

Estimation of effectiveness of three methods of feral cat population control by use of a simulation model

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Objective—To predict effectiveness of 3 interventional methods of population control for feral cat colonies.

Design—Population model.

Sample—Estimates of vital data for feral cats.

Procedures—Data were gathered from the literature regarding the demography and mating behavior of feral cats. An individual-based stochastic simulation model was developed to evaluate the effectiveness of trap-neuter-release (TNR), lethal control, and trap-vasectomy-hysterectomy-release (TVHR) in decreasing the size of feral cat populations.

Results—TVHR outperformed both TNR and lethal control at all annual capture probabilities between 10% and 90%. Unless > 57% of cats were captured and neutered annually by TNR or removed by lethal control, there was minimal effect on population size. In contrast, with an annual capture rate of $\geq 35\%$, TVHR caused population size to decrease. An annual capture rate of 57% eliminated the modeled population in 4,000 days by use of TVHR, whereas > 82% was required for both TNR and lethal control. When the effect of fraction of adult cats neutered on kitten and young juvenile survival rate was included in the analysis, TNR performed progressively worse and could be counterproductive, such that population size increased, compared with no intervention at all.

Conclusions and Clinical Relevance—TVHR should be preferred over TNR for management of feral cats if decrease in population size is the goal. This model allowed for many factors related to the trapping program and cats to be varied and should be useful for determining the financial and person-effort commitments required to have a desired effect on a given feral cat population. (*J Am Vet Med Assoc* 2013;243:502–511)

Feral cats are present worldwide, and in the United States the number of feral cats likely rivals or exceeds the number of owned cats.^{1,2} Unfortunately, many of these cats will die prematurely from disease, starvation, or trauma.³ Feral cats, as opposed to other free-roaming cats, are generally unadoptable as pets. As an artificially introduced opportunistic predator, feral cats are a major factor in the death of birds, small mammals, reptiles, amphibians, and fish and have been directly responsible for extinction of some species.^{4–8} Feral cats are a potential public nuisance, may spread disease to other species, and are of concern to human health.^{1,4} The AVMA “strongly encourages and supports actions to eliminate the problem of free-roaming abandoned and feral cats.”³

Management of feral cat populations is a matter of great controversy, with many parties invested in the debate. The goals of intervention may be different depending on the location and nature of the population as well as financial resources and perspective of the funding agency. Nuisance issues such as urine mark-

ABBREVIATIONS

LC	Lethal control
TNR	Trap-neuter-release
TVHR	Trap-vasectomy-hysterectomy-release

ing, fighting, and fecal deposition are irrelevant on an isolated island but may be the main reason for intervention in an urban area. Even a small population of feral cats can be a major problem if located in an ecologically sensitive location. Although many methods have been used to control feral cat populations, the goal in North America has generally been humane extirpation, maximizing the quality of life for the cats but eliminating the existing colony over time.^{1,2,4,9}

Management of feral cat populations by TNR has gained popularity in recent years. Depending on the program involved, a variety of other services may also be provided, including assessment for infectious diseases, treatment of illnesses and injuries, vaccination, and removal of socialized cats for adoption.^{10,11} The rationale for TNR programs is eventual population decrease through attrition and territorial defense by neutered resident cats to prevent immigration of sexually intact cats that would breed and repopulate the site.^{10,12} The Humane Society of the United States recommends TNR for feral cat control, and 76% of US respondents strongly or mostly support these programs.^{9,13} Complaints

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about feral cats generally decrease after implementation of TNR.¹²

Despite the current popularity of TNR programs and, in some instances, the application of substantial resources over prolonged periods of time, there are few data to support their effectiveness in eliminating feral cat populations, other than small colonies in controlled environments with active caregivers.^{6,12,14} It is difficult or impossible to capture all resident cats, and because feral cat populations have high intrinsic growth rates, sexually intact cats that have not been captured quickly repopulate an area. Trap-neuter-release programs may increase both adult and kitten survival rates, which counteracts attempts at population control.^{15,16,a} Immigration of new cats, usually by abandonment, is common and results in failure of population decline.^{17,18} Cost of TNR programs is high, with estimates in the United States of between \$15 and \$40/cat neutered.^b The AVMA's position on TNR is that the effect of these programs as presently used is insufficient to eliminate the overall problem, and research into the issue is encouraged.³ Wildlife advocates generally oppose TNR programs as ineffective.^{6,19}

Lethal control methods such as hunting, trapping, poisoning, and introduction of disease can cause rapid temporary depopulation but have rarely proven effective in the long term. Lethal control has been used to eradicate cats on several islands worldwide, but most of these islands were small (< 5 km²), unpopulated by humans, and involved small cat numbers.^{2,4,5} Lethal control is unacceptable to a large proportion of people.^{2,4,5}

Management of feral cat colonies by TVHR has not been suggested previously and may be more effective at decreasing population size because cats retain reproductive hormones and normal social behavior is maintained.^{20,21,c} Vasectomy does not alter a male cat's sexual drive or social status, so cats maintain their position in the breeding hierarchy, may better prevent immigration of intruding males into the colony, compete for females as before surgery, and continue to copulate but in an unproductive fashion.^{15,20,22–24} Coitus initiates a prolonged, nonreceptive 45-day pseudopregnancy period in females, thereby reducing the chance of a fertile mating.^{25–27} After TVHR, female cats continue to attract males and compete with sexually intact females for male courting and breeding time. Unlike TNR, TVHR does not increase kitten and adult survival rates, which counteracts attempts at population control.

The possibility of greater potential effectiveness of TVHR, compared with TNR and LC, is supported by the following mathematical argument. For a given population size, TVHR would not affect the number of matings, but the fraction of matings that can produce offspring is $(1 - m)(1 - m) = 1 - 2m + m^2$, where m is the fraction of feral cats captured previously. For TNR, as long as an adequate number of sexually intact males exist, the number of matings (all of which can produce offspring) depends on the fraction of sexually intact females and is thus proportional to $(1 - m)$. The same argument holds for LC if removed females are considered as being nonreproductive individuals. Between $m = 0$ and $m = 1$, the curve $1 - 2m + m^2$ is always below $1 - m$. In particular, when m is small, the effect of TNR

and LC on reducing productive matings is proportional to m , and the impact of TVHR is proportional to $2m$. Furthermore, the difference between $(1 - m)$ and $(1 - m)^2$ is greatest at $m = 0.5$. Consequently, we predict that TVHR would be superior to TNR and LC and that the differences would be greatest in the midrange of capture rates.

Although direct long-term observations of populations yield the most accurate information on the effect of different interventional methods, obtaining such observations requires years of data collection. Alternatively, computer-based population modeling may be used to rapidly compare predicted outcomes of various management strategies.^{28,29} On the basis of model predictions, the most promising alternatives can be tested subsequently in the field. The goal of the study reported here was to use computer-based population modeling to compare the predicted efficacy of neutering by vasectomy (rather than castration) and hysterectomy (rather than ovariectomy) for controlling feral cat populations. The hypothesis was that different interventional methods will have different outcomes on populations of feral cats; specifically, TVHR will result in a more rapid decrease in population size than traditional methods, particularly at intermediate capture rates.

Materials and Methods

With commercially available software,^d an individual-based, stochastic simulation model^e was developed to evaluate different interventions on feral cat populations. As an individual-based model, each cat was tracked on a day-by-day basis, updating its status as required. As new cats were born, they were added to the population; dead cats were removed.

Each run simulated the cat population over a fixed number of days; 6,000 days was the number used, which is substantially greater than the mean lifetime of a feral cat.^{24,a} To allow the cat population to reach a steady state both in terms of population size and age distribution, the trapping program was not initiated until well into the simulation, on day 2,000. Simulations were applicable to temperate-zone cats; that is, there was seasonal breeding of 9 months' duration. Although any size population could be studied, this study evaluated a population of cats with approximately 200 individuals in the absence of any control strategy because this is the population size likely to be targeted for control. The model allowed for many factors related to both the trapping program and the cats to be varied. A pseudocode (**Appendix**) describes the basic steps and structure of the computer simulation.

Input parameters—Three methods of population control were considered: LC, castration of males and ovariectomy of females followed by release back into the population (TNR), and vasectomy of males and hysterectomy of females followed by release back into the population (TVHR). The program allowed specification of how many trapping episodes occurred each year (T), the number of consecutive days trapping was performed in each trapping episode (D), and the probability that a cat would be captured on a given day (π).

All cats were considered equally trappable. The annual probability of trapping an individual cat (P) was calculated as follows:

$$P = 1 - (1 - \pi)^{DT}$$

A population of cats is not the homogeneous body that many simple population models assume. Instead, it consists of individuals in various phases of life. The number of phases or categories is increased when population control policies such as those depicted in this study are applied. In the present study, males were allocated into 11 classes on the basis of age and reproductive status; associated with each stage was a daily survival rate derived from data from the literature (Table 1).^{15,30-34,a} In only 2 of these classes is the individual sexually active, namely sexually intact adult males and adult males after a vasectomy. Age of sexual maturity in male cats was specified as 319 days.^{26,35-38}

The situation for females is more complex, largely because of female cats' reproductive cycle. For females, 17 classes were created, also with state-specific daily survival rates derived from published literature (Table 2).^{15,30-34,a} In

15 of these classes, females were sexually inactive, and in the remaining 2 (sexually intact receptive adult and receptive adult after hysterectomy), females were sexually active. The length of time an individual stays in a given class is specified by development time and reproductive cycle. To predict female sexual maturity, a piecewise linear mathematical model with an expected mean age of sexual maturity of 10.5 months (319 days) was used. On the basis of this model, there was a 50% chance of a cat being sexually mature at 212 days of age, 75% chance at 319 days, and 100% chance at 426 days of age. Because female cat reproduction is characterized by induced ovulation, the presence of female cats in the 2 sexually active classes required the model to include a record of recent copulations to determine whether the cats were ovulating or had entered pseudopregnancy. On the basis of the model, there was a 21% chance of ovulation after a single copulation, 51% chance after 2 copulations, and 81% chance after ≥ 3 copulations. Minimum and maximum litter sizes, copulations required for ovulation, maximum number of copulations per day, time to estrous cycling after parturition, and pregnancy probabilities per mating were specified on the basis of available information from the literature. When multiple values were available, the median value was used, but preference was given to values obtained from field studies on feral cats (Table 3).^{10,25-27,30,35-37,39-60}

With each model run, an initial population of 40 male and 40 female cats was randomly distributed among the various age classes. Female cat society is divided into social units that affect the way males and females interact. For this analysis, a female social unit was defined as a female cat with each of its female offspring. Each female cat was considered to be a lifelong member of the social unit into which it was born. The initial population was divided into 20 social units. For males, daily access to female social units was determined by level of dominance, with only 1 male accessing a social unit per day. In the model, male dominance level was a function of age, being 0 until the age of 319 days, then increasing linearly to 1.0 (greatest dominance) at the age of 1,080 days, and remaining at 1.0 thereafter. Sexually active males were limited to a specified maximum number of copulations per day (8). The specified mating system was polygamous.

Table 1—Estimated daily survival probabilities associated with age category, reproductive status, and sexual activity of feral male cats undergoing population control.

Age category (age)	Reproductive status	Sexual activity	Daily survival probability
Adult (> 319 d)	Sexually intact	Yes	0.997406*
	Castrated	No	0.999051†
	Vasectomized	Yes	0.997406
Older juvenile (184–319 d)	Sexually intact	No	0.997406
	Castrated	No	0.999051
	Vasectomized	No	0.997406
Young juvenile (43–183 d)	Sexually intact	No	0.991244‡
	Castrated	No	0.991244
	Vasectomized	No	0.991244
Kitten (0–42 d)	Sexually intact	No	0.991244

*Value based on median survival time of 267 days in sexually intact males. †Value based on median survival time > 730 days in neutered males. ‡Value based on 20% survival rate to 6 months of age.^{15,30-34}

Table 2—Estimated daily survival probabilities associated with age category, reproductive status, and sexual activity of feral female cats undergoing population control.

Age category (age)	Reproductive status	Sexual activity	Daily survival probability
Adult (> 319 d)	Sexually intact, receptive	Yes	0.998832*
	Sexually intact, not receptive	No	0.998832
	Sexually intact, pseudopregnant	No	0.998832
	Sexually intact, pregnant	No	0.998832
	Sexually intact, nursing	No	0.998832
	Hysterectomized, receptive	Yes	0.998832
	Hysterectomized, not receptive	No	0.998832
	Hysterectomized, pseudopregnant	No	0.998832
	Spayed	No	0.999051†
	Older juvenile (184–319 d)	Sexually intact, not receptive	No
Hysterectomized, not receptive		No	0.998832
Spayed		No	0.998832
Young juvenile (43–183 d)	Sexually intact, not receptive	No	0.991244‡
	Hysterectomized, not receptive	No	0.991244
	Spayed	No	0.991244
Kitten (0–42 d)	Sexually intact, not receptive	No	0.991244

*Value based on median survival time of 593 days in sexually intact females. †Value based on median survival time > 730 days in spayed females. ‡Value based on 20% survival rate to 6 months of age.^{15,30-34}

Table 3—Reproductive input parameters used in a simulation model for feral cat populations.

Parameter	Input
Reproductive cycle	Seasonal polyestrous ^{25–27,39,40}
Mating system	Polygynous ^{41–44}
Pregnancy duration	65 d ^{26,27,39,40,45,46}
Weaning age	45 d ^{26,47}
Estrus duration	5 d ^{26,27,39,45,48}
Diestrus duration	8 d ^{26,27,39,49,50}
Seasonal anestrus duration	90 d ^{26,27}
Pseudopregnancy	45 d ^{26,27,49,50}
Litter size	Minimum, 3.0; mean, 3.6; maximum, 4.0 ^{30,40,51–54}
Male copulations/d	8 ^{42,48,55,56}
Copulations required for ovulation	3 ^{26,37–39,57,58}
Pregnancy probability/mating probability	0.2 ^{42,45,54–56}
Age of sexual maturity	10.5 mo ^{26,27,30,35–37,39,45,46}
Social unit size	7 ^{10,48,59,60}
Time to cycling after parturition	45 d ^{27,51}

It was assumed that daily survival rates were density dependent. The daily survival rate, $s(p)$, for all cats other than kittens and young juveniles, is given by the following relationship:

$$s(p) = s_0 - (s_0 - s_k)p/K$$

where $p = p(t)$, which is the population size on day t , K is carrying capacity of the population, s_0 is the daily survival rate at low population size, and s_k is the daily survival rate at carrying capacity. Carrying capacity was defined as the population size before any intervention; $s(p)$ was chosen as a linear function of p because no data to support a more complex relationship were available. The s_k values were obtained from the literature and were different for the different classes of cats (Tables 1 and 2). In contrast, because of the absence of published data from field studies, s_0 was set at 0.9991, a value somewhat larger than any of the s_k values for all classes of cats, thus ensuring that $s(p)$ was a decreasing function of p .

The survival rate of cats during their first 6 months may increase with the fraction of the adult population that is neutered.¹⁵ Specifically, approximately 76% of kittens survived to 6 months in colonies with a neutering prevalence of approximately 75%, whereas in colonies without neutering, only 32% of kittens survived to 6 months. This release of density-dependent feedback (defined as the density of sexually intact cats) on survival rate has the potential to strongly affect cat population dynamics (Figure 1). To evaluate this effect when comparing TNR, in which an increase in kitten survival rate occurs, and TVHR, in which it does not, a linear function of the fraction of cats neutered, f , was used to modify the kitten and young juvenile survival rates (s^*), as follows:

$$s^*(p,f) = s_0 - (1 - bf)(s_0 - s_k)p/K$$

for $bf \leq 1$ and $s^* = s_0$ for $bf > 1$, where b is the parameter governing the strength of the neutering effect on survival; when b is large, kitten and young juvenile survival rate is higher. When either $b = 0$ or $f = 0$, this reduces to the previous model.

By use of this formula, b can be estimated as follows:

$$b = [s^*(p,f) - s^*(p,0)]/f[s_0 - s^*(p,0)]$$

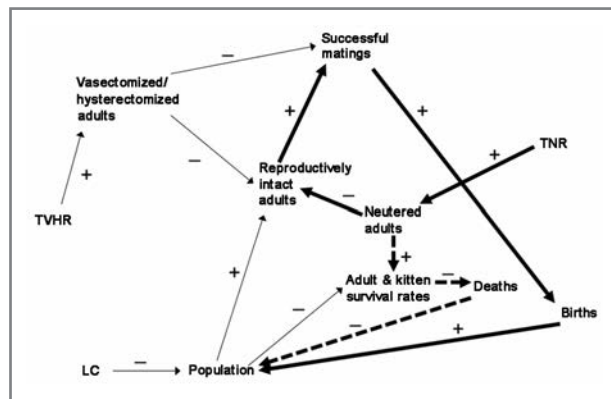


Figure 1—Signed (+, -) digraph model of a feral cat system indicating alternative population control strategies (TVHR versus TNR versus LC). Intended (bold solid lines) and unintended (bold dashed lines) consequences of TNR population control programs are highlighted. Notice that TNR increases both adult and kitten survival rates, potentially causing the unintended consequence of increasing population size.

Given that, according to Gunther,¹⁵ 32% of cats survive to 6 months of age in colonies with no neutered individuals, and noting that 6 months represents approximately 180 days, then $s^*(p,0)^{180} = 0.32$ or $s^*(p,0) = 0.9937$. In the present model, $s_0 = 0.9991$ and $s^*(K,0) = 0.9912$. The approximate mean survival rate is therefore calculated as follows:

$$s^*(p,0) = [s_0 + s^*(K,0)]/2 = (0.9991 + 0.9912)/2 = 0.9952$$

The 2 values are reasonably close, so their mean (0.9945) was used. Similarly, from the data of Gunther¹⁵, 76% of cats survived to 6 months of age if 75% of colony members were neutered by TNR, so $(s^*[p,0.75])^{180} = 0.76$, so $s^*(p,0.75) = 0.9985$. The estimate for b is therefore as follows:

$$b = (0.9985 - 0.9945)/(0.75[0.9991 - 0.9945]) = 1.16$$

Program output—Because the model is stochastic, 2 runs of the model with the same input data will produce different results. Consequently, each scenario was run 20 times and the mean of the data was calculated to give the reported results. The program output included the population histories from individual simulations, the mean population size over time over a

number of simulations, and the cat-days for individual or mean population histories. Cat-days was defined as the area under the population history curve after day 2,000 (when the trapping program begins; ie, the total number of cats alive each day summed over day 2,000 to day 6,000). Cat-days was a proxy for the cumulative exposure of the cat population to the environment and also allowed finer resolution of the relative effectiveness of the alternative control methods.

Checks for validity—To validate that the model represents realistic biological behavior of a feral cat population, several characteristics of the modeled population were compared with data available in the literature. Specifically, the relative proportions of males, females, adults, and pregnant or nursing females were evaluated. The effect of no intervention was included in the analysis to ensure that the assumption of reproductive and population parameters resulted in a steady-state population.

Statistical analysis—No statistical analyses were done to compare the treatments because significance values from statistical tests are a combination of effect size and sample size, and the larger the sample size, the smaller the effect size that can be detected as significant. As a result, all lines might be considered significantly different because we can increase the number of replicates until we have a small *P* value. Consequently, *P* values arising from this type of statistical evaluation would be trivial.

Results

At annual capture rates $\leq 19\%$, all methods were ineffective at decreasing population size (Figure 2). At annual capture rates $\geq 97\%$, each method was effective at reducing population size, but LC was most effective, followed by TVHR, and finally TNR. At all intermediate annual capture rates tested (ie, between 19% and 97%), TVHR outperformed both alternative treatments. If 57% of cats could be captured and neutered annually by use of TNR or removed by LC, there was an approximately 25% decrease in population size. In contrast, with an annual capture rate of only 35%, TVHR caused an approximately 50% decrease in population size. From the various annual capture rates modeled, for TVHR, an annual capture rate between 35% and 57% caused complete elimination of the population in 4,000 days, compared with a rate $> 82\%$ for both TNR and LC. At no annual capture rate did TNR perform better than either of the alternative methods.

Evaluation of the effects of different management methods on cat-days revealed that TVHR outperformed TNR and LC at all annual capture probabilities from 10% to 90%, with the greatest difference at approximately 50% annual capture probability (Figure 3). Lethal control was the most effective technique at annual capture probabilities $>$ approximately 90%. Variability in estimates of mean cat-days was lowest at low capture rates, ranging from 3% to 8% for annual capture probabilities of approximately 0.20. At intermediate capture probabilities (0.4 to 0.64), SD was highest for TVHR (21% and 27% of the mean, respectively), with lower variability for TNR and LC; at the higher capture rates, SDs were relatively high but similar for all control methods.

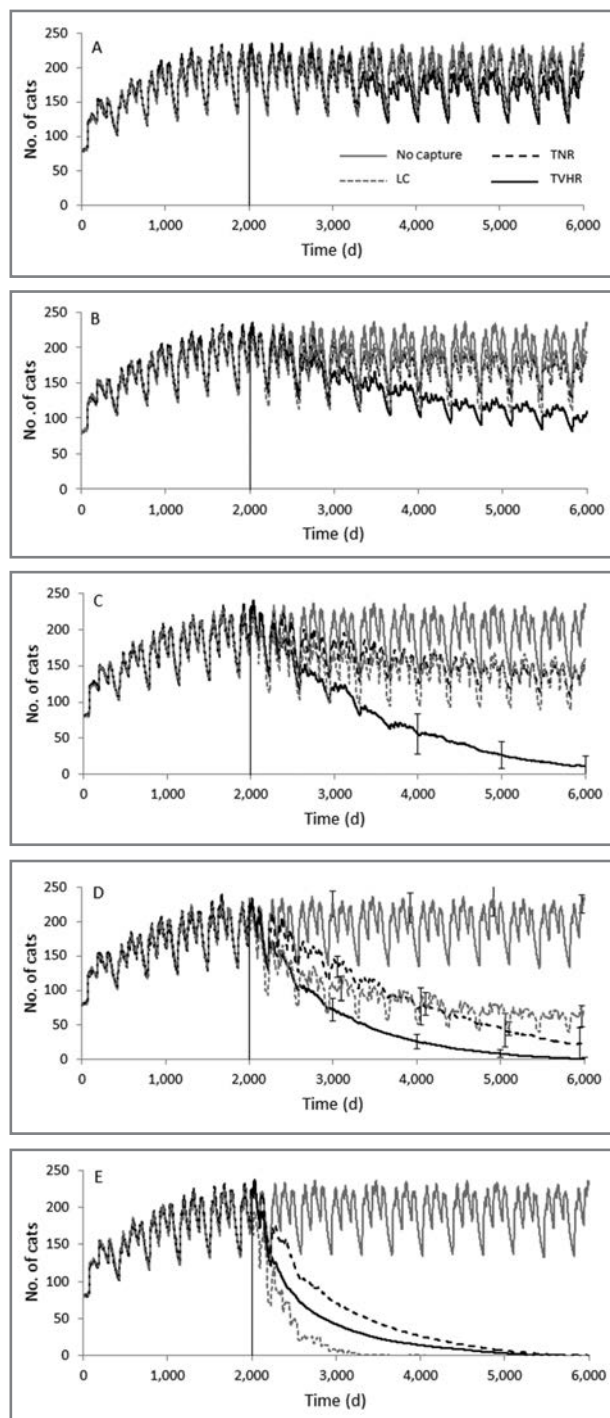


Figure 2—Predicted feral cat population size for 3 population control methods with 5 rates of annual capture success. Each line is the mean of 20 model runs. Notice the somewhat cyclic pattern to the lines caused by the 9-month breeding season, which causes population growth, with subsequent decreases during the nonbreeding season. The initial population has a carrying capacity of approximately 200 cats, and there is no effect of fraction of adult cats neutered on kitten and young juvenile cat survival rate. In each plot, there is no intervention for the first 2,000 days of the model; on day 2,000 (vertical bar), each control method begins. A—Daily capture probability = 0.03; 7-day capture period with 1 capture period/y; annual capture probability = 0.19. B—Daily capture probability = 0.03; 7-day capture period with 2 capture periods/y; annual capture probability = 0.35. C—Daily capture probability = 0.03; 7-day capture period with 4 capture periods/y; annual capture probability = 0.57. Bars indicate SD. D—Daily capture probability = 0.03; 14-day capture period with 4 capture periods/y; annual capture probability = 0.82. Bars indicate SD. E—Daily capture probability = 0.06; 14-day capture period with 4 capture periods/y; annual capture probability = 0.97.

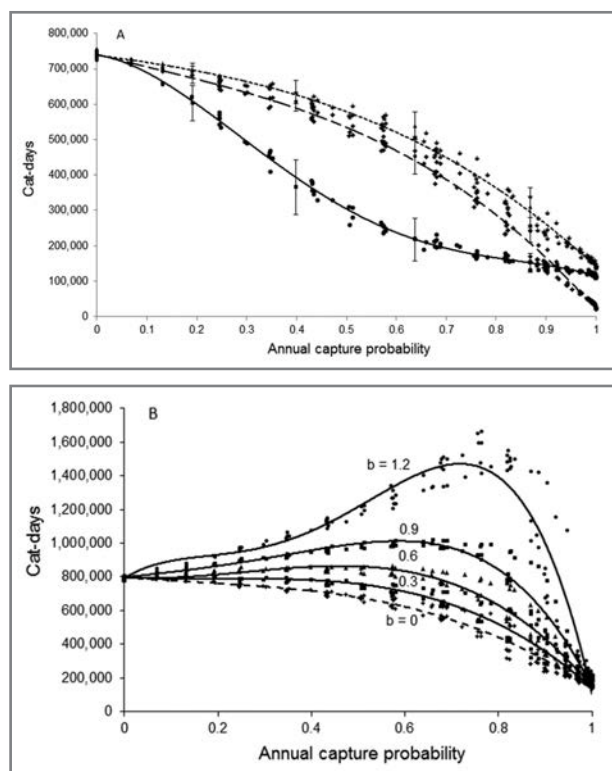


Figure 3—Predicted number of cat-days for 3 feral cat population control methods with different annual trapping probabilities. Cat-days indicates the total number of cats alive each day summed over day 2,000 (when each control method begins) to day 6,000. The initial population has a carrying capacity of approximately 200 cats. Each point represents the mean of 20 runs of the simulation model. Bars indicate SD. A—In this model, there is no effect of fraction of adult cats neutered on kitten and young juvenile survival rate. B—Predicted number of cat-days for TNR with different annual capture probabilities and 5 levels of effect (*b*) of fraction of adult cats neutered on kitten and young juvenile survival rate. *b* = 0 represents no effect; other values for *b* represent the predicted effect.

When the effect of fraction of adult cats neutered on kitten and young juvenile survival rate was included in the analysis, TNR performed progressively worse (Figure 3). This density-dependent feedback release peaked at approximately 60% to 70% annual capture probability, with cat-days more than doubling between *b* = 0 and 1.2. Because of this density-dependent release, TNR was actually counterproductive, such that cat-days increased, compared with no intervention, for all but high annual capture rates if *b* was > 0.60.

Tests for validity indicated that with no intervention, approximately 40% of the modeled population was male, and 40% of cats were kittens or juveniles. Approximately 81% of adult females were pregnant or nursing. When no treatment was applied, the modeled colony had steady-state numbers.

Discussion

For the present study, an individual-based stochastic computer simulation model was developed to evaluate the effectiveness of 3 alternative strategies for controlling feral cat populations. In contrast to traditional mathematical population models, individual-based sto-

chastic simulations are bottom-up analysis tools. They describe the behavior of individuals in the population as well as their interactions with other individuals and allow the resultant population-level behavior to emerge. The stochastic nature of some of the model parameters (survival rate, litter size, and pregnancy probability) reflects the essential unpredictability of individual behaviors and fates. This modeling approach tries to capture as many of the relevant biological features of the system as is practical. Only recently has the extensive computational requirements of such models ceased being forbidding. The goal was that the model would be more biologically meaningful and the results more credible than those provided by population-level models.

Results of the simulation model suggested a clear superiority of TVHR, compared with TNR and LC, if a decrease in population size and consequent effects on local wildlife is the goal. Trap-vasectomy-hysterectomy-release resulted in a decrease in feral cat populations at lower capture rates than either TNR or LC, and exposure of cats to the environment (cat-days) decreased more rapidly with increased capture rates for TVHR than for TNR or LC. At no annual capture rate was TNR superior to TVHR or LC, and only at annual capture rates > approximately 90% was LC more effective.

The annual probability of capturing an individual cat was used frequently as an outcome parameter in the analysis to evaluate success of different interventions. It should be noted that the same annual capture probability might be obtained in different ways. Specifically, increased annual capture probability can be obtained by increasing the probability that a cat is captured on a given day (possibly by increasing the number of traps set) or by increasing the frequency or duration of a specific capture program. Because of the stochastic nature of several of the input parameters, changing the way a given annual capture probability is obtained may have different relative effects on alternate control methods. The model allows for unlimited specification of any of these variables.

Although they have not been included in previous feral cat population control models, social behaviors, including dominance, are important in feral cat colonies.^{48,55,59,61} Dominance status is complex and may differ in different populations but is most frequently associated with age and body weight.^{34,55,59,61–63} Dominant males that are castrated in a TNR program become sexually inactive and are subsequently replaced in the breeding hierarchy by the next most dominant male, so unless every male in a colony can be captured and castrated, continued reproduction with maintenance of population size is inevitable. Unlike castration, vasectomy does not alter a male cat's sexual drive or social status.^{20,22} Cats that have undergone vasectomy maintain their position in the breeding hierarchy, compete with other males for females as before surgery, prevent less dominant males from breeding, and continue to copulate but in an unproductive fashion.

In the middle latitudes, breeding season is determined by photoperiod and approximately 21 periods of sexual receptivity are theoretically possible.^{25,26} If nonproductive coitus induces ovulation, such as with a male that has undergone vasectomy, the estrous period

is followed by a 45- to 51-day pseudopregnancy, and only 4 to 5 periods of sexual receptivity would then be possible during a breeding season, reducing the chances and number of fertile matings.^{25–27,46,49,64}

Population management by means of TVHR likely provides a group of sexually active but nonfertile male and female cats that compete equally with their fertile counterparts for copulations. If an individual male courts a large number of females, the effect of vasectomy on population control is likely greater because more females are brought into nonreceptive 45-day pseudopregnancy, but the effect of hysterectomy is likely less because a lower percentage of a male's total courting effort will be unproductive. Alternately, if a large number of males court a single estrous female, the effect of vasectomy is probably less because it is more likely that at least 1 sexually intact male will ultimately court and mate successfully, whereas the effect of hysterectomy is likely greater because more males use up mounting time and energy on a single unfertile female.

An important difference among the methods of control we tested was their relative effect on survival rate of cats remaining in the population. In this regard, LC and TVHR had no effect, whereas TNR increased survival rate of both adults and kittens.^{15,a} Multiple studies^{65,66} have suggested that decreased survival rate is more effective than decreased fecundity in reducing population size. Increased survival rate in neutered adult males occurs because they lose interest in mating with females, so they roam less and are less likely to be injured by trauma. In addition, they have fewer agonistic interactions with other males and sustain fewer infections.^{11,15,16,59,61,67} Increased survival rate of neutered adult females may relate to diminished stress associated with repeated hormonal cycling, pregnancy, and rearing kittens.¹⁶ In 1 study,^a median survival time of sexually intact adult males was 267 days and for sexually intact females was 593 days, compared with > 730 days for both neutered males and spayed females. In another study,⁶⁸ 54% of feral cats were less than ideal weight before neutering, compared with 14% one year later. Cats in that study⁶⁸ had a mean increase in weight of 40% and body condition score of 1 after neutering.

Kitten survival rate is a separate and important consideration when comparing methods of population control and in fact may be the major factor limiting population size.³⁴ High mortality rates are reported for kittens in hormonally intact feral cat populations with the rate of survival to 6 months of age ranging from 12% to 33%.^{15,30–34,a} Survival rate of kittens may improve when TNR is instituted, possibly because of increased tolerance by other cats.¹⁵ A recent study^{15,69} found that in identical living conditions, 32% of kittens survived to 6 months in hormonally intact colonies, compared with 76% in colonies where 75% of the members had been neutered. When the effect of TNR on kitten survival rate was included in the analysis in the present study, TNR performed even worse as a population control measure and was actually counterproductive, such that cat-days were greater, compared with no intervention, for all but high (> 90%) annual neutering rates if density-dependent feedback release was as predicted from the literature.^{15,69}

Elimination of a targeted population is often the goal of wildlife or pest management programs, but even small changes in population size may be important in reducing effects on local wildlife. Cat-days is an indicator of the potential environmental impact of a feral cat population and, as such, an important determinant of management success. There is little debate that feral cats are a major factor in the deaths of hundreds of millions of birds, small mammals, reptiles, amphibians, and fish annually.^{3–7} Feral cats consume a mean of approximately 328 g of food/d, and a study⁷⁰ in the United Kingdom estimated that 9 million cats there kill at least 81 to 98 million native wildlife in the summer months alone. The Wisconsin Department of Natural Resources⁷¹ estimated that an individual urban feral cat kills 14 to 28 birds/y, and a rural feral cat kills 91 to 360 birds/y. On the basis of estimates such as these, even small changes in population control by any management method may represent a large change in environmental impact.

Computer-based modeling has been used to assess predicted effects on feral cat population size after TNR and LC and has uniformly predicted failure to eliminate a targeted population unless unrealistically high annual capture rates can be maintained for long periods.^{65,72–74,a} Nutter^a reported that in the absence of immigration, an annual harvest rate of 55% to 60% by LC or annual neutering rate of 75% to 85% by means of TNR was required to have any effect on population size. For TNR, if the 75% to 85% neutering rate could be maintained, estimated time for elimination of all cats was 12.8 years.^a Anderson⁶⁵ predicted that for LC, a 50% annual reduction in the female population would likely cause the population to decrease by approximately 10% yearly; with use of TNR, > 75% of the female population would need to be neutered annually to stabilize population growth. A similar model was used to compare the theoretical effect of a 3-year single-treatment nonsurgical contraception program with traditional TNR, and outcomes indicated that for TNR, cessation of population growth would require annual surgical neutering of > 51% of both adult and juvenile (age, < 1 year) sexually intact female cats.⁷³ Once the population was stabilized, this would equate to neutering approximately 14% of the total female population/y or having 71% of the total female population neutered at all times.⁷³ In another assessment, Foley et al⁷² predicted the effects that would occur after implementation of TNR on the basis of data from 2 TNR programs. Results suggested that the critical neutering rate would be 94% for one area and 71% for the other. It was concluded that neither TNR program achieved the needed rate, so continued growth was predicted.⁷² Finally, Schmidt et al⁷⁴ predicted the relative effects of TNR and LC with different capture and immigration rates on an actual feral cat colony. With no immigration, population size was expected to decrease 46% for either LC or TNR after 25 years of implementation.⁷⁴ Immigration decreased performance of both methods, but more so for TNR.⁷⁴

None of these previous models included the effects of feral cat social behavior, changes in adult survival rate with loss of hormones, density-dependent decrease of kitten mortality rate associated with TNR, or season-

ality of reproduction. Social behaviors play important roles in feral cat population dynamics, and both adult and kitten survival rates have important effects on feral cat population size in the presence of TNR. Most feral cat interventions occur in areas of the world where cats have a prolonged period of anestrus associated with shortened day length during winter, so by assuming yearlong reproduction, these models are likely to overestimate population increases without intervention and underestimate the positive effects of attempts at control. By including seasonality, the present model allowed a more accurate representation of colony dynamics under management alternatives and allowed the potential to investigate the effect of applying interventions at different times of the fertile-nonfertile cycle.

Validation checks of the present model agreed well with data available in the literature. Most feral cat populations have approximately equal numbers of males and females,^{10,11,53,73} and in the simulated population, approximately 60% of cats were female.^{10,11,53,73} Age distribution may vary considerably because of seasonal breeding, but kittens and juveniles usually represent 15% to 56% of cats in wild populations.^{10,41,43,53,55,57} In the present model, 40% to 50% of cats were consistently in this age group. On the basis of real populations, most adult females should be pregnant or nursing during the breeding season,⁴¹ and in the simulated population, this was the case. When no intervention was included, the model projection resulted in a steady-state population limited by the carrying capacity, further validating the model as representative of a wild feral cat population.

The use of vasectomy or hysterectomy to control feral cat populations has been mentioned in the literature, but rarely has it been investigated clinically.^{21,23,24,c} One study^c failed to confirm a reduction in the number of stray cats when all captured males underwent vasectomy, but the study was limited in sample size, was unable to accurately count all cats, and may have preferentially euthanized older dominant males. Vasectomy was performed in a study^a investigating lifespan, immigration patterns, and home range of feral cats, but the benefit of vasectomy on population control was not evaluated. Hysterectomy was used to stabilize a population of feral cats at a zoological garden, but no comparison was made with alternative techniques.²¹

Although the results of the present study suggested a distinct superiority of TVHR with regard to decreasing population size, potential disadvantages also exist. Vasectomy allows persistent undesirable male behaviors such as fighting, vocalization, and urine marking, and in some situations, elimination of these behaviors is the main impetus for the control program itself.⁶⁹ Fortunately, in most feral cat populations worldwide, this is not the case, and if vasectomy results in a more rapid and persistent population decline, negative behaviors may be acceptable in the short term. Neutering by vasectomy is a somewhat more time-consuming and difficult surgical technique than routine castration but is easily learned by any veterinarian with basic surgical skills. Finally, any technique that uses surgical neutering requires trapping of cats, and in this regard, TVHR is no different than TNR.

Hysterectomy in female cats allows continued hormone production, so vocalization will be more

prominent than in cats that have been neutered.^{51,75} Although attempts are made at surgery to remove the entire uterus, small amounts of persistent tissue may provide a site for development of cystic endometrial hyperplasia-pyometra complex. In reality, this condition appears to be exceptionally rare, even in non-neutered female feral cats.⁷⁵ The pathological effects of multiple pseudopregnancies are unknown.

Lethal methods of feral cat control are sometimes recommended by wildlife advocates to manage feral cat colonies.⁶ Results of the present study suggested that TVHR outperforms LC at all rates of annual capture up to approximately 90%. Eliminating 90% or more of the cats in a large and wild population is unlikely. Most feral cats cannot be tamed and are not suitable as pets, so LC involves methods such as hunting, poisoning, or introduction of disease, which are unacceptable to many people, as indicated by legal protection in some countries and cities.¹⁸ Lethal control has been effective at eradication of cats on several islands, but most of these islands were small (< 5 km²), unpopulated by humans, and involved small cat numbers.^{2,4,5} Probably the most successful eradication program with LC was performed on Marion Island, South Africa, where approximately 2,500 feral cats were eliminated by introduction of feline panleukopenia virus, trapping, and hunting.⁵ Eradication was successful but required intensive effort for 15 years.⁵ Trap-vasectomy-hysterectomy-release should be recommended as a humane and more effective method of decreasing population size.

Limitations exist with all models, in part because of accuracy and variances of available demographic and behavioral data on the target species.⁷ There are gaps in available data on the basic reproductive structure and behavior in feral cat populations. Although we did include the predicted effect of density dependence on survival rate, we did not incorporate an effect on reproductive rate. Similar to other wildlife, reproductive success may increase as population size decreases, especially where availability of food and shelter are limited.⁷⁶ Parameter estimates were generated from the literature, but there may be variation in these parameters on the basis of colony size, density, age structure, location, climate conditions, available food sources, and management activities. Regardless of these variations, the model allowed flexibility for input of data to evaluate any group of feral cats, provided population-specific vital data are available.

Although computer-based modeling is useful to rapidly predict the outcomes of different control methods on feral cat populations, direct clinical trials would be beneficial to document or refute the relative advantage of different control strategies. Group-randomized trials, where similar communities in an area receive different interventions have been recommended but not performed.¹⁴ Feral cat control programs should gather basic data through standardized methods and report outcomes to allow valid comparisons among studies, improve parameter estimates, and decrease potential variance. This, combined with experimental studies, would allow for adaptive management in feral cat control.

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Appendix

Pseudocode for basic steps and structure of a computer simulation model of feral cat populations.

```

Read in method of population control
Read in trapping program parameters
Read in cat parameters
Read in population parameters
For day 0 simulation
  For cat in initial (day 0) population
    Assign sex
    Assign age at day 0
    Assign class
    Assign social unit for female
  Next cat
For day 1 to last day simulations
  Determine if day is trapping day
  Determine all dominant males
  Determine dominant males order for access to receptive females
  Set all female social units to available
  Determine all receptive females
  For each living male cat
    Determine if it survives the day
    If it survives
      Update status
    If not winter
      Determine daily sexual activity of dominant males
  For each living female cat
    Determine if it survives the day
    If it survives
      Update status
    If not winter
      Determine daily sexual activity of receptive females
      Determine resulting pregnancies and pseudo-pregnancies
      Determine births of males and females
      Carry out various population calculations and information gathering
  Next day
Display results

```