

## Effects of sterilization on movements of feral cats at a wildland–urban interface

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Trap–neuter–release (TNR) programs, in which feral cats are sterilized and fed in unconfined colonies, have been advocated as a humane and effective way to reduce the impacts of feral cats on native wildlife. Little is known, however, about the effects of sterilization on feral cat movements and space use, particularly where colonies are located near natural areas. We determined home-range area and overlap and characterized the long-range movements of 14 sterilized and 13 intact radiocollared cats on Catalina Island, California, from 2002 to 2004. Male home ranges were significantly larger than those of females, but no significant differences were revealed in home-range areas or overlap between sterilized and intact cats. Cats regularly moved between natural habitats in the interior of the island and human-populated areas regardless of sex or treatment status, although most (68%; 17/25) of the cats that moved long distances were female. Island-wide, the cat population was estimated to be 600–750 cats, with >70% associated with developed areas, including existing TNR colonies. The influx of subsidized cats to natural habitats, combined with their high vagility and low trappability, makes TNR an unlikely solution for controlling feral cats on a large, rugged island like Catalina and, more generally, in other locations where human populations abut ecologically sensitive areas. DOI: 10.1644/09-MAMM-A-111.1.

Key words: California Channel Islands, Catalina Island, feral cats, home range, invasive predators, island conservation, trap–neuter–release

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Domestic cats (*Felis catus*) have been introduced to islands and continental areas worldwide where they have been implicated in the extinction of native species (Dickman 1996; Nogales et al. 2004). Free-roaming cats harm native wildlife in several ways. First, cats are opportunistic predators, with large effects on prey that are naïve to cat predation (Courchamp and Sugihara 1999). Second, free-roaming cats can compete with native predators for prey. Human-subsidized cats can reach densities exceeding several hundred cats/km<sup>2</sup> (Liberg et al. 2000), and individuals can spill over into less densely populated wildland areas where they reduce prey for native predators (George 1974). Finally, free-roaming cats often carry diseases and parasites that can spread to wildlife (Jessup et al. 1993; Riley et al. 2004).

The introduction of feral cats has been particularly devastating for island species (Nogales et al. 2004). Although eradication and control of invasive predators has been successful on uninhabited islands, such efforts are more complicated on islands inhabited by humans and their pets and by nontarget wildlife (Levy and Crawford 2004). A nonlethal approach to controlling cat populations, known as trap–neuter–release (TNR), involves trapping and sterilizing cats and returning them to unconfined “colonies,” where they are

fed daily by volunteer caretakers. Longcore et al. (2009), however, point out that the TNR phenomenon is received by the public as an issue of animal welfare, not one of environmental impact. As a result, although TNR is considered only an interim solution to cat overpopulation (Slater 2002), it has been widely implemented to control feral cat populations in urban, rural, and wildland areas, often with detrimental effects on native wildlife (Jessup 2005). In reality, most TNR programs are volunteer-based, understaffed, and cannot sterilize all cats in a colony or monitor colony health or population changes over time (Jessup 2004). Even in intensively managed colonies with a high rate of sterilization (75–80%), the estimated time to extinction of a TNR colony may be more than a decade (Nutter 2005). Finally, TNR research fails to address critical issues such as spillover predation by cats in adjacent wildland areas, zoonotic and wildlife disease risks, and the health and welfare of feral cats (Castillo and Clarke 2003). Thus, many of the actual



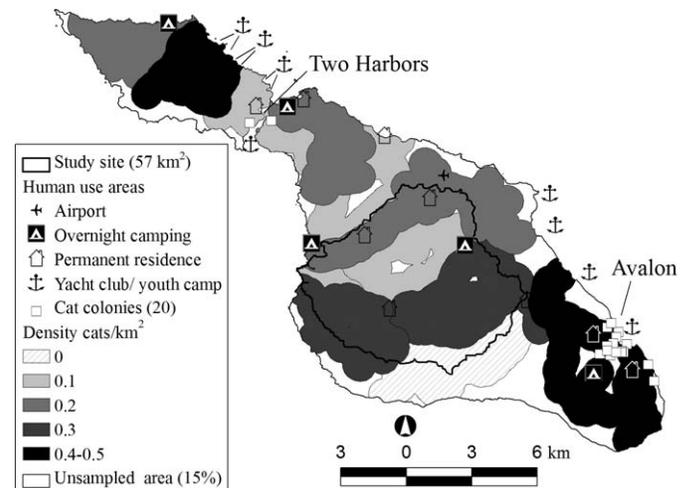
consequences of TNR remain poorly documented, making it difficult to assess the true efficacy of such programs.

The feral cat population on Catalina Island provides an ideal opportunity to assess the impact of TNR on cat populations living at the wildland–urban interface. Cats likely were first introduced to the Channel Islands off California, during the 19th century (Phillips and Schmidt 1997), and feral populations are currently resident on 3 of the 8 Channel Islands: San Nicolas, San Clemente, and Santa Catalina (hereafter, Catalina). Catalina has a human population of approximately 4,000 permanent residents and a tourism-based economy with effectively no regulation of exotic or domestic animals brought to the island (Guttilla 2007). Human activity is restricted primarily to the periphery of the island, with the interior of Catalina consisting of rugged, relatively intact native habitat. At the same time, for >20 years, the Catalina Island Humane Society has practiced TNR at designated cat colonies in Avalon and Two Harbors, the 2 largest human settlements on the island. Proponents of TNR have argued that colony-fed sterilized cats pose little threat to native species in the adjacent wildland interior and that because sterilized cats roam less than reproductively intact cats but retain their territorial behavior (Hawkins et al. 2004; Zaunbrecher and Smith 1993), they should prevent immigration of new cats (i.e., the vacuum effect—Mahlow and Slater 1996; Neville and Remfry 1984), thereby eventually leading to population decline due to attrition.

To explore the effects of sterilization on the persistence of feral cat populations we examined the home-range behavior and movements of sterilized and intact radiocollared feral cats living in the interior of Catalina. We predicted that home ranges of sterilized cats would be smaller than those of intact cats because the former would not wander as far in search of mates. In addition, we predicted that sterilized cats would be more sedentary and less territorial and would therefore exhibit greater overlap in their home ranges than intact cats (Castillo and Clarke 2003; Lee et al. 2002). We also examined the extent of movement of cats between the interior and developed areas, including TNR colonies, to determine whether these areas are a source of cats for other parts of the island. Last, we used our livetrapping efforts to estimate the population size of feral cats on Catalina Island. Although our results apply most directly to the management of cats on Catalina, they should improve our understanding of the consequences of maintaining large, unrestricted populations of human-subsidized cats adjacent to ecologically sensitive continental areas.

## METHODS

**Study site.**—Catalina is the 3rd largest (194 km<sup>2</sup>) of the California Channel Islands, which are located approximately 35 km off the coast of Southern California (Fig. 1). The island is 13 km wide and 22 km long, with rugged terrain ranging in elevation from sea level to 631 m. It has a Mediterranean climate characterized by hot, dry summers and cool, wet winters. Annual temperatures range from 9°C to 24°C, with a



**FIG. 1.**—Feral cat densities estimated from 2004 island-wide stratified trap efforts on Catalina Island. Filled areas represent bands of different cat densities, on the basis of the number of captures in different trap lines (see text for procedure used to estimate area sampled for determination of densities). Human-inhabited areas and known TNR (trap–neuter–release) colonies are shown because of the higher cat densities observed near those areas. The dark line represents the boundary of targeted trapping efforts, which was approximately 57 km<sup>2</sup> or 30% of the island.

mean ( $\pm 1$  SD) annual precipitation of 300 ( $\pm 146$ ) mm (Catalina Island Conservancy, [www.catalinaconservancy.org](http://www.catalinaconservancy.org)). The predominant types of vegetation are coastal sage scrub, island chaparral, and grassland (Knapp 2005). The wet season (November–April) generally corresponds to the cat breeding season, with little reproduction by feral cats reported during the drier part of the year (May–October).

**Animal capture and handling.**—To capture cats for radio-tracking we conducted targeted trapping in the Middle Canyon and Cottonwood Canyon watersheds (57 km<sup>2</sup>) on the eastern half of Catalina (Fig. 1). Targeted trapping consisted of setting traps along roads, trails, canyon bottoms, and ridge tops where we detected fresh cat sign; trapping efforts were not standardized with respect to duration or trap placement. In 2004, these efforts were expanded with island-wide transects (250–350 m) placed systematically along the interior road system. We trapped cats with wire-mesh live traps (Model 106; Tomahawk Live Trap Co., Tomahawk, Wisconsin) that were custom-manufactured with smaller mesh to reduce tooth injuries. Traps were covered with industrial shade cloth and equipped with bite bars consisting of nontoxic plastic hose affixed to the back of traps with wire (Guttilla 2007). Traps were lined with grass and baited with wet and dry commercial cat food. We anesthetized cats in traps with an intramuscular injection of ketamine HCl (10 mg/kg) and acepromazine (0.1 mg/kg). Cats were weighed and tested for exposure to feline immunodeficiency virus (FIV) and feline leukemia virus (FeLV). Tests for FIV and FeLV antibodies were run in-house using a commercially available enzyme-linked immunosorbent assay test kit (Snap Combo kit; IDEXX Veterinary Laboratory, West Sacramento, California). FeLV- and FIV-

positive cats were euthanized to prevent infected cats from suffering disease symptoms, to reduce opportunities for disease transmission to other cats and wildlife, and to minimize the loss of experimentally sterilized cats.

We marked adult cats with passive integrated transponder tags (AVID, Inc., Norco, California; Biomark, Inc., Boise, Idaho), which were implanted subdermally between the shoulder blades. A subset of 27 of the adult cats captured was equipped with 45-g radiocollars (Communication Specialists, Orange, California). Fourteen (7 male, 7 female) of the radiocollared cats were sterilized using standard spaying and neutering procedures (Guttilla 2007). The remaining 13 (5 male, 8 female) were left intact as controls. Cats were selected for sterilization opportunistically, as determined by the availability of a veterinarian (on contract with the Institute for Wildlife Studies, Arcata, California) on-island and the timing of cat captures (Guttilla 2007). All radiocollared cats were negative for both FIV and FeLV and weighed at least 1.5 kg. To identify cats as having been sterilized, approximately 1 cm of the distal portion of left ear was cut (tipped). Ear-tipping is common practice in TNR programs (Scott et al. 2002), and TNR colony cats on Catalina have their right ear tipped (Guttilla 2007). All procedures were consistent with guidelines set by the American Society of Mammalogists (Gannon et al. 2007) and were approved by the Institutional Animal Care and Use Committee at California State University Fullerton.

*Radiotelemetry.*—Before radiotracking cats we placed radiocollars at known locations to determine accuracy of directional bearings in estimating cat locations, giving an estimated bearing error of 12° (White and Garrott 1990). We radiotracked cats from November 2002 to July 2004 using an R-1000 radio receiver and hand-held 3-element Yagi antenna (Communication Specialists, Orange, California). Most locations (83%;  $n = 1,614$ ) were recorded between sunset and sunrise when cats are most active (Barratt 1997). We attempted to obtain 3 locations per cat per week. For each fix a single observer moving on foot or by vehicle triangulated the location of the cat. Mean ( $\pm 1$  SD) time between the 1st and last bearings for a fix was 21 ( $\pm 16$ ) min ( $n = 2,004$  locations). We tracked individual cats for 1–4 wet/dry seasons (mean  $\pm 1$  SD:  $2 \pm 1$  seasons); tracking continued until either collar failure or death of the collared cats.

*Home-range analyses.*—We plotted telemetry fixes in location of a signal (LOAS 2.07; Ecological Software Solutions, Urnäsch, Switzerland) using the maximum likelihood estimator (MLE) algorithm, with best biangulation as the default estimator when MLE failed. LOAS converts radiolocation estimates into a geographic information systems format so that home-range analyses can be performed. Home-range boundaries were determined in ARCVIEW 3.2a, using the spatial analyst (Environmental Systems Research Institute Inc., Redlands, California) and animal movement (Hooge and Eichenlaub USGS, Anchorage, Alaska) extensions. Home-range boundaries were calculated using minimum convex polygon (MCP) and fixed kernel procedures (KHR, optimized

by least-squares cross validation—Worton 1989); 2 procedures were used to better account for differences in the precision and assumptions associated with each estimator (Harris et al. 1990). Home-range area was calculated from 95% of the radio fixes for each animal (95% MCP, 95% KHR), assuming that the remaining 5% of fixes, as determined by the software, were outliers that represented excursions. Core home-range, defined as the area used disproportionately more than other areas (Samuel et al. 1985), was estimated using 50% KHR.

All statistical analyses were performed in SAS v. 9.1 (SAS Institute Inc., Cary, North Carolina). Home-range data were analyzed by season (breeding, nonbreeding), with 18–50 fixes ( $28 \pm 6$ ; mean  $\pm 1$  SD) per cat per season tracked. We used Pearson correlations ( $r$ ) to determine if a relationship existed between the number of fixes and home-range area that would indicate that we had sufficient numbers of fixes to estimate home-range areas. Initial inspection of these data also indicated that they did not meet the assumptions of parametric tests, and thus estimates of home-range area were natural log-transformed before analysis. We used a 2-way analysis of variance (ANOVA) and Tukey honestly significant difference (HSD) tests to determine the effects of sex and reproductive status (treatment = intact versus sterilized) on the areas of the home ranges occupied by our study animals during the breeding and nonbreeding seasons. We used  $t$ -tests to compare home-range areas of cats, pooling across sexes and treatments, and Pearson correlations to determine the relationship between home-range area and body size.

Home-range overlap was calculated for all pairs of overlapping cats during a given season and year, using both 50% and 95% KHR estimates. The area of overlap for a given pair of cats was calculated as the percentage of each cat's home range during a given season and year. Percentage overlap data were normalized by arcsine-square root transformation. We used 3-way ANOVAs to determine the effects of season, reproductive status (sterilized versus intact), and sex on percentage overlap followed by Tukey HSD test for pairwise comparisons subsequent to significant ANOVA outcomes.

*Long-distance movements.*—We recorded long-distance movements of radiocollared cats from their home ranges in the island interior to areas associated with human activities. These were calculated as the linear distance between the last observation within a cat's home range and the 1st observation in a new area, and were equivalent to  $\geq 2$  diameters of a given cat's home range. Long-distance movements also were recorded for uncollared TNR colony cats trapped in the interior of the island; these animals were identified visually on the basis of their right-tipped ears. These cats came from TNR colonies located in Avalon and Two Harbors. We estimated the linear distance from trap locations to both Avalon and Two Harbors and recorded the shorter of the 2 distances. All estimates of movements and distance traveled were conservative because they did not take into account the route traveled or the topography of the island.

**TABLE 1.**—Estimates of the numbers of free-roaming feral cats in the interior of Catalina Island, California, between 2002 and 2004 on the basis of trapping, direct observations, and spotlight counts. Spotlight surveys were conducted in November 2003 and January–September 2004 (Stapp and Guttilla 2006). The estimated population size assumes that only 50% of the interior population was trapped in a given year.

Method	Year		
	2002	2003	2004
Targeted and systematic trapping	50	70	75
Known to be alive (visuals or radiocollars)			
but not trapped	53	66	9
Monthly spotlight surveys		5	22
Total known individuals	103	141	106
Estimated population size	128	176	144

*Population size and density.*—We estimated population density of feral cats from targeted and systematic trapping efforts as the number of individual cats captured divided by the effective trapping area. The effective trapping area was calculated by assuming that the area covered by each trap was equivalent to the mean 95% MCP home-range area ( $1.56 \text{ km}^2$ ), resulting in a 705-m radius buffer around each location; areas then were summed for each trapping transect. The total area of coverage from targeted efforts ranged from 39 to  $77 \text{ km}^2$ , whereas systematic, island-wide efforts in 2004 had an effective area of  $165 \text{ km}^2$  (85% of the island). Trap success was adjusted to exclude disturbed traps or those that captured nontarget species. To estimate the size of feral cat population in the interior of the island we combined capture records from targeted and systematic trapping with information on radiocollared cats known to be alive (Stapp and Guttilla 2006). We also surveyed TNR colony caretakers in Avalon and Two Harbors and interior rural residents to estimate the number of colony and feral cats that were dependent on human foods. These two values were summed to estimate the total number of free-roaming cats on Catalina.

## RESULTS

We trapped 142 cats between May 2002 and October 2004. Forty-one (28.9%) of 134 cats tested positive for FeLV and/or FIV (30/73 male, 11/61 female) and were euthanized (FeLV prevalence = 15.7% [13 male, 8 female]; FIV prevalence = 17.9% [20 male, 4 female]). These included 3 (17%) of 18 previously sterilized TNR colony cats that were caught in the interior of the island. Of the remaining 101 cats, 35 sterilized (15 previously sterilized; 20 sterilized in our study) and 66 intact animals were released at the point of capture. Fourteen of the sterilized individuals (7 male, 7 female) and 13 of the intact animals (5 male, 8 female) were the radiocollared animals used to assess home-range size and overlap.

Trap success for both targeted and island-wide trapping (9,242 trap-nights) was low (combined mean  $\pm 1 \text{ SD} = 2.7\% \pm 0.4\%$ ;  $n = 3$  years). Cat densities from targeted trapping

( $0.8 \pm 0.4 \text{ cats/km}^2$ ) were higher than those for island-wide efforts ( $0.3 \pm 0.1 \text{ cats/km}^2$ ). The highest densities during island-wide trapping were near areas of human settlement (Fig. 1). The west end of the island, which supports several camps and yacht clubs, also had high cat densities ( $0.5/\text{km}^2$ ), although estimated densities near Two Harbors ( $0.1\text{--}0.2 \text{ cats/km}^2$ ), the location of several TNR colonies, were surprisingly low.

Feral cats were difficult to recapture; nearly 50% of cats known to be alive in 2002 and 2003 evaded traps (Table 1). Under the simple model that only 50% of the population was trappable in a given year, estimates from all sources suggested that the feral population in the interior ranged from 128 to 176 cats across years. Similarly, if we extrapolate the range of feral cat densities generated from trapping ( $0.3\text{--}0.8 \text{ km}^{-2}$ ) to the entire island ( $194 \text{ km}^2$ ), estimates of the interior feral cat population size ranged from 58 ( $0.3 \text{ km}^{-2}$ ) to 155 ( $0.8 \text{ km}^{-2}$ ) cats. Assuming that the numbers of TNR colony (471) and interior feral cats (85) reported by residents were stable over time, we suggest that approximately 614–732 free-roaming cats were on the island during our study.

We recorded 2,004 fixes for the 27 animals monitored via radiotelemetry between November 2002 and July 2004. Four cats were tracked during all 4 seasons, 9 cats were tracked for 3 consecutive seasons, 4 cats were tracked for 2 consecutive seasons, and the remaining 10 cats were tracked for 1 season. To account for differences in the number of seasons during which individuals were monitored, mean seasonal home-range sizes were calculated for the 13 cats that were tracked for 2 dry or 2 wet seasons. Mean ( $\pm 1 \text{ SD}$ ) number of fixes per season per cat was  $29 \pm 6$ , with no significant correlation between the number of fixes and home-range area ( $n = 61$ ; 95% MCP:  $r = -0.005$ ,  $P = 0.975$ ; 95% KHR:  $r = -0.062$ ,  $P = 0.682$ ).

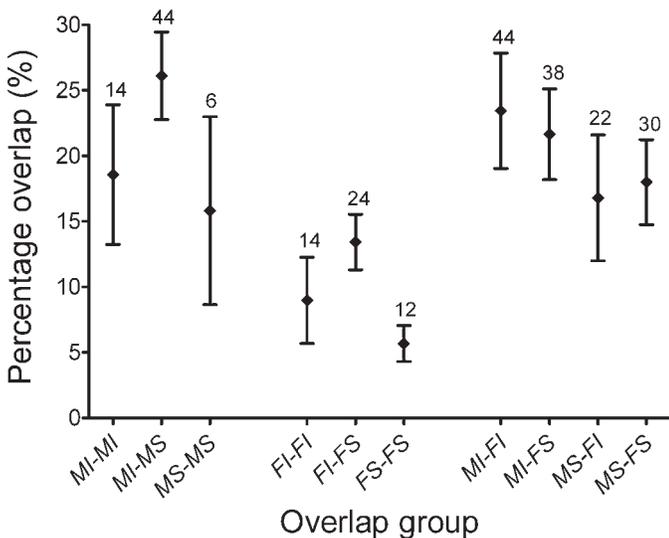
For all 3 home-range estimators used (95% MCP, 95% KHR, 50% KHR), sex was the only factor that significantly affected home-range area, and only during the dry, nonbreeding season (dry season: overall model,  $d.f. = 3, 16$ ,  $P \leq 0.027$ , sex effect  $P \leq 0.004$ , treatment, sex  $\times$  treatment effects  $P \geq 0.299$ ; wet season: overall model  $d.f. = 3, 20$ ,  $P \geq 0.089$ ). Combining treatments, mean home-range area for males was 2–4 times larger than that for females, depending upon the estimator (Table 2;  $t$ -tests, dry season,  $P \leq 0.002$ ; wet season,  $P < 0.064$ ). Although seasonal home ranges of intact and sterilized females were similar, home ranges of intact males tended to be larger (although not statistically different;  $P \geq 0.173$  for the 3 estimators) than those of sterilized males during both seasons (Table 2). The large variation in 95% KHR estimates of home ranges for intact males was largely the result of 1 individual that had a home range in both the breeding ( $13.6 \text{ km}^2$ ) and nonbreeding ( $18.7 \text{ km}^2$ ) seasons that was 2–4 times larger than the average for intact males. Home-range area was not correlated with body mass for males ( $n = 12$ ,  $P \geq 0.550$  for the 3 estimators), and correlations between home-range area and mass for females were marginally nonsignificant for 50% KHR ( $n = 15$ ,  $r = -0.49$ ,  $P = 0.065$ ) and 95% KHR ( $r = -0.45$ ,  $P = 0.089$ ).

**TABLE 2.**—Home-range area estimates (km<sup>2</sup>; mean ± 1 SE) of sterilized and intact feral cats radiotracked during dry (nonbreeding) and wet (breeding) seasons on Catalina Island between November 2002 and July 2004.

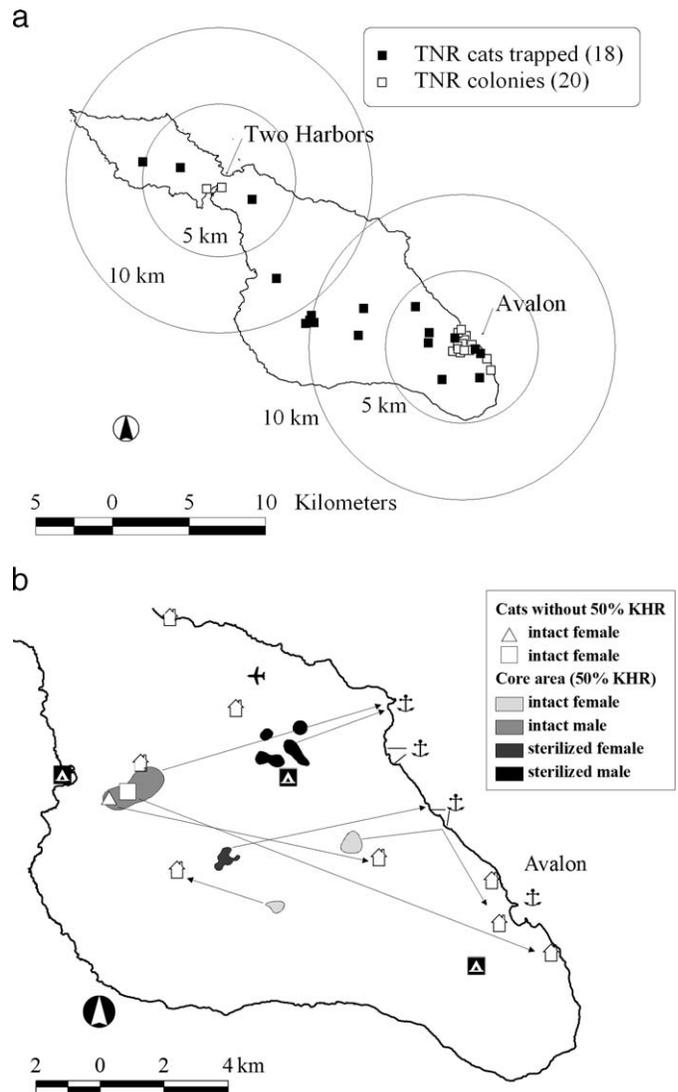
Treatment group	Dry (nonbreeding) season			Wet (breeding) season		
	<i>n</i>	95% MCP	95% KHR	<i>n</i>	95% MCP	95% KHR
Female intact	6	0.8 ± 0.2	1.5 ± 0.3	7	1.7 ± 0.6	1.9 ± 0.4
Female sterilized	6	0.9 ± 0.2	1.7 ± 0.4	6	1.3 ± 0.5	3.1 ± 1.4
Male intact	4	2.8 ± 1.0	8.2 ± 3.9	5	3.7 ± 1.2	7.4 ± 2.1
Male sterilized	4	2.1 ± 0.3	3.8 ± 0.3	6	2.2 ± 0.6	4.1 ± 1.1
All males	8	2.5 ± 0.5	6.0 ± 2.0	11	2.9 ± 0.6	5.6 ± 1.2
All females	12	0.9 ± 0.1	1.6 ± 0.3	13	1.5 ± 0.4	2.5 ± 0.7
All cats	20	1.5 ± 0.2	3.4 ± 0.9	24	2.1 ± 0.4	3.9 ± 0.7

We observed no difference in home-range overlap between seasons, sex, or treatment groups for 50% KHR (*n* = 58 pairs; overall  $F_{7,50} = 1.39$ ,  $P = 0.231$ ). For 95% KHR, sex was the only factor that was significantly associated with differences in overlap (*n* = 248 pairs; overall  $F_{9,238} = 2.00$ ,  $P = 0.040$ ; sex effect:  $F_{2,238} = 4.88$ ,  $P = 0.008$ ). Males overlapped significantly more with other males (mean ± 1 SE: 23.5% ± 2.7%) and with females (20.6% ± 2.0%) than females overlapped with each other (10.3% ± 1.5%; Tukey HSD test,  $P < 0.05$ ). Neither season ( $F_{1,238} = 0.06$ ,  $P = 0.811$ ), reproductive status ( $F_{2,238} = 1.47$ ,  $P = 0.232$ ), nor the interaction of sex and reproductive status ( $F_{4,238} = 1.09$ ,  $P = 0.363$ ; Fig. 2) significantly influenced the degree of home-range overlap.

Eighteen previously sterilized cats (13% of captures, identified by tipped right ears) were trapped in the island interior (Fig. 3a) ≥10 km from Two Harbors and Avalon. Most of these were females (12, versus 6 males). Long-distance movements from the island interior into peripheral, human-populated areas were recorded for 7 (26%) of the 27 radiocollared cats, including animals of both sexes (2 males, 5



**FIG. 2.**—Mean percent home-range overlap (± SE) of intact and sterilized feral cats, grouped by sex, estimated by fixed kernel (95% KHR). Sample sizes of overlapping groups are listed above error bars. MI = intact male; MS = sterilized male; FI = intact female; FS = sterilized female.



**FIG. 3.**—a) Trap locations of sterilized colony cats (TNR cats; *n* = 18) captured in the interior of Catalina Island in 2003–2004. Circles denote distances of 5 and 10 km from TNR colonies in Avalon and Two Harbors. b) Long-distance movements of 7 radiocollared cats from the wildland interior into human areas. Polygons are 50% KHR core area (50% KHR) of cats before movements in the direction of the arrows. The open triangle and square denote trap locations of 2 intact females for which core areas could not be calculated before movements. See Fig. 1 for description of other symbols of human use areas.

females) and both intact and sterilized cats (5 intact, 2 sterilized). The mean ( $\pm$  *SD*) distance moved by radiocollared cats was 8 ( $\pm$  4) km (Fig. 3b), although movements exceeding 14 km were recorded. On average, females (9  $\pm$  4 km) tended to move farther than males (6  $\pm$  3 km), although sample sizes were too small for meaningful statistical analysis.

## DISCUSSION

Home ranges of male feral cats were significantly larger than those of females, a finding that has been reported elsewhere (Liberg et al. 2000). However, contrary to our predictions, we found no significant differences in home-range areas of sterilized and reproductively intact cats of either sex. We caution that although we tracked many cats across multiple seasons, sample sizes, especially for males, were relatively low. We expected males to vary more in ranging behavior, suggesting that very large numbers of individuals might be needed to estimate range size with any precision. Our results, however, provide little evidence that sterilization markedly reduces ranging behavior for either sex, at least for cats sterilized as adults.

Previous studies (e.g., Fettman et al. 1997) have revealed that sterilization does not reduce feeding activity and may actually increase longevity (Levy and Crawford 2004). Together with these findings, our results suggest that sterilization likely would not reduce the impact of feral cats on native prey, which, on Catalina, includes a variety of small mammal, bird, amphibian, reptile, and invertebrate species (Guttilla 2007). In addition, the removal of diseased cats before sterilization—a common practice in some TNR programs (Hughes and Slater 2002)—may result in a healthier population than one where sterilization is not conducted. Although this may benefit free-roaming pet cats that interact with feral ones (and ultimately, wildlife), returning healthy cats, even if sterilized, to the environment has no clear ecological benefits.

Our results also revealed that, contrary to our predictions, sterilization had no effect on the degree of home-range overlap among individuals. Because uncollared cats were known to be present in our study area, our measurements of home-range overlap might have underestimated the actual overlap among feral cats. Extensive overlap among male cats has been reported for other islands (Harper 2004; Konecny 1987), although the lower frequency of male–male overlap observed for core areas relative to 95% use areas suggests that core areas may be defended. Sterilized and intact males behaved similarly, however, suggesting that territorial behavior was not affected by being neutered (see also Nutter 2005). Because home ranges of sterilized cats did not overlap more than those of intact cats, sterilization alone would not necessarily lead to an increase in cat densities.

On the surface our finding that sterilization did not significantly change the spatial distribution of feral cats appears to support the argument that sterilization prevents immigration of new animals (i.e., the vacuum effect) and

therefore may lead to population decline via attrition. This argument, however, assumes that no consistent source of new, unsterilized cats exists. We found evidence of considerable long-distance movement of both sterilized and intact cats between the wildland interior and developed areas; most of the cats moving long distances were females. The presence of TNR colony cats in the island interior was either the result of cats dispersing from unnaturally high densities near feeding areas or from the deliberate, illegal release of unwanted colony cats into the interior. The number of radiocollared cats observed moving from wildland to populated areas, however, suggests that long-distance movements may be common and that these populations are not distinct.

Our study also provides the 1st estimates of population size for feral cats on Catalina (600–750 cats). These data suggest that the numbers of cats dependent on humans may be 3–4 times larger than the feral population in the island interior. The low trappability of cats in our study population suggests that this estimate is likely conservative. The higher cat densities observed near some developed areas may be spillover from overcrowded conditions associated with TNR colonies and unsterilized pets, which may affect native prey populations in areas immediately adjacent to colonies. For example, low trap success near TNR colonies at Two Harbors, where some 175 stray and colony cats were present but not caught (Guttilla 2007), corroborates previous studies (e.g., Nutter et al. 2004) suggesting that cats become trap-wary, making them difficult to capture and complicating sterilization and control efforts.

From a management perspective our study revealed that hundreds of stray and feral cats live on Catalina. Collectively, our findings suggest that an island-wide TNR program would probably fail to alleviate threats of feral cats to wildlife and would run counter to efforts to protect vulnerable species and restore native ecosystems. TNR also does not address public health risks and nuisance issues in populated areas of Catalina, and sterilized cats are still susceptible to diseases and parasites that can be transmitted to wildlife, humans, and pets (Lee et al. 2002). For these reasons and out of consideration of the welfare of the cats themselves, many animal welfare organizations, including the American Society for the Prevention of Cruelty to Animals, People for the Ethical Treatment of Animals, American Veterinary Medical Association, and Humane Society of the United States currently oppose TNR programs in and adjacent to ecologically sensitive areas where wildlife may be at risk (Guttilla 2007).

We believe that efforts to minimize the effects of feral cats on the interior of Catalina depend upon effective management and control of high-density cat populations in Avalon, Two Harbors, and other coastal areas. Until resources are available to implement more proactive control measures in these areas, cats trapped in the island interior should be removed and delivered to a shelter; if they are deemed adoptable, cats should be sterilized and added to the adoption pool on the mainland. If they are not adoptable or if there are insufficient resources to support relocation, they should be euthanized. Because TNR colonies in human-populated areas of the island

are a likely source of feral cats to maintain an interior cat population, steps should be taken to reduce and eliminate these colonies and adopt and enforce stricter policies for responsible pet ownership and regulation of the importation of exotic animals to the island.

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