of all feral cats suggested the presence of three clusters (ln(L) = –2037; not shown) with membership in each cluster ranging from $q = 0.35$ to $q = 0.95$ (mean $q = 0.75$). Females were split into two clusters (ln(L) = –818) with membership ranging from $q = 0.59$ to $q = 0.98$ (mean $q = 0.88$). Female cats from HAVO and NMK created one cluster while WMK females created another. For males, a single cluster ($K = 1$) was the most likely (ln(L) = –1261).

Assignment tests correctly assigned most individuals to the area in which they were trapped (GENECLASS2: 62.4%; STRUCTURE: 56.4%). Considering the two closest populations (18 km apart), 23.1% (GENECLASS2) and 10.3% (STRUCTURE) of individuals captured in NMK were assigned to WMK. Of those misassigned in WMK, 25.8% (GENECLASS2) and 41.9% (STRUCTURE) were assigned to HAVO (Table 3). In GENECLASS2, two individuals were identified as samples that could not be grouped into a population, and thus were likely to be migrants from an unsampled population (Cegelski *et al*. 2003). Another two individuals were identified in both tests as being likely migrants (probability of assignment (P) >0.80) from WMK into both HAVO and NMK.

Effective population size

The overall $Ne(D)$ estimates for HAVO, NMK, and WMK (with 95% CI) were 24.2 (19.2–54.2), 35 (27.5–46.4), and 26.9 (21.2–35.4), respectively. In HAVO, the $Ne(D)$ estimates from 2000–02 samples ($n = 6$) and 2003–05 samples ($n = 9$) increased from 6.4 (4.0–12.2) to 18 (10.0–55.3), respectively. In NMK, the $Ne(D)$ estimates from 2004 samples ($n = 18$) and 2005 samples ($n = 21$) increased from 29.2 (19.1–54.2) to 30.8 (20.8–53.5), respectively. Although not significant, these estimates may suggest population growth for HAVO and NMK (Fig. 2).

Gene flow and migration rate

Nm estimates suggested high gene flow between feral cat populations with the effective number of migrants per generation ranging between 6.3 and 10.6 (Table 4). Number of migrants per generation was lowest between HAVO and NMK and highest in the adjacent populations on Mauna Kea. The mean posterior probabilities of migration rates showed that most individuals were native to their capture locations in all populations, with the most originating in WMK (0.708–0.927) (Table 5). 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

Assignment t-test results supported male-biased dispersal and female 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

Table 3. Assignment of feral cats to populations on Hawai'i Island

Assignment of feral cats to the three sampled populations (capture locations) in Hawai'i Volcanoes National Park (HAVO), North Mauna Kea (NMK) and West Mauna Kea (WMK) using GENECLASS2 (Piry *et al*. 2004) and STRUCTURE assignment tests (Pritchard *et al*. 2000)

Location	n	Number assigned to population					
		HAVO		NMK		WMK	
		GENECLASS2	STRUCTURE	GENECLASS2	STRUCTURE	GENECLASS2	STRUCTURE
HAVO	15	11	12	2	1	2	2
NMK	39	7	13	22	22	9	4
WMK	31	8	13	3	4	19	14

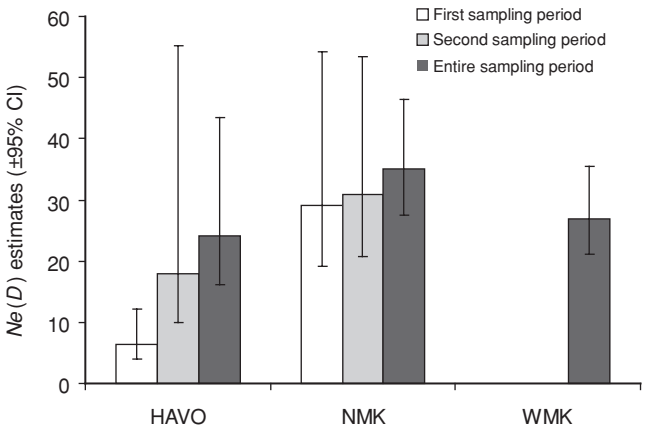

Fig. 2. Effective population size (*Ne*(*D*)) estimates for three feral cat populations sampled in Hawai'i Volcanoes National Park (HAVO), North Mauna Kea (NMK) and West Mauna Kea (WMK), Hawai'i, with corresponding 95% confidence intervals for first (white bars), second (light grey bars) and entire (dark grey bars) sampling periods. The first and second sampling periods for HAVO were between 2000–02 and 2003–05. The first and second sampling periods for NMK were 2004 and 2005, respectively. The entire sampling period for WMK was in 2003.

(mAI_c = –0.900, 1.23, P = 0.007, respectively). The estimate of f was significantly higher for males (F = 0.085) than for females (F = –0.007) (P = 0.008) and the average θ estimate across the populations for males (θ = 0.013) was significantly lower than that calculated for females (θ = 0.053) (P = 0.028).

We found no differences in relatedness between female and male cats within and among populations (Fig. 3). Mean r_{xy} values suggested little to no relatedness within and among populations (as shown by the negative estimates) and both male and female cats in HAVO were less related to each other than to cats in other populations, most likely owing to the larger sampling area of HAVO compared with the other populations. Among populations, pairwise r_{xy} values were significantly (P < 0.0001) correlated with geographic distance, having a greater inverse correlation for female cats (Mantel test r = –0.161) than for all cats (Mantel test r = –0.131) and very little inverse correlation for male cats (Mantel test r = –0.095). Within populations, r_{xy} values and distance were not correlated for male cats (P > 0.5 in all populations). For females, r_{xy} values declined significantly with distance in HAVO and WMK (HAVO, Mantel test r = –0.576, P = 0.005; WMK, Mantel test r = –0.386, P = 0.002), although not in NMK (Mantel test r = –0.05, P = 0.587).

The most related individuals (r_{xy} = 0.86), an adult and a juvenile female, were captured within 15 days of each other at a distance of 1.4 km in WMK. It is likely that this was a mother–daughter pair. The most closely related individuals (r_{xy} = 0.62) separated by the greatest distance (65.9 km) were two females captured in HAVO and NMK and were likely siblings or a mother–daughter pair.

Table 4. Genetic structure and connectivity of feral cat populations on Hawai'i Island

Pairwise F_{ST} (θ) estimates above the diagonal, estimated number of migrants per generation (N_m) between populations below the diagonal, and expected heterozygosities (H_E) along the diagonal from three feral cat populations sampled in Hawai'i Volcanoes National Park (HAVO), North Mauna Kea (NMK) and West Mauna Kea (WMK), Hawai'i

Location	HAVO	NMK	WMK
HAVO	0.756	0.038	0.028
NMK	6.30	0.736	0.023
WMK	8.81	10.56	0.716

Table 5. Migration rates of feral cats on Hawai'i Island

Means of the posterior distributions of the migration rate (with 95% confidence intervals) into each of the three feral cat populations sampled in Hawai'i Volcanoes National Park (HAVO), North Mauna Kea (NMK) and West Mauna Kea (WMK), Hawai'i. Migration rates 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

Location	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)

Discussion

Genetic structure suggests that feral cats on Hawai'i Island exhibit long-distance dispersal between populations and their movements are not inhibited by current control efforts or barriers such as extensive lava flows. As expected, given their European ancestry, the genetic diversity of feral cats we examined in Hawai'i (A = 7.57–9.00, H_O = 0.70) was similar to that of European domestic cats (A = 14.2, H_O = 0.70: Pierpaoli *et al*. 2003) but was greater than that reported for feral cats recently introduced from France to a subantarctic island (A = 3.67–7.00, H_O = 0.53: Pontier *et al*. 2005) and also for cat colonies in France (A = 4.38–7.78, H_O = 0.61) that experience low dispersal rates owing to barriers such as heavy-traffic roads (Say *et al*. 2003). We also found very little genetic differentiation (θ = 0.028) between populations and dispersal was not spatially

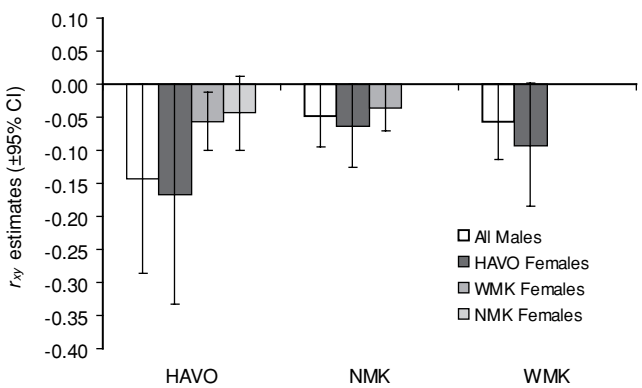

Fig. 3. Estimated pairwise relatedness (r_{xy}: Lynch and Ritland 1999) with 95% confidence intervals of male feral cats (white bars) within, and female feral cats (shaded bars) within and among, three populations from Hawai'i Volcanoes National Park (HAVO), North Mauna Kea (NMK) and West Mauna Kea (WMK), Hawai'i.

limited. Generally, F_{ST} values below 0.05 suggest high levels of gene flow and population connectivity (Thulin *et al*. 2006). Therefore, we conclude that the three populations were not founded independently, there was rapid colonisation from initial founders owing to high growth rates, and ongoing gene flow has occurred (Abdelkrim *et al*. 2005; Pontier *et al*. 2005). Apparently, feral cats in Hawai'i have not differentiated markedly from their initial founders (Pontier *et al*. 2005). 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 those of European wildcats (*Felis silvestris*) (Lowe *et al*. 2000; Beaumont *et al*. 2001).

We found some evidence of inbreeding in the Mauna Kea populations ($f > 0.09$) and between all populations ($F = 0.03$), although this was low compared with estimates of isolated feral cat populations in urban France ($F = 0.14$) (Say *et al*. 2003) and on a subantarctic island ($f > 0.11$) (Pontier *et al*. 2005). Inbreeding may be the result of factors that cause low population density, such as kitten mortality due to feline leukemia virus, feline immunodeficiency virus, and toxoplasmosis (Molsher 1999), all of which have been documented in feral cats on Mauna Kea (Danner *et al*. 2007). Inbreeding may also reduce fitness and resistance to diseases (Coltman *et al*. 1999), mating success (Slate *et al*. 2000) and juvenile survival (Coltman *et al*. 1998).

Despite the positive inbreeding coefficients, WMK and NMK, separated by the shortest distance (18 km), had high levels of gene flow between them, with 10.6 cats migrating per generation. Kaeuffer *et al*. (2004) estimated that the mean generation time for feral cats in France was 3.38 years. This suggests that >10 cats migrated between WMK and NMK and successfully reproduced in 3 years. Given the home-range sizes of feral cats reported from similar environments in Australia (Edwards *et al*. 2001), it is not surprising that cats disperse long distances. Often populations in close proximity receive a greater number of migrants than populations farther apart (Whitlock and McCauley 1999), and, accordingly, less gene flow occurred between Mauna Kea and HAVO. It is surprising, though, that an estimated 6.3–8.8 cats per generation may have migrated between these populations given the harsh environment between these areas. However, our estimates of indirect gene flow are presented only as an index of relative measures of connectivity between populations and some assumptions of this analysis may have been violated (Whitlock and McCauley 1999; Cegelski *et al*. 2003).

As for other carnivores, the spatial organisation of cats is determined by the abundance and distribution of available prey and receptive mates and the proximity to human habitation (Pontier *et al*. 1995). The density of cats may be higher on Mauna Kea, particularly WMK, than in HAVO owing to abundant prey (Hess *et al*. 2007), which may facilitate increased reproduction, survival, and dispersal to other locations. Accordingly, migration rates showed that most dispersing cats originated and immigrated from WMK into the other populations with little migration occurring into WMK. Also, only 45–61% of individuals captured in WMK were correctly assigned to their origin. The 'misassigned' individuals were likely migrants from an unsampled population or offspring of migrants (Cegelski *et al*. 2003; Rollins *et al*. 2006). In fact, two migrants were captured in both HAVO and NMK and assigned to WMK. This suggests that cats may not be able to easily integrate with some residents and may disperse long distances to fill empty territories created by current predator-removal efforts. Also, cats may disperse more during the seabird breeding season to prey upon these burrow-nesting endangered species (Hu *et al*. 2001).

Mauna Kea populations had significantly more successfully breeding individuals than did HAVO, as shown in the larger N_e estimates (DeYoung and Honeycutt 2005). Because we trapped consistently between 2000 and 2005, our samples had overlapping generations and immediate evaluation of N_e would have been difficult using more common temporal methods that require at least two non-overlapping generations (Waples 1989). Bartley's linkage disequilibrium method (Bartley *et al*. 1992) has an advantage in that population trends can be evaluated (Leberg 2005) and only one sampling period is required regardless of generation length (Bartley *et al*. 1992). Both HAVO and NMK apparently experienced population expansion with increasing N_e estimates, indicating insufficient control efforts between trapping periods. However, our sample sizes were small and our results should be used only to evaluate control strategies, as sample sizes over 90 may be necessary to obtain precise estimates of N_e when using the linkage disequilibrium method (Bartley *et al*. 1992). Also, Mauna Kea populations may be experiencing introgression from adjacent unsampled populations which would explain both the increase in N_e estimates and misassigned individuals (Roman and Palumbi 2003; Spencer and Hampton 2005).

Although our results support high gene flow, population structuring was evident in the Bayesian clustering results that showed three clusters of cats. Cats captured in HAVO had a greater proportion of individuals correctly assigned to that population whereas individuals in Mauna Kea had more ambiguous assignments. The discrepancies between genetic structure and assignment tests could be a result of several reasons such as the distance and terrain separating populations, predator-control efforts reducing encounter rates, and sampling individuals that have mixed or indistinct ancestry (Cegelski *et al*. 2003). When analysing individual sexes, population structuring suggested two clusters of females and only one of males. Also, assignment *t*-tests and relatedness estimates supported male-biased dispersal, which is common in many mammal species (Goudet *et al*. 2002). More unusual was the similar relatedness we found between males and females. However, relatedness of females, but not males, decreased significantly with geographic distance, further supporting female philopatry. Similar to other research, we found that sex-biased dispersal estimates derived using genetic-based assignment techniques mirrored radio-telemetry findings, and did not require as much field effort (DeYoung and Honeycutt 2005). Goudet *et al*. (2002) suggested that short-distance dispersal may be sex-biased to avoid inbreeding. Alternatively, long-distance dispersal may be a means to colonise empty patches and is unlikely to be sex-biased. In fact, Spong and Creel (2001) reported that ~20% of female lions (*Panthera leo*) in Africa emigrate to new territories. This is consistent with our finding that the most closely related individuals separated by the furthest distance were two females.

Our results can be used to design an effective plan for feral cat control. Although complete eradication of feral cats has

occurred on several small islands (Nogales *et al*. 2004), Hawai'i Island would require large-scale control programs, which are typically difficult to implement (Pontier *et al*. 2005). One major limitation for control efforts is the ability of the invasive species to disperse from neighbouring populations and recolonise (Abdelkrim *et al*. 2005). The genetic structure of feral cats in Hawai'i indicates great dispersal ability, therefore control will be very difficult and recolonisation seems highly likely. The reproductive biology and life history of the invasive species can also determine the ease of control and potential for recolonisation (Myers *et al*. 2000). Female cats reach sexual maturity between 6 and 8 months and males between 8 and 10 months and can breed 2–3 times a year. However, reproduction can be delayed (Jones and Coman 1982; Say *et al*. 1999) as shown by Bester *et al*. (2002), who reported that a drastic decrease of feral cats following eradication efforts on sub-antarctic Marion Island caused a decline in pregnancy rates and fecundity, possibly owing to a lower encounter rate between the sexes. Control efforts need to minimise gene flow to no more than one migrant per generation in order to decrease genetic diversity (Wright 1969) and thus create small or fragmented populations in which inbreeding is more likely to occur. Targeting the source population for control is important when the animal disperses long distances on unknown pathways (Rollins *et al*. 2006). On Hawai'i Island, control efforts on Mauna Kea may benefit endangered wildlife at other locations by reducing dispersing feral cats. Also, the sex that disperses the most could be targeted for control (Rollins *et al*. 2006); however, we do not recommend targeting male feral cats as both sexes exhibited some dispersal.

To minimise risk of failure in controlling invasive species and to reduce management cost and loss of native species, genetic monitoring of the invasive species should be a preliminary step in the management process in order to assess the effectiveness of control efforts (Robertson and Gemmell 2004; Abdelkrim *et al*. 2005; Rollins *et al*. 2006). For example, a decrease in genetic diversity, increase in inbreeding, and decrease in effective population size would all indicate successful control strategies (DeYoung and Honeycutt 2005). Assignment tests can be used to identify captured individuals as either control survivors or recolonisers following control efforts (Robertson and Gemmell 2004). Management of other invasive vertebrates may benefit by employing these population genetic tools.

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