

Use of matrix population models to estimate the efficacy of euthanasia versus trap-neuter-return for management of free-roaming cats

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Objective—To evaluate the efficacy of trap-neuter-return and trap-euthanize management strategies for controlling urban free-roaming cat populations by use of matrix population models.

Design—Prospective study.

Sample Population—Estimates of free-roaming cat populations in urban environments.

Procedure—Data from the literature describing the biology of free-roaming cat populations in urban environments were gathered. A matrix population model was developed with a range of high and low survival and fecundity values and all combinations of those values. The response of population growth rate to a range of management actions was assessed with an elasticity analysis.

Results—All possible combinations of survival and fecundity values of free-roaming cats led to predictions of rapid, exponential population growth. The model predicted effective cat population control by use of annual euthanasia of $\geq 50\%$ of the population or by annual neutering of $> 75\%$ of the fertile population. Elasticity analyses revealed that the modeled population was most susceptible to control through euthanasia.

Conclusions and Clinical Relevance—Free-roaming cat populations have a high intrinsic growth rate, and euthanasia is estimated to be more effective at reducing cat populations than trap-neuter-return programs. (*J Am Vet Med Assoc* 2004;225:1871–1876)

Free-roaming cats represent challenges to the veterinary profession and society. Free-roaming cats contribute to a public health hazard through the risk of transmitting rabies and other zoonotic agents.¹⁻⁶ These cats may be infected with a variety of feline pathogens and function as a reservoir of infection for owned cats.^{1,2,7,8} The welfare of free-roaming cats concerns society because they are frequent victims of vehicular collisions and fights between themselves and other animals.^{1,3,5,6,9,10} Cats also are efficient predators, and results of numerous studies^{2,3,5,11,12} indicate their detrimental

impacts on native wildlife. For example, the British population of 9 million cats has been estimated to be responsible for the deaths of 57 million mammals, 27 million birds, and 5 million reptiles and amphibians per year¹¹; because the US cat population has been estimated at 100 million,¹² the potential impact of domestic cats on American wildlife is high. There also are emotional and financial costs to society caused by concern for these cats, their prey, and the attempts to mitigate the perceived and real damages caused by unmanaged populations of free-roaming cats.^{6,9,10,13} Despite recognition of the problems, there is no consensus on how such populations should be managed.

Two management schemes predominate. Traditional animal control plans manage free-roaming cats through capture and removal. Whereas some captured cats are returned to their owners or adopted as pets, most are euthanized as unwanted, excess cats. Traditional animal control is often constrained by resources and rarely sustains active cat population management on a broad scale. A more recently proposed management alternative is to maintain stable, nonbreeding populations. These programs are founded on capturing, neutering, and releasing cats with additional management processes of disease testing, vaccination, feeding, adoptions, and monitoring being components of some programs. Although trap-neuter-return (TNR) programs are presented as an alternative to euthanasia and an effective means of population management,^{1,4,6,10,14,15} these programs have not been developed on a large scale, limiting their assessment as a tool for decreasing cat populations. Further, TNR programs are often instituted because of society's aversion to euthanasia as a method of control. Thus, much of the debate surrounding the use of euthanasia or TNR has a substantial emotional component. Therefore, an objective evaluation of TNR and alternative strategies for managing cat populations would make a valuable contribution toward sound management.

Matrix population models are a primary tool used in wildlife management to set annual guidelines on hunting, trapping, and fishing; explore population dynamics; and develop management plans for endangered species.¹⁶⁻²⁹ These models use estimates of age- or stage-specific vital rates (reproduction and survival) to project future population structure. Analysis of these models allows objective comparison of the efficacy of different management actions and permits identification of key factors influencing population dynamics.^{18,29,30}

For our study, published data from studies of urban, free-roaming cat populations were used to parameterize

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a matrix population model¹⁷ and explore how cat populations may respond to various forms of control. The primary objective was to compare the efficacy of TNR programs versus euthanasia programs as methods of cat population management. Because TNR programs affect reproduction and euthanasia programs affect survival, these 2 approaches should be fundamentally different with respect to their impact on the growth rate of cat populations. To address this hypothesis, an elasticity analysis of the matrix population models was conducted to explore how alterations in the estimates of stage-specific vital rates would influence population growth rate. Elasticity analysis is a form of perturbation analysis that allows determination of the rate of change of population growth rate in response to changes in individual vital rates.¹⁷ This allows vital rates to be ranked in order of their influence on population growth.

Materials and Methods

Model description and construction—The matrix population model^{31,32} allows classification of the population either by age or stage classes (eg, larva, juvenile, adult). The model advances a given population structure ahead through 1 time interval to a new projected population structure. Through that time interval, reproduction and survival occur within each age or stage class in the population at rates specific to that age or stage class. For instance, young animals, such as juveniles, have a probability of surviving (usually < 1) to the reproductive adult stage, thereby increasing the numbers in the adult stage and decreasing the numbers in the juvenile stage. Similarly, reproduction by different stages at time t would contribute to the number of young present at time $t + 1$. Thus, the survival probabilities and reproductive rates of each age or stage class would contribute to a new population structure at time $t + 1$.

Under this model, changes in population structure are denoted by the equation $n(t + 1) = An(t)$, where n represents a vector of age or stage classes describing the population structure at times $t + 1$ and t , respectively, and the population projection matrix A contains the survival probabilities and reproductive rates acting on the population through each time interval. The dominant eigenvalue of the population projection matrix, denoted by λ , is the intrinsic or asymptotic growth rate of the population. If $\lambda = 1$ there is no net change in the population size. Values > 1 mean that the population is increasing; values < 1 mean that the population is decreasing.¹⁷

Model parameter estimation—Vital rate data were gathered from published studies of free-roaming cats in urban environments; preference was given to studies of unmanipulated populations. Given the variability of the vital rate data, low and high extremes of parameter estimates and all combinations of those extremes were used in the analysis. The available data were insufficient for an age-structured classification but amenable to a stage-structured model with 2 stages: individuals ≤ 1 year old, called juveniles, and individuals > 1 year old, called adults. This classification of the population model conformed to the level of detail of the management actions that were evaluated. The model time step was 1 year. The model considered only the female population; this is appropriate if the population is not mate-limited or if the vital rates of the 2 sexes are identical.¹⁷

Reproduction in cats is relatively well documented, and values from the literature were used to develop the model. Fetus number has been reported as mean \pm SD of 3.6 ± 0.2 kittens/dam in a program to spay free-roaming cats.¹⁵ This can be conservatively considered a typical litter size and is comparable to values found in other studies.²⁹ Mean number of litters per female per year has been reported to be from 1.1 to

2.1.^{10,15} Puberty in female cats varies with time of year of their birth, but first conception has been reported to be at a mean of 212 days of age.² Sex ratios are consistently near 50:50.¹⁵

Based on these values, the fecundity of adult female cats was estimated as a product of kittens per litter, litters per year, and sex ratio at birth. Thus, our low estimate of fecundity was $3.6 \times 1.1 \times 0.5 = 1.98$ female offspring/y; our corresponding high estimate was $3.6 \times 2.1 \times 0.5 = 3.78$ female offspring/y. Juvenile females have reduced mean fecundity because most are prepubertal. This reduction is equal to the factor $(365 - 212)/365$, which yielded 0.83 female offspring/y to 1.58 female offspring/y for the low and high estimates of juvenile fecundity, respectively.

Survival probabilities have not been as thoroughly documented. In a long-term study,² annual juvenile survival was reported as approximately 75%. In another report,³³ it was suggested that annual survival is closer to 50%. Published figures for survival rates of adults include 33% survival over a 42-month period³⁴ and 67% survival over an 18-month period.⁴ Anecdotal reports estimate adult life span of feral cats at 2 to 3 years.

Survival rates were computed under the assumption that the juvenile and adult classes reported in the various studies were consistent with this model's juvenile and adult classes. The low estimate of survival for juveniles was therefore 0.5, and the high estimate was 0.75. Reported survival rates for adults were determined over periods longer than 1 year; annual survival rates were estimated by use of the geometric probability distribution as an approximate discrete lifetime distribution.³⁵ This method assumes that survival probabilities remain constant over the entire period for which they are being estimated. This assumption may not be true if there are age-dependent effects on survival. For example, if younger adults learn as they age, survival may be enhanced with time, whereas senescence may cause the opposite effect in older adults, reducing survival over time. It is likely that both processes occur, but the available data did not allow us to address this issue. The distribution function for the geometric distribution was $P = 1 - S^t$, where S is the per-time-unit survival rate, and P is the probability that an individual will die by time t . Thus, the expression for S given t and P was $S = \exp(\ln[1 - P]/t)$.

This expression was used to obtain 4 estimates of annual survival rates for the adult class based on 3 values of P . Calculations based on a 2-year and 3-year life span, assuming that $P = 0.50$, yielded annual survival rates of 0.707 and 0.794, respectively. A monthly survival rate of 0.974 was calculated from a survival probability of 0.33 over 42 months (ie, $P = 0.67$ and $n = 42$), and this monthly rate was converted to an annual rate of 0.729 (ie, 0.974 to the 12th power). Similarly, a monthly survival rate of 0.978 results from a survival probability of 0.67 over 18 months ($P = 0.33$ and $n = 18$). This monthly rate converts to an annual survival rate of 0.766 (0.978 to the 12th power). Thus, by use of 4 reported estimates of adult survival, the estimated annual rate of adult survival varied from 0.707 to 0.794. Therefore, the low and high values for adult survival rates used in the model were 0.7 and 0.8, respectively.

Although breeding is skewed towards the first half of the year and only a few litters are born during the months of October through December, cats essentially can breed throughout the year.^{2,9,15} Continuously breeding populations are most easily modeled by assuming that all births take place at the midpoint of the time interval.¹⁷ Under this assumption, parental individuals must survive to that midpoint and the resultant offspring must survive through the remaining half of the time interval. Half-year survival rates are equal to the square root of the annual rate. Thus, the matrix elements are as follows:

$$\begin{bmatrix} S_0 \cdot F_0 & \sqrt{S_0} \cdot F_1 \cdot \sqrt{S_1} \\ S_0 & S_1 \end{bmatrix}$$

where S_0 and S_1 are annual rates of survival for the juvenile and adult stage classes, and F_0 and F_1 are the estimates of fecundity for those same stage classes. The composite matrix elements in the top row of the matrix are equal to the stage-specific reproductive rates (R_0 and R_1) for juveniles and adults, respectively.

Model analyses—Analyses were performed with software written in a standard programming language.^a Intrinsic rates of increase (λ) were calculated with all combinations of high and low fecundity and survival rates. Fecundity was reduced by 10%, 25%, 50%, and 75% to simulate TNR programs of increasing rigor. Trap-euthanate programs were modeled through several combinations of reductions of juvenile and adult survival by 10%, 25%, 50%, and 75%.

The geometric mean of λ , computed across all combinations of fecundity and survival rates, was used as a summary statistic in assessment of population management strategies. Elasticity analysis was used to provide a broader view of the demographic basis of the effects of the different management strategies. All elasticity values were calculated with a computer program.^{30a}

Uncertainty in vital rate estimates may influence the outcome of computations of the elasticity values. These possible effects may be accounted for by computing elasticity values for a large number of simulated population projection matrices, in which the vital rate values are randomly chosen to lie between predetermined limits. The upper and lower bounds chosen for the vital rates were the high and low estimates, respectively, for each rate.

Results

The high and low vital rate values resulted in 8 possible matrices that each yielded $\lambda > 1$ (Table 1). Population growth rate ranged from a high of 2.49 for the highest estimates of fecundity and survival for both juvenile and adult classes to a low of 1.34 for the lowest combinations. All remaining combinations of parameters led

Table 1—Baseline population projection matrices used in simulations of free-roaming cat populations and their intrinsic rates of increase (λ). Each scenario corresponds to a different estimate of fecundity and survival.

Scenario	Fecundity	Juvenile survival	Adult survival	Matrix	λ
1	High	High	High	$\begin{bmatrix} 1.189 & 2.928 \\ 0.75 & 0.8 \end{bmatrix}$	2.49
2	High	High	Low	$\begin{bmatrix} 1.189 & 2.739 \\ 0.75 & 0.7 \end{bmatrix}$	2.40
3	High	Low	High	$\begin{bmatrix} 0.792 & 2.391 \\ 0.5 & 0.8 \end{bmatrix}$	1.89
4	High	Low	Low	$\begin{bmatrix} 0.792 & 2.236 \\ 0.5 & 0.7 \end{bmatrix}$	1.80
5	Low	High	High	$\begin{bmatrix} 0.622 & 1.534 \\ 0.75 & 0.8 \end{bmatrix}$	1.79
6	Low	High	Low	$\begin{bmatrix} 0.622 & 1.435 \\ 0.75 & 0.7 \end{bmatrix}$	1.70
7	Low	Low	High	$\begin{bmatrix} 0.83 & 1.252 \\ 0.5 & 0.8 \end{bmatrix}$	1.61
8	Low	Low	Low	$\begin{bmatrix} 0.415 & 1.171 \\ 0.5 & 0.7 \end{bmatrix}$	1.34

For juvenile fecundity, low = 0.83 female offspring/female per year, high = 1.58 female offspring/female per year; for adult fecundity, low = 1.98 female offspring/female per year, high = 3.78 female offspring/female per year. For juvenile survival, low = 0.5, high = 0.75; for adult survival, low = 0.7, high = 0.8.

For each matrix, upper left value represents juvenile reproductive rate, upper right value represents adult reproductive rate, lower left value represents juvenile survival, and lower right value represents adult survival.

to intermediate intrinsic rates of population increase. The geometric mean of these 8 baseline values of λ was 1.84.

The geometric mean intrinsic rates of increase for the matrices simulating a TNR (ie, with reduced fecundity values), even for quite large reductions in fecundity, were still > 1 (Table 2). A 75% reduction in fecundity for all reproductive females (corresponding to ongoing spaying 75% of the female population) yielded $\lambda = 1.08$.

The geometric mean intrinsic rates of increase for the matrices simulating a euthanasia program (ie, with reduced survival values) revealed that reductions of $\leq 25\%$ were not sufficient to lead to predictions of declining cat populations (Table 2). However, reductions in both juvenile and adult survival by $\geq 50\%$ yielded a geometric mean intrinsic rate of increase < 1 . A 75% reduction in both adult and juvenile survival led to $\lambda = 0.47$, meaning that a cat population subjected to such a program would be approximately halved every year.

In nearly all scenarios, λ was more sensitive to changes in survival than fecundity (Figure 1). A 25%

Table 2—Geometric mean λ for free-roaming cat populations with either reduced fecundity, simulating the effects of a trap-neuter-return program, or reduced survival, simulating the effects of a euthanasia control program. Geometric means were calculated over the 8 baseline matrix models in Table 1 with fecundity or survival reduced by the percentage indicated.

Fecundity	Juvenile survival (%)	Adult survival (%)	λ
Baseline	Baseline	Baseline	1.84
10	NC	NC	1.73
25	NC	NC	1.59
50	NC	NC	1.35
75	NC	NC	1.08
NC	10	10	1.63
NC	10	25	1.53
NC	25	10	1.46
NC	25	25	1.36
NC	50	50	0.91
NC	50	75	0.73
NC	75	50	0.62
NC	75	75	0.47

NC = No change in the vital rate from the baseline values.

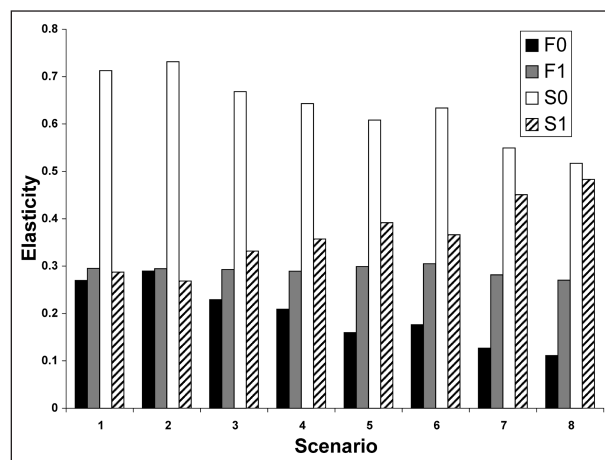


Figure 1—Elasticity of the intrinsic rate of population increase in response to changes in survival and fecundity rates of free-roaming cats under 8 scenarios corresponding to the matrices in Table 1. Survival and fecundity rates that yield larger elasticity values are expected to have a greater influence on the intrinsic rate of population increase. F_0 = Juvenile fecundity. F_1 = Adult fecundity. S_0 = Juvenile survival. S_1 = Adult survival.

Table 3—Elasticity of λ in free-roaming cat populations for mean vital rates and random matrices derived from a range of values for each vital rate.

Vital rate	Elasticity of λ for mean vital rates	Elasticity of random matrices		
		Minimum	Maximum	Mean (SD)
Juvenile fecundity	0.34	0.12	0.33	0.20 (0.045)
Adult fecundity	0.28	0.26	0.33	0.30 (0.016)
Juvenile survival	0.76	0.55	0.72	0.65 (0.034)
Adult survival	0.24	0.28	0.45	0.36 (0.035)

reduction in fecundity of the cat population led to a growth rate of 1.59, whereas a 25% reduction in survival reduced growth rate to 1.36 (Table 2). Fifty percent and 75% reductions in survival similarly led to greater reductions in population growth than did the 50% and 75% reductions in fecundity. Elasticity values ranged from as high as 0.73 for juvenile survival in 1 scenario to as low as 0.11 for juvenile fecundity in another scenario. Elasticity for the survival rates ranged from 0.27 to 0.73, whereas elasticity for the fecundities remained < 0.30 . This result was mirrored by the stochastic analyses of λ (Table 3). Elasticity values for the mean vital rates ranged from 0.24 to 0.76, and the mean elasticity values for the random matrices ranged from 0.20 to 0.65. The highest elasticity values were for juvenile survival, suggesting that population growth is most sensitive to this vital rate, followed by adult survival. Control strategies that target survival of free-roaming cats should be more effective at reducing cat populations than those that target fecundity.

Discussion

Matrix population models have been used successfully in many population management strategies.^{18,20,22,23,29,36} Such models have been used to assess the viability of populations of endangered plants^{19,26} and animals,^{21,22} to assess the impacts of wildfires²⁴ and pollutants on natural populations,^{25,27,28} and to study the pathogenicity of an external parasite.³⁷ Matrix models are often preferred in management applications because of the degree of development of the underlying mathematics, the level of realism of the models, and the ease of parameter estimation.³⁸

The geometric mean growth rate rather than the arithmetic mean is the appropriate measure of the most likely growth rate of a stochastic population growth process. The geometric mean best represents the expected rate of growth of a population in which one of the possible population matrices is randomly chosen at each time step. In other words, if one of the different possible population projection matrices considered was randomly selected and a population was to grow according to that matrix for that time step, and another matrix was randomly selected for the following time step, then over time, the population's long-term growth rate would be the geometric mean, not the arithmetic mean, of the set of possible growth rates.^{17,30} Thus, the use of the geometric mean of λ as the summary measure directly and explicitly recognizes the uncertainty in the parameter estimates.

Demographic elasticity analysis is a way of calculating the effect of small changes in the vital rates of a

population on the population's rate of growth. Analytically, this can be computed as the partial derivative of λ with respect to each individual vital rate, holding the others constant. These partial derivatives are referred to as sensitivity values; when these values are multiplied by the ratio of the vital rate in question to λ (to scale for differences in the vital rates themselves), they are referred to as elasticity values.¹⁷ The elasticity of λ can be calculated with respect to particular vital rates or with respect to the matrix elements themselves. In this analysis, the elasticity of λ was calculated with respect to each vital rate (ie, stage-specific fecundity and survival) because the matrix element for fertility was a composite of several vital rates.

Examination of elasticity values is valuable in assessing management strategies for free-ranging populations. Such strategies nearly always have age-specific effects, representing a perturbation in a particular vital rate, and are aimed at either increasing or reducing the target population's growth rate. Management strategies intended to alter vital rates with particularly high elasticity values are more likely to achieve their goal than strategies that target vital rates with low elasticity.³⁰

Management programs for free-roaming cat populations typically focus on either survival (euthanasia programs) or fecundity (TNR programs). Because these 2 approaches target different vital rates, they may have fundamentally different outcomes with respect to their influence on cat population growth rate. Under scenarios lacking control, feral cat populations were predicted to grow rapidly because all values of λ are substantially > 1 . The model results further suggested that a reduction in survival might have a more profound effect on cat population growth rate than a reduction in fecundity. A 50% reduction in annual survival rate was predicted to result in a cat population that declined by approximately 10% per annum, whereas a large reduction in annual fecundity (75%) in both the juvenile and adult stages was predicted to result in an increasing population. The interpretation that survival had a greater predicted influence on population growth rate also was supported by results of the elasticity analyses; cat population growth rate was more sensitive to survival regardless of the control scenario.

Juvenile survival has been identified as a key population management target in matrix-modeling studies of other species.^{18,21} Given the uncertainty of the vital rate estimates, the sensitivity of urban cat populations to changes in adult and juvenile survival cannot be confidently distinguished. Nevertheless, changes in survival are always predicted to have a greater influence on population growth than changes in fecundity.

Matrix population models have also been applied to owned populations of pet dogs and cats.³⁹⁻⁴¹ An age-structured matrix of pet cats yielded a λ of 1.21 for cats through the first 5 years of life.³⁹ This value is lower than any growth rate calculated for the unmanaged population structures used here; however, those authors were modeling pet populations in which responsible owners had a substantial number of cats neutered or prevented breeding by fertile cats. A spay

rate of 88% would be needed to stabilize population growth if all fertile cats were free to breed.³⁰ In a separate study,⁴¹ a growth rate of 1.02 was calculated for a citywide pet cat population with a spay rate of 85.7%. This result is similar to the most intensive fecundity reduction used in this study, in which a 75% reduction in fecundity yielded a geometric mean λ of 1.08. These results suggest that management actions that reduce fecundity in excess of 75% of the fertile population would need to be maintained, on an ongoing basis, to cause a population decrease in a TNR program. Thus, TNR programs are not likely to convert increasing cat populations into declining populations or even stable populations until the neutering rate is quite high.

Nevertheless, population decreases under TNR programs have been recorded. In 1 study,⁴ a 26% population reduction over an 18-month period with an approximately 70% neuter rate was reported. This reduction also included a population reduction of 25% through a concurrent adoption program. Another study¹⁰ revealed profound population reduction in a managed cat population with essentially a 100% neuter rate and adoptions occurring at a high rate (approx 47% of the population). Adoption programs are similar in effect to euthanasia because these cats are permanently removed from the free-roaming population.

Feral or free-roaming cat populations are subject to additional population processes that were not considered here. The survival rates used may account for extrinsic factors that would be expected to cause death (eg, intraspecific aggression or disease), but the estimates of fecundity used did not incorporate a measure of density dependence, which might be expected to lower reproductive rates at high population densities. Density dependence was omitted for 2 reasons. First, there are no reliable estimates of the reduction in fecundity that would be expected at high population densities; second, small populations would not be influenced by density dependence to any great degree. Emigration also is apt to be a substantial population factor that was not considered. Emigration between cat colonies has been reported,^{1,4,10} and a substantial number of owned cats are reported to be adopted strays.^{5,33,41} Evaluating the efficacy of euthanasia versus TNR programs would benefit from additional field studies that estimate other population processes and from well-designed monitoring programs run in parallel with control programs.

^aMATLAB, The MathWorks Inc, Natick, Mass.

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