Analysis of the impact of trap-neuter-return programs on populations of feral cats

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Objective—To evaluate 2 county trap-neuter-return (TNR) programs for feral cat population management via mathematical modeling.

Design—Theoretical population model.

Animals—Feral cats assessed from 1992 to 2003 in San Diego County, California (n = 14,452), and from 1998 to 2004 in Alachua County, Florida (11,822).

Procedure—Data were analyzed with a mathematical Ricker model to describe population dynamics of the feral cats and modifications to the dynamics that occurred as a result of the TNR programs.

Results—In both counties, results of analyses did not indicate a consistent reduction in per capita growth, the population multiplier, or the proportion of female cats that were pregnant.

Conclusions and Clinical Relevance—Success of feral cat management programs that use TNR can be monitored with an easily collected set of data and statistical analyses facilitated by population modeling techniques. Results may be used to suggest possible future monitoring and modification of TNR programs, which could result in greater success controlling and reducing feral cat populations. (*J Am Vet Med Assoc* 2005;227:1775–1781)

Populations of feral cats are large, have high intrinsic rates of growth, and are highly adaptable to different and sometimes harsh habitats. Feral cats often are regarded as pests on the basis of their predatory habits and the negative effect they may have on wildlife populations.[1-4] They may function as hosts for diseases and vectors that can infect humans, domestic animals, or wildlife[5-7]; yet, colonies of feral cats often are maintained through feeding and care by people who have strong affection for these cats.[8]

There have been many attempts to eradicate populations of feral cats or to regulate their population sizes at low numbers. Such projects have included intentional release of panleukopenia virus, poisoning, predator introduction, euthanasia, and neutering.[9-13] Often, despite intense effort, attempted control programs fail because growth rates within the population do not decline or because of additional recruitment of cats into the population, although some programs have reported[14-16] successful reduction in feral populations with humane trapping programs. The general public often finds extermination programs for feral cats unacceptable, yet also often is intolerant of cat predation on wildlife. It has proven difficult to assess program success; theoretical models would be helpful to guide interpretation of data from control programs and to provide motivation for changes that could increase success.

Feral cats are territorial animals, and their highest potential for population increase occurs when populations are low. The maximum per capita rate of increase is the maximum mean number of female cats produced annually from each female cat, including the cat and its female kittens. A cat population size tends to increase until a carrying capacity is reached. This carrying capacity depends mainly on food and appropriate area for territories. After the carrying capacity has been reached, density dependence forces the per capita growth rate to drop to 0. Matrix methods are used to study the sensitivity of long-term population growth rates to perturbations in survivorship and fecundity and have been used to evaluate feral cat population dynamics.[17] By use of a logistic (Ricker) model to lower feral cat populations, 2 general approaches are possible: the carrying capacity can be decreased (eg, by discouraging public feeding of feral cats), or the maximum per capita rate of increase can be lowered (eg, by increasing mortality rate[18] or by neutering female cats). For feral cat populations to decline, the maximum per capita rate of increase needs to decrease to < 0. Temporarily lowering the population size below the carrying capacity yields no long-term population reduction if this is not accomplished. The cat population will simply increase back to carrying capacity.

The objective of the study reported here was to use data from 2 **trap-neuter-return (TNR)** programs to evaluate development and implementation of models that could determine program success and calculate the rate of neutering needed to decrease the feral cat population.

Materials and Methods

Modeling—Statistical analyses and modeling were performed with computer software.[a,b] For all statistical tests, a value of $P < 0.05$ was considered significant. Cat population regulation was modeled on the basis of a Ricker model:

$$R_t = e^{r_m(1-\frac{N_1}{K})}$$

where R_t is an annual population multiplier or net fundamental reproductive rate, r_m is the maximum per capita rate of increase, N_1 is the population size at time 1, and K is the carrying capacity. If $R_t = 1$, the net annual growth of

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the population r_t is 0 (ie, the population size is multiplied by 1.0).

To apply the model to TNR data, results from trapping were inserted into the model as index values (linear multipliers of the actual values) and interpreted with the assumption that trapped cats represented some fraction of all cats in the county; this fraction was divided into an index value (eg, the index carrying capacity) to yield an estimated county-wide value. The county-wide feral cat population size was approximated; there were 1,040,149 households in San Diego County in 2000, of which 8.9% of those interviewed reported that they fed a mean of 2.6 feral cats/household.[19] Thus, a minimum county-wide estimate of feral cat population size for 2000 was 240,690 feral cats. In Alachua County, 12% of interviewed households reported that they fed a mean of 3.6 feral cats each. There were 84,963 households in 1999 and approximately 36,398 feral cats.[20]

Estimates of feline population growth rate (R_t) were obtained from the trapped cat data. The R_t was calculated as follows:

$$R_t = N_{t+1}/N_t \text{ and } r_t = \ln R_t$$

where N_t and N_{t+1} are indices of the actual population size, equal to the total number of cats neutered at clinics for that year. It was not necessary to estimate either K or N_t directly because the growth rates describe population trajectories independent of absolute or index values of population size and carrying capacity. The regression of per capita growth rate on population size provided the estimate of maximum per capita rate of increase (y-intercept) and, for convenience, an index of carrying capacity (x-intercept).[21] The actual carrying capacity was obtained by multiplying the index carrying capacity by the estimated total feral cat population in that county and dividing by the total cats trapped.

Program success was evaluated with several methods. Evidence for density-dependent population regulation was sought by plotting per capita growth rate as a function of year to determine a significant reduction in per capita growth rate as detected by a significant negative linear regression of per capita growth rate on time. Similarly, evidence of reduced fecundity was sought by use of linear regression for the proportion of female cats pregnant when neutered over time. The Malthusian parameter r_m (maximum per capita rate of increase) calculated for each county was used to obtain a Malthusian multiplier, $R_m = e^{r_m}$.

Management of feral cat R_m means getting a new value, R_m'. Population decline occurs when R_m' is < 1.0; R_m can be written as the sum of survivorship (p) and offspring production ($R_m - p$). The critical fraction (s) of cats that would need to be neutered in a population to induce a decline can be obtained by solving the following equation:

$$1 = R_m' = p + (R_m - p)(1 - s)$$

to get

$$s = \frac{R_m - 1}{R_m - p}$$

One can also approximate the proportion of cats that must be neutered each year (M) to gradually reach $M = s \bullet N$ neutered cats. Neutered cats accumulate in the population because they survive at rate p from year to year. If the number of cats neutered annually is m and the program continues many years, when neutered individuals are counted right after neutering but before death,

$$M = m\sum_{i=0}^{\infty} p^i = m\frac{1}{1-p}$$

To achieve the neutering level s = M/N, the annual neutering rate s_a must satisfy the following equation:

$$s_a = \frac{m}{N} = s(1 - p)$$

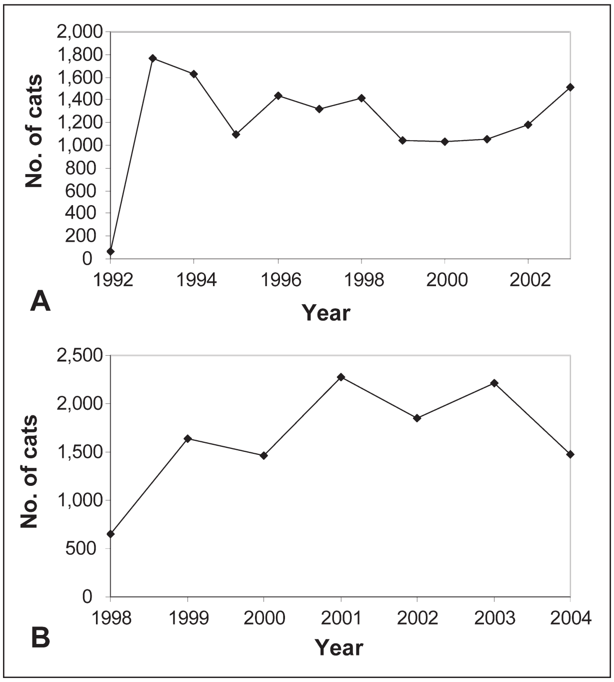

Figure 1—Yearly distribution of all feral cats evaluated for neutering in San Diego County (A) and Alachua County (B).

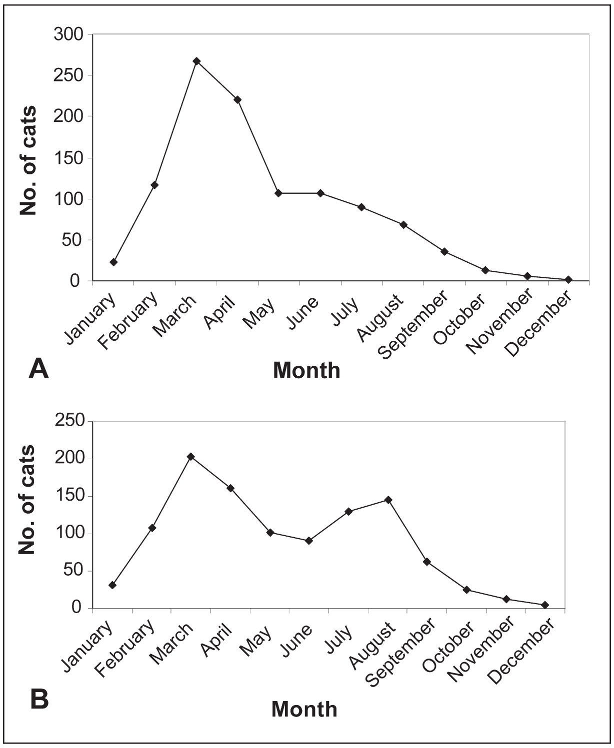

Figure 2—Monthly distribution of pregnant feral female cats evaluated for ovariohysterectomy in San Diego County (1992 to 2003, all years summed [A]) and Alachua County (1998 to 2004, all years summed [B]).

When survivorship (p) is close to 1.0, this is a much lower burden for the neutering program. The calculation is only approximate because N is not constant over the lifetime of the neutering program, survivorship may differ between neutered and non-neutered cats, and cats do not live indefinitely. In the absence of field data, the annual survival rate ($\hat{p}$) can be estimated from the mean cat life span as follows:

$$\hat{p} = 1 - \frac{1}{\text{mean life span}}$$

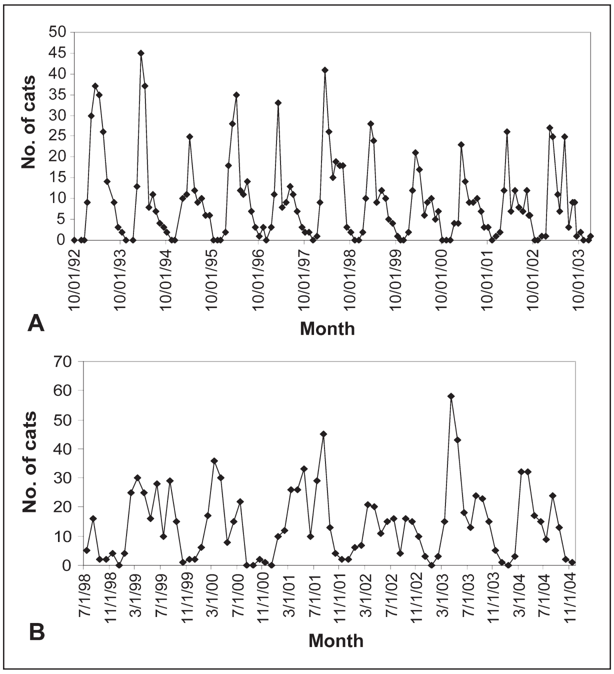

Figure 3—Monthly distribution of pregnant feral female cats evaluated for ovariohysterectomy in San Diego County (1992 to 2003 [A]) and Alachua County (1998 to 2004 [B]).

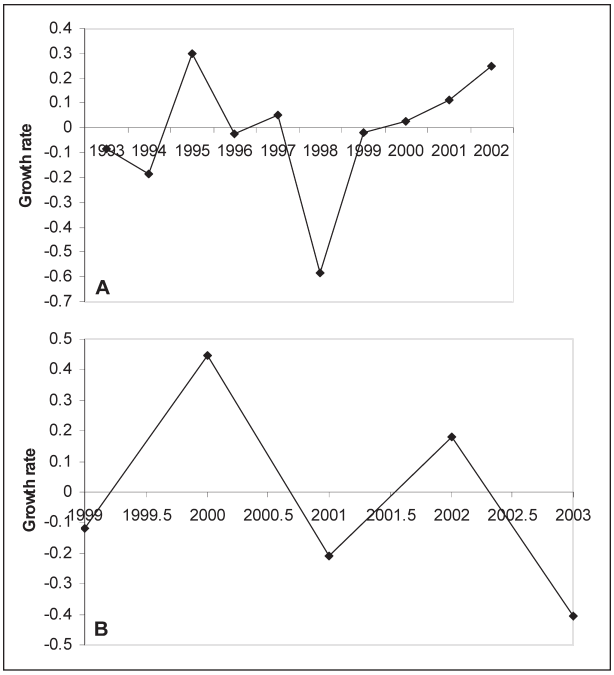

Figure 4—Annual per capita feral cat population growth rate by year for feral cats evaluated for neutering in San Diego County (1992 to 2003 [A]) and Alachua County (1998 to 2004 [B]).

and if such data were available, the life span and annual survival rate should be estimated at low population sizes.

Data—Data from the Feral Cat Coalition were acquired during a trapping program involving volunteers from across San Diego County, California, from 1992 to 2003 and from a similar program from 1998 to 2004 run by Operation Catnip Inc in Alachua County, Florida. Cats were live-trapped, transferred approximately once per month to participating veterinary clinics, examined, vaccinated, surgically neutered, and returned to their colonies after a short postoperative recovery period. For each day that clinics were held, data compiled included clinic number and date, location of the clinic, number of males neutered, number of females neutered, number of cats already neutered when trapped, and total females subdivided into the categories pregnant and not pregnant. Data regarding San Diego County demographics were obtained from the California Department of Finance[22] and included number of humans in the county and number of households. For Alachua County, demographic data were obtained from the US Census Bureau. Data regarding cat ownership, feeding of feral cats, approximate county-wide cat numbers, and number of feral cats were obtained or calculated from published surveys of San Diego and Alachua County households.[19,20]

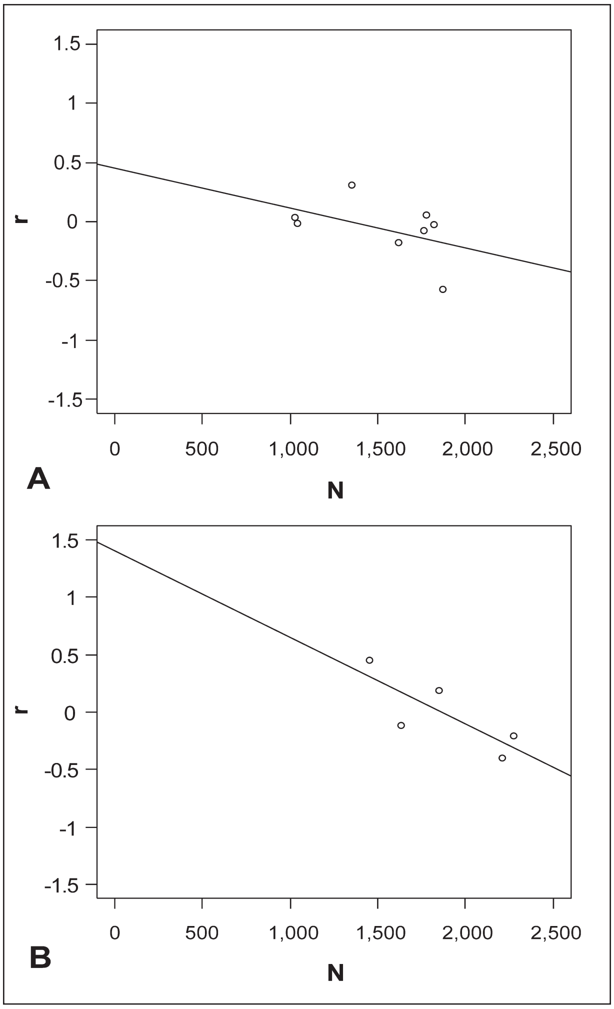

Figure 5—Regression of annual per capita growth (r) on annual index population size (N) for feral cats evaluated for neutering in San Diego County (1992 to 2003 [A]) and Alachua County (1998 to 2004 [B]).

Results

Feral cat demographics—From 1992 to 2003, 14,452 cats were submitted as feral cats to veterinary clinics in San Diego County for neutering (**Figure 1**; data for 1992 represent only part of the year, when the program began). Of these cats, 565 (4%) had already been neutered; 14,129 surgeries were performed on 6,494 (46%) male and 7,635 (54%) female cats. The number of cats neutered over the months of the year did not vary significantly ($P = 0.13$), but the presence of pregnant cats was strongly seasonal, with numbers increasing in spring, compared with winter and fall **(Figures 2 and 3)**. Overall, 17.2% of trapped female cats were pregnant.

In Alachua County, 11,822 cats were submitted for neutering from 1998 to 2004 (Figure 1). Of these, 258 (2%) cats had previously been neutered; 11,564 surgeries were performed on 4,928 (43%) male and 6,636 (57%) female cats. Evaluation of pregnant cats revealed a double peak, with increases in March and August (Figures 2 and 3). Sixteen percent of trapped female cats were pregnant.

Model results—Per capita growth rate in San Diego County ranged from –0.58 to 0.30, with a value of 0.25 for 2002 **(Figure 4)**. Values for Alachua County were similar. Regressing per capita growth rate on population size yielded estimates of the index carrying capacity (x-intercept) and maximum per capita rate of increase (y-intercept) of 1,323 and 0.45 ($P = 0.09$), respectively, for San Diego County and 1,855 and 1.41, respectively, for Alachua County ($P = 0.1$; **Figure 5**). In the last year of data for each county, the total numbers of trapped cats were 1,514 (0.63% of the total estimated feral cats) in San Diego County and 2,213 (9.6%) for Alachua County. Thus, the county-wide carrying capacities were estimated as 210,325 and 19,323 feral cats,

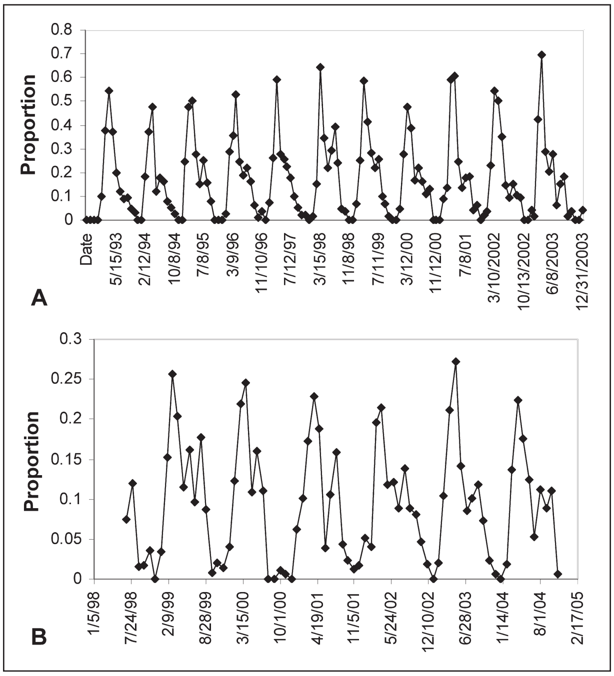

Figure 6—Monthly distribution of pregnant feral female cats evaluated for neutering in San Diego County (1992 to 2003 [A]) and Alachua County (1998 to 2004 [B]).

Table 1—Critical overall neutering rate required to bring growth rate in a feral cat colony to 1.0 for various growth rate, life span, and survivorship (p) estimates.

	Mean life span (y)											
Growth rate and p	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
p	0.00	0.50	0.67	0.75	0.80	0.83	0.86	0.88	0.89	0.90	0.91	0.92
1.0	0	0	0	0	0	0	0	0	0	0	0	0
1.5	0.33	0.50	0.60	0.67	0.71	0.75	0.78	0.80	0.82	0.83	0.85	0.86
2.0	0.50	0.67	0.75	0.80	0.83	0.86	0.88	0.89	0.90	0.91	0.92	0.92
2.5	0.60	0.75	0.82	0.86	0.88	0.90	0.91	0.92	0.93	0.94	0.94	0.95
3.0	0.67	0.80	0.86	0.89	0.91	0.92	0.93	0.94	0.95	0.95	0.96	0.96
3.5	0.71	0.83	0.88	0.91	0.93	0.94	0.95	0.95	0.96	0.96	0.96	0.97
4.0	0.75	0.86	0.90	0.92	0.94	0.95	0.95	0.96	0.96	0.97	0.97	0.97
4.5	0.78	0.88	0.91	0.93	0.95	0.95	0.96	0.97	0.97	0.97	0.97	0.98
5.0	0.80	0.89	0.92	0.94	0.95	0.96	0.97	0.97	0.97	0.98	0.98	0.98

Table 2—Critical annual neutering rate required to bring growth rate in a feral cat colony to 1.0 for various growth rate, life span, and p estimates.

	Mean life span (y)											
Growth rate and p	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
p	0.00	0.50	0.67	0.75	0.80	0.83	0.86	0.88	0.89	0.90	0.91	0.92
1.0	0	0	0	0	0	0	0	0	0	0	0	0
1.5	0.33	0.25	0.20	0.17	0.14	0.13	0.11	0.10	0.09	0.08	0.08	0.07
2.0	0.50	0.33	0.25	0.20	0.17	0.14	0.13	0.11	0.10	0.09	0.08	0.08
2.5	0.60	0.38	0.27	0.21	0.18	0.15	0.13	0.12	0.10	0.09	0.09	0.08
3.0	0.67	0.40	0.29	0.22	0.18	0.15	0.13	0.12	0.11	0.10	0.09	0.08
3.5	0.71	0.42	0.29	0.23	0.19	0.16	0.14	0.12	0.11	0.10	0.09	0.08
4.0	0.75	0.43	0.30	0.23	0.19	0.16	0.14	0.12	0.11	0.10	0.09	0.08
4.5	0.78	0.44	0.30	0.23	0.19	0.16	0.14	0.12	0.11	0.10	0.09	0.08
5.0	0.80	0.44	0.31	0.24	0.19	0.16	0.14	0.12	0.11	0.10	0.09	0.08

respectively. The calculated values for R_m for each county were 1.57 for San Diego County and 4.1 for Alachua County.

Critical neutering rates depend on R_m and survivorship (**Tables 1 and 2**). Reported[9,23] mean life spans in feral cats range from 2 to 8 years. By use of a median life span of 5 years for San Diego County, the critical neutering fraction (s) would be approximately 71% (94% for Alachua County). The needed annual neutering fraction (s_a) was 14% for San Diego County and 19% for Alachua County. Hypothetical feral cat populations would decrease between these values.

To assess the success of the TNR program, data were evaluated for density-dependent population regulation and a significant reduction in the proportion of female cats that were fertile. When per capita growth rate was regressed on year, there were no indications of a significant reduction in per capita growth rate (ie, evidence for density dependence) in either of the counties ($P = 0.24$ and 0.1 for San Diego and Alachua counties, respectively; Figure 4). The proportion of pregnant females cycled annually, but an overall reduction in either of the counties was not detected (**Figure 6**).

Discussion

Feral and stray cats represent more than 40% of all cats in the United States, are fed by an estimated 10% to 20% or more of households, and are rarely neutered.[20,24,25] It is desirable to reduce feral cat populations because of welfare concerns for the cats, concern about the effects of feral cats on vulnerable wildlife, and public health considerations. The American Association of Feline Practitioners supports appropriately managed feral cat colonies, but that group's position statement indicates that the goal of colony management should be the eventual reduction of the colony.[24] Additionally, feral cat colonies should not be located near at-risk wildlife. Although several control methods including TNR have been proposed and implemented, assessment of their efficacy has typically been missing or at most anecdotal. This is unfortunate given the substantial investment of resources required to run an effective program and the skepticism with which TNR is regarded by many people.

Feral cat populations are extraordinarily capable of reaching local carrying capacities as a function of reproductive mechanisms that emphasize breeding efficiency. These include induced ovulation, weaning of kittens as young as 50 days old, an age of first reproduction as early as 8 months, and many (approx 130) days pregnant per year.[9,26] Consequently, cats have some of the highest maximum per capita rates of increase among carnivores, estimated in 1 study[27] at 23.3%. Population sizes, home range size, and local carrying capacity of feral cats all vary extensively, depending on habitat type and availability of food and safe den sites. Intrinsic control of feral cat populations may occur by density-dependent mechanisms including starvation, predation, control of reproductive success, and disease. Although cats, particularly males, are territorial,[28,29] feral cat colonies receiving abundant food supplementation may have a reduction in apparent territoriality as cats co-occupy territories or attempt to maintain small territories (sometimes accompanied by stress and fighting).[30]

The purpose of TNR programs is rarely articulated in the language of population ecology but often is motivated by an attempt to reduce population size (N_t) and per capita growth rate (r_t) by reducing reproduction. Additional goals of TNR may include provision of veterinary care and vaccines to reduce the threat of feline and zoonotic diseases, improve the quality of life of homeless cats, avoid euthanasia as a control method, and, in some programs, reduce the population size.[14,31] In many TNR programs, including those described here, direct assessment of possible changes in population size is not possible because data collection and population structure do meet assumptions of capture-recapture or other similar methods of estimating population size. Although index values were necessarily used for parameters because actual population counts were not available or practical, the trajectories of populations (whether or not populations were declining) could be determined from calculation of maximum per capita rate of increase without accurately detecting population size or carrying capacity.

The models reported here also have the flexibility of providing statistics that could be used to evaluate success of control programs, methods for calculating the fraction of cats that must be neutered to force population decline, and the annual neutering rate required to eventually achieve the required neutered fraction. The assessment statistics are R_m (multiplier for the maximum per capita rate of increase), which can be calculated from the time series and, as a multiplier, must be < 1.0 for the population to be in decline; the proportion of cats that are pregnant, which should be declining significantly in a successful program; and the proportion of trapped cats that already are neutered, which should increase. This last statistic was not evaluated in the data given here because the TNR programs specifically avoided retrapping cats, which was unfortunate because keeping account of previously ear-tipped cats would have made the calculation of the proportion neutered more accurate.

The present study yielded mixed results regarding the success of large TNR programs in San Diego and Alachua counties. Results of the programs had previously been summarized[16] regarding the number of cats neutered, but the effect of neutering on the free-roaming cat population had not been analyzed. Our analysis indicated that any population-level effects were minimal, with R_m (the multiplier) ranging from 1.5 to 4, which indicated ongoing population growth (similar to values in previous studies), and critical needed values of neutered cats (ie, the proportion of all cats that needed to be neutered to reduce R_m to < 1.0) of 71% to 94%, which was far greater than what was actually achieved. There are several potential limitations to the data; the net reproductive rate was estimated under the assumption that trapping effort and efficiency were unbiased across sites and trapping periods. Retrapping success for feral cats probably was underestimated because cats were marked after neutering by removal of a small distal portion of the pinna and ear-tipped cats usually were released from cages without counting. The estimate of total numbers of feral cats was somewhat inaccurate because it was calculated from general surveys of how many people feed how many feral cats. However, this statistic was not used in the model itself but rather provided an estimate of the calculated proportion of all available feral cats that were being neutered, to allow for interpretation of model successes. The regression of per capita growth rate on population size was not significant for either San Diego or Alachua counties, possibly reducing confidence in the estimate of population growth rates. However, this was not surprising given that a time series of at least 20 years is typically required before such a regression is found to be significant.[32] Nevertheless, the coefficient of regression (y-intercept) still represented the maximum likelihood estimator for maximum per capita rate of increase.

In some ways, results were similar to those obtained in an earlier, stage-structured matrix model of feral cat demographic features.[17] The matrix model forced $\lambda < 1$, analogously with the Ricker model forcing $R_m < 1$, for the population to decline. Implementation of the stage-structured model suggested that no plausible combinations of life history variables would likely allow for TNR to succeed in reducing population size, although neutering approximately 75% of the cats could achieve control (which is unrealistic), a value quite similar to results in the present study. An important distinction between the 2 models was the incorporation of density-dependent reduction of fecundity and possible saturation of the population with neutered cats in the present model.

Feral cat control programs are notoriously difficult, and in many cases, short-term control has been followed by a long-term return to precontrol conditions. Attempted control of a feral cat population on Marion Island in the Indian Ocean had poor success for many years.[9] The population size on the island was estimated by use of a line transect at approximately 2,200 cats, and in 1979, virulent panleukopenia virus was released on the island. Although in 1 study[9] it was concluded that the population density of cats had declined, this conclusion was based on questionable statistical analyses. Within 5 years, intrinsic population growth rates were reported to have increased 4 times, and although population sizes had supposedly declined, predation on seabirds continued. Hunting was instituted, and ongoing population estimates were assessed by use of the highly biased index of cat sightings.[10] The authors acknowledged that control (ie, suppression) would only succeed with ongoing intensive hunting. Feral cats have been eliminated from at least 48 islands, including Marion Island, primarily through hunting (sometimes with dogs), trapping, poisoning, and disease and typically on fairly small islands with low cat density.[33]

In contrast with hunting, disease, or other methods of feral cat control that increase mortality rates, TNR has the potential advantage of allowing niches to become saturated with neutered individual cats. If, concurrently with the reduction in maximum per capita rate of increase, carrying capacity is reduced (typically by reduction of food oversupplementation) and immigration is controlled, there may be a humane, gradual reduction in overall cat numbers. Future feral cat management programs could potentially achieve better success with a few modifications of the TNR paradigm. Despite the substantial expenditure of resources to operate the 2 TNR programs described here, they probably were performed on too large a scale; many cats were neutered, but this constituted a very small overall proportion of the cats. Moreover, feral cats within a county surely do not constitute a single population, further diluting the enormous overall effort into numerous smaller efforts with less impact. Trap-neuter-return programs should be focused on well-defined, preferably geographically restricted, cat populations, rather than diluting effort across multiple populations. In future TNR studies, it would be helpful if trapping efforts were standardized to allow for the least biased index estimates of population size from trapping efficiency (catch per unit effort[34]), although with such an intelligent species, cats may modify behavior after experience with the traps. If population growth actually is declining, then per capita growth rate should decline consistently. Also, retrapping statistics, which were not obtained in these programs, are particularly valuable because they allow for comparison of observed retrapped (neutered) proportions with the critical proportions needed to reduce R_m to < 1.0.

Focused TNR programs have had some success. A survey-based assessment[8] of TNR for small colonies (mean, 7 cats) revealed moderate success, with reduction of mean colony size by as much as half. A two-thirds reduction in population size was obtained in a feral cat colony on a university campus where every cat was specifically included in the census.[16] Although causes of loss from the population included euthanasia of sick cats, adoption, and deaths (often vehicular trauma), increases in population were attributable to immigration but not births because virtually all resident cats were neutered. For these programs, managers were able to evaluate success because every cat could be counted. In larger programs, such enumeration is impossible and index-level assessment, such as that described here, becomes necessary.

Statistical assessment of the impact of TNR programs on population size is critical to help gain credibility for such programs. Because of the increasing will to address humane, conservation, and public health concerns associated with free-roaming cats, tools to evaluate program success will increasingly contribute to achieving management goals.

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