CSIRO PUBLISHING
www.publish.csiro.au/journals/wr *Wildlife Research*, 2009, **36**, 117–125

Evaluation of euthanasia and trap–neuter–return (TNR) programs in managing free-roaming cat populations

Paige M. Schmidt[A,D], *Todd M. Swannack*[A], *Roel R. Lopez*[A] *and Margaret R. Slater*[B,C]

[A]Department of Wildlife and Fisheries Sciences, Texas A&M University, 2258 TAMU, College Station, TX 77843-2258, USA.
[B]College of Veterinary Medicine, Texas A&M University, 4458 TAMU, College Station, TX 77843-4458, USA.
[C]Present address: Animal Services Program Office, The American Society for the Prevention of Cruelty to Animals, 1717 South Philo Ave, Suite 36, Urbana, IL 61802, USA.
[D]Corresponding author. Email: pmhill@tamu.edu

Abstract. Global estimates of the number of domestic cats (*Felis catus*) are >400 million. Issues associated with free-roaming cats are of global importance because of animal-welfare and public-health concerns and impacts on native wildlife through predation, competition and disease transmission. In the United States, proposed control solutions for managing urban free-roaming cat populations include euthanasia and trap–neuter–return (TNR) programs. We evaluated control methods using a demographic population model for a 25-year period, with parameters estimated from an unmanaged, free-roaming cat population in Texas. We modelled euthanasia and TNR at 25%, 50% and 75% implementation rates and a 50 : 50 combination of euthanasia and TNR at 25%, 50%, 75% and 100% implementation rates for 0%, 25% and 50% maximum immigration rates. We compared final population size, total number of cats treated and treatment effort relative to population reduction. Population decreases were comparable among euthanasia, TNR and a 50 : 50 combination for all treatment rates when the immigration rate was 0%; however, they were higher for euthanasia at 25% and 50% maximum immigration rates. Euthanasia required higher treatment effort than TNR. Our results indicate that immigration must be prevented and high (>50%) treatment rates implemented to reduce free-roaming cat populations.

Introduction

The USA population of owned cats has recently been estimated to be 90.5 million (Association of Pet Manufacturers 2004) and the number of unowned cats has been speculated to be ~10–50 million (Mahlow and Slater 1996) for a total cat population of >100 million (Clarke and Pacin 2002). With an estimated 400 million domestic cats worldwide (Jarvis 1990), issues associated with free-roaming cats are of global importance. Free-roaming cat populations include owned cats allowed outdoors, recently owned, lost or abandoned cats, and feral cats (Slater 2002). Problems associated with free-roaming cat populations in both urban and rural areas are well documented (see Patronek 1998 and Slater 2002), including animal-welfare concerns (starvation, disease, abuse or depredation), public-health and nuisance concerns and impacts on native wildlife through predation, competition and disease transmission. Management of free-roaming cats is an issue of much debate that pivots upon whether management solutions should use lethal or non-lethal control strategies. In the USA, the two main population-management strategies for free-roaming cat populations are euthanasia and TNR (trap–neuter–return) programs (e.g. Neville and Remfry 1984; Zaunbrecher and Smith 1993; Centonze and Levy 2002; Scott *et al*. 2002; Levy *et al*. 2003), whereas recreational harvest of free-roaming cats was recently proposed in Wisconsin and denied (Wisconsin Department of Natural Resources 2005). Proponents for both euthanasia and TNR argue that each preferred solution is more effective and appropriate than the opposition's; however, studies comparing the effectiveness of euthanasia and TNR at reducing free-roaming cat populations are controversial and are not based on standard wildlife-research techniques (Neville and Remfry 1984; Passanisi and Macdonald 1990; Zaunbrecher and Smith 1993; Patronek 1998; Clarke and Pacin 2002; Gibson *et al*. 2002; Hughes *et al*. 2002; Stoskopf and Nutter 2004). Lethal and non-lethal population-control strategies are expected to alter vital rates (Conover 2002); therefore, the evaluation of population-control methods for unmanaged cat populations ideally should be conducted *a priori* using vital-rate estimates from unmanaged cat populations (White 2000). Wildlife ecologists commonly use population models as decision-making tools to assess various management scenarios to control invasive and introduced species (Gogan *et al*. 2001), including free-roaming cats (Andersen *et al*. 2004; LaFever *et al*. 2008).

For the treated segment of the population, euthanasia will affect population parameters by an increase in mortality above the natural rate, whereas implementation of a TNR program will decrease fecundity rates. Implementation of euthanasia or TNR would realistically include treatment of male and female cats. The effects of each control scenario on male and female vital rates and the subsequent effects on population growth have not been considered in prior modelling attempts (Andersen *et al*. 2004).

10.1071/WR08018 1035-3712/09/020117

For example, if we assume equal capture rates for male and female cats, applying treatment rates to females only will overestimate reductions in fecundity, thus biasing model results. Inclusion of both sexes is also important if male and female vital rates are different (Andersen *et al*. 2004). For our study population, we found evidence that male and female mortality rates differed (Schmidt *et al*. 2007*a*), thus requiring a population model evaluating male and female contributions to population growth rates. In addition, population control efforts may be expected to have compensatory rather than additive effects on parameter estimates for populations with high rates of male mortality or for populations with a large proportion of non-breeding males. Models that use natality estimates derived from fetus counts and the number of litters per female per year do not account for kitten mortality (Andersen *et al*. 2004), and inflate net reproductive rate above zero for cats that die before the age of first reproduction.

TNR advocates often cite the 'vacuum theory' arguing that surgically altered cats will maintain or occupy habitat or resources, thereby reducing the ability of immigrants to establish themselves (Neville and Remfry 1984; Passanisi and Macdonald 1990; Zaunbrecher and Smith 1993; Mahlow and Slater1996; Gibson *et al*. 2002). In areas treated with TNR, non-reproducing individuals will maintain the population closer to carrying capacity, reducing fecundity rates in non-treated individuals and reducing immigration rates, thus reducing the population over time. However, TNR programs encourage provision of supplemental food sources for managed cat colonies and often encourage provision of artificial shelters that may raise the carrying capacity of free-roaming cat populations. Prior attempts to use population models to compare euthanasia and TNR did not account for density dependence or immigration of cats into management areas from outlying areas (Andersen *et al*. 2004).

Data on the effectiveness of euthanasia and TNR on unmanaged, free-roaming cat populations typically found in urban areas are lacking. Therefore, our objectives were to (1) determine population growth using vital-rate estimates from an unmanaged, free-roaming cat population, (2) evaluate density dependence and the role of immigration for this population and (3) evaluate euthanasia, TNR and euthanasia + TNR combinations at different levels of intensity for reducing free-roaming open populations of cats.

Material and methods

Study area

Caldwell is a small, suburban community of ~3400 residents located in Burleson County, Texas, USA. Caldwell has no zoning laws, resulting in a highly heterogeneous community with single- and multi-family dwellings (6–10 houses ha^{-1}) intermixed with commercial, industrial and agricultural development (Marzluff *et al*. 2001). Our study area was ~822 ha and was surrounded by agricultural fields, woodlots and pasture. Spotlight surveys indicated free-roaming cat densities were lower in surrounding areas than within our study area (P. Schmidt, pers. obs.). Residents generally tolerate unowned cats (P. Schmidt, unpubl. data). Nuisance animals reported to the part-time animal control officer are trapped, held according to state law and euthanised if unclaimed. Socialised cats may be held longer until they are adopted or euthanised.

Model overview

To determine quantitatively how different levels of euthanasia and/or TNR affected the population of cats in Caldwell, we developed a discrete-time simulation model representing the population. We obtained the model's parameter estimates from a radio-marked population of free-roaming cats ($n = 43$) studied in Caldwell (Table 1; Schmidt *et al*. 2007*a*, 2007*b*). The model was formulated as a stochastic, stage-structured compartment model based on difference equations (Δt = 1 year) and programmed in STELLA7 (STELLA Research 2002). We examined the effects of 11 different combinations of euthanasia and TNR (Table 2), at three different levels of immigration (0%, 25% and 50%), using 100 replicate stochastic iterations of each combination for 25 years of simulated time. The conceptual model is shown in Fig. 1.

Table 1. Parameter estimates used to simulate the effects of euthanasia and trap–neuter–release (TNR) to control free-roaming cat populations

Parameter estimates were obtained from a radio-telemetry study of an unmanaged, free-roaming cat population in Caldwell, Texas, USA, from October 2004 through December 2005

Parameter	Estimate	Source
Natality		
Feral females	1.75 (s.e. = 0.25, n = 2) 1 litter year^{-1}	Schmidt *et al*. (2007*a*)
Semi-feral females	2.75 (s.e. = 0.48, n = 4) 1.6 litter year^{-1}	Schmidt *et al*. (2007*a*)
Per capita rate	$[1.75(1) + 2.75(1.6)]/2 = 3.075$	
Survival		
Unowned (feral and semi-feral) males	0.57 (s.e. = 0.13, n = 27)	Schmidt *et al*. (2007*a*)
Unowned (feral and semi-feral) females	0.88 (s.e. = 0.12, n = 16)	Schmidt *et al*. (2007*a*)
Initial abundance		
Mark–resight estimator	(n = 744, 95% CI 518–1135)	Schmidt *et al*. (2007*b*)
Distance estimator	(n = 296, 95% CI 262–333)	Schmidt *et al*. (2007*b*)
Model parameter	$(744 + 296)/2 = 520$	
Carrying capacity	$K = 724$	

Table 2. Rates of euthanasia and trap–neuter–release (TNR) used during each simulation for control of a free-roaming cat population in Caldwell, TX, USA

For Scenarios 4, 7 and 10, which utilised a combination of euthanasia and TNR, individuals were only treated once (i.e. killed cats were not available for TNR and cats treated via TNR were not killed)

Scenario	Treatment rate (%)	
	Euthanasia	TNR
1	0	0
2	0.25	0
3	0	0.25
4	0.125	0.125
5	0	0.50
6	0.5	0
7	0.25	0.25
8	0.75	0
9	0	0.75
10	0.375	0.375
11	0.5	0.5

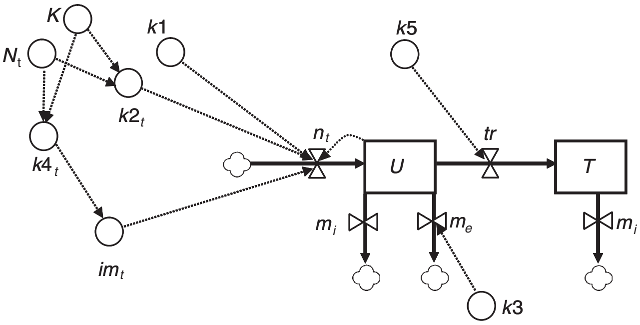

Fig. 1. Conceptual model representing the dynamics of untreated and treated cats in Caldwell, Texas, USA. For simplicity, details are shown for a single gender (i). U and T represent the number of untreated and treated cats, respectively. n represents natality, m_i represents sex-specific natural mortality, m_e represents mortality through euthanasia, tr represents individuals treated with TNR. $k1$, $k3$ and $k5$ are constants and represent the per capita birth rate and treatment levels for euthanasia and TNR, respectively. $k4_t$ represents the unutilised opportunity for population increase at time t. $k2_t$ and im_t represent a density-dependent reduction of natality and immigration, respectively, and both depend on the carrying capacity K and total population size N_t at time t. Symbols follow those described by Forrester (1961)

The simulated population consisted of the following four stages: untreated males (U_m), untreated females (U_f), treated males (T_m) and treated females (T_f). We assumed equal trapability among all individuals; therefore, all individuals are equally susceptible to lethal and non-lethal management strategies (Fig. 1). Forms of equations for each gender were identical, but mortality rates were sex-specific. Untreated cats were represented as:

$$U_{i,t+1} = U_{i,t} + (n_{i,t} + i_{i,t} - m_{i,t} - me_{i,t} - tr_{i,t})\Delta t, \qquad (1)$$

where $U_{i,t}$ represents the number of untreated individuals of gender i at the beginning of time t, $n_{i,t}$, the number of young of gender i born into the population during time t, and $i_{i,t}$, $m_{i,t}$, $me_{i,t}$, $tr_{i,t}$ represent the number of individuals immigrating into the population, dying through natural causes, euthanised or treated (TNR, see below) of gender i during time t, respectively, and Δt represents the change in time, in this case 1 year. Our estimate of natality ($n_{i,t}$) represents the number of 12-week-old kittens and not the number of newborns; therefore, an estimate of kitten mortality is included in the $n_{i,t}$ term. Treated cats were represented as:

$$T_{i,t+1} = T_{i,t} + (tr_{i,t} - mt_{i,t})\Delta t, \qquad (2)$$

where $T_{i,t}$ represents the number of treated individuals of gender i at time t, $tr_{i,t}$ represents the number of untreated animals receiving the TNR treatment during time t, and $mt_{i,t}$ represent the number of previously treated animals succumbing to natural mortality during time t. The total population size for any time t was calculated as:

$$N_t = \sum U_{i,t} + \sum T_{i,t}. \qquad (3)$$

Natality

Natality was calculated as:

$$n_{i,t} = (U_{f,t})(k1)(k2_t), \qquad (4)$$

where $U_{f,t}$ is the number of reproductively mature females, $k1$ is the number of cats born per female to survive to 12 weeks of age (3.075) calculated for the population (Table 1; Schmidt *et al.* 2007*a*) and the sex ratio at birth was assumed to be 1M : 1F. Natality was stochastic and at each time step a natality rate was chosen from the per capita rate and standard deviation reported in Schmidt *et al.* (2007*a*; Table 1). Most cats are sexually mature and reproduce within their first year (Jones and Coman 1982; Nutter *et al.* 2004); therefore, we assume the natality rate applies to females so that between birth and their first birthday cats reproduce at the given rate.

Density dependence

Preliminary exploration of model dynamics indicated the population grew to unreasonable sizes because of the extremely high fecundity rates reported for this population (Table 1). Therefore, we assumed the population grew logistically. $k2_t$ represents a density-dependent reduction of natality and we assumed a linear relationship between $k2_t$ and population size,

$$k2_t = 1 - (1/K)N_t, \qquad (5)$$

where N_t represents the population size at time t and K represents the carrying capacity of the environment. When the population reaches K, we assumed all available niches were full and that no breeding could occur.

Mortality

The model represents two sources of mortality: mortality that occurs naturally and mortality that occurs through euthanasia. Natural mortality was stochastic and at each time step a mortality rate was chosen from a normal distribution created from the mean and standard deviation of survival rates reported in Schmidt *et al*. (2007*a*; Table 1), as follows:

$$m_{f,t} : \mu = 0.12, \quad \sigma = 0.12, \tag{6}$$

and

$$m_{m,t} : \mu = 0.43, \quad \sigma = 0.098, \tag{7}$$

where $m_{f,t}$ and $m_{m,t}$ represent annual mortalities chosen from normal distributions (truncated at 0 and 1) of mean μ and standard deviations of σ of females and males, respectively. We assumed that treated and untreated adults had the same natural mortality rates.

Mortality resulting from euthanasia was represented as a proportion of the untreated individuals and was identical for males and females, as follows:

$$m_e = k3(U_{i,t}), \tag{8}$$

where $U_{i,t}$ represents untreated individuals of gender *i* at time *t*, and *k*3 represents a proportion of untreated individuals to be euthanised. The proportion of individuals euthanised was a constant, which was reparameterised for each simulation (Table 2).

Immigration

We assumed our population was open and cats immigrating into the population were untreated, sexually mature individuals. Immigration into the population was assumed to be a linear function of the unutilised opportunity for increase (Krebs 2001), as follows:

$$k4 = (K - N_t)/K, \tag{9}$$

where *k*4 represents the proportion of available habitat not currently occupied by cats. Immigration rates are not available for this population. We assumed immigration into the population would be a percentage (*x*) of maximum available niche-space so we evaluated the model for several values of *x*, including zero immigration, to determine how immigration affected population dynamics (see model evaluation below). We assumed equal immigration between genders (*i*), and immigration at time *t* was calculated as

$$im_{i,t} = (x)(K)(k4). \tag{10}$$

TNR

TNR was represented as a proportion of untreated individuals and was a constant, which was re-parameterised for each simulation (Table 2). TNR treatments were calculated as:

$$tr_{i,t} = k5(U_{i,t} - m_{i,t} - me_{i,t}) \tag{11}$$

where ($U_{i,t} - m_{i,t} - me_{i,t}$) represents the number of untreated individuals of gender *i* at time *t* that did not die naturally or were not euthanised and *k*5 represents the TNR treatment level (Table 2).

Model evaluation

To determine the effect of parametric uncertainty on model projections, we conducted a sensitivity analysis on the parameters for which we did not have empirical estimates, i.e. carrying capacity (*K*) and immigration (*im*). We evaluated the baseline model (i.e. no treatments) at eight different levels of *K* (300, 400, 600, 750, 1000, 1250, 1500, 2000) at each of six different levels of immigration (0.0, 0.1, 0.2, 0.3, 0.4, 0.5) for a total of 48 different parameterisations. For each parameterisation, we ran 100 replicate stochastic simulations. We determined a sample size of 100 replicates for each parameterisation provided enough variation to determine a statistical difference of two cats among repetitions (Ott and Longnecker 2001).

Model application

After we evaluated the results from the 48 parameterisations used for model evaluation, we chose to apply the treatments (euthanasia, TNR, combination) to three different parameterisations of the model. We ran each of 11 treatments at three levels of immigration and a $K = 724$ (explained below) to determine the effects of the treatment groups (100 replicate stochastic simulations per treatment). We calculated (1) mean population size and (2) mean number of cats (male, female, total) treated for each model scenario for the 25-year period. Both were averaged across the 100 repetitions per scenario. We subtracted the final population size for each treatment scenario from the baseline population size and divided by the final baseline population size to calculate the total percentage population decrease. To evaluate the treatment effort required to reduce cat populations for each scenario, we divided the total percentage population decrease by the mean total number of cats treated for each scenario.

Results

Model evaluation

Our simulation results indicated that the mean final population size was more sensitive to changes in *K* than it was to changes in immigration and the mean final population size was more variable when *K* was larger. When *K* was large, the population growth exhibited 'overshoot and collapse' dynamics that resulted from the interaction of the high per capita fecundity rate and population sizes being relatively near carrying capacity. For any given level of *K*, we observed general trends in immigration. For example, there were no statistical differences between immigration rates of 0 and 0.10, 0.20 and 0.30, and 0.40 and 0.50; however, there were statistical differences among those groups. Because we observed straightforward trends associated with changing carrying capacity, we selected the carrying capacity that represented the upper bound of a 95% confidence interval for our estimate of abundance ($K = 724$) (Schmidt *et al*. 2007*b*; Table 1).

We assume the environment is limited and that carrying capacity will remain unchanged. Neither carrying capacity nor immigration has been estimated for this population; therefore, on the basis of our model evaluation we made a simplifying assumption that the population grew logistically (Verhulst 1838; Pearl 1927) and that the birth rate decreased linearly as the population approached *K* (via the feedback mechanism *k*2). Further, we assumed immigration was a percentage of the unutilised capacity for increase (Krebs 2001) and therefore, at specific levels of *K*, *im* could not exceed the carrying capacity minus current population size ($K - N_t$).

Model results

Without control effort and no immigration, the baseline population increased from an initial abundance of 520 cats to a mean final population size of 663 (s.d. 81.8) cats, a 27% increase. Without control effort and a maximum immigration rate of 25%, the mean final population size was 669 (s.d. 100.1) cats, a 28.6% increase. Without control effort and a maximum immigration rate of 50%, the mean final population size was 703 (s.d. 127.1) cats, a 35.1% increase. The mean final population size for each scenario is summarised in Fig. 2*A–C*. Mean final population size was smallest for the 75% euthanasia rate with no immigration ($\bar{x} = 355$, s.d. 23.6), and largest for the baseline population with no treatment and a 50% maximum immigration rate ($\bar{x} = 703$, s.d. 127.1). For all scenarios, the final sex ratio was female-biased.

Mean final population size for euthanasia was comparable to or smaller than for TNR and a combination of euthanasia and TNR at all treatment and immigration rates, with the exception of the 25% treatment rate with a 50% maximum immigration rate (Fig. 2*A–C*). After 1 year, populations treated with euthanasia generally decreased whereas populations treated with TNR either remained unchanged or decreased slightly (Table 3). When the population was closed to immigration, treatment rates >50% were required for lethal and non-lethal control strategies to maintain the population below initial abundance (Fig. 2*A*). When populations experienced maximum immigration rates between 25% and 50%, euthanasia rates at or above 75% were required to reduce the population below initial abundance (Fig. 2*B*, *C*).

For each treatment scenario and rate, we summarised the total number of cats treated by sex (Fig. 3). Implementation of euthanasia at a 75% rate when the maximum immigration rate was 50% resulted in the highest mean total number of animals treated (Fig. 3; $\bar{x} = 6450$, s.d. = 97.6). Excluding the baseline scenarios, implementation of TNR at a 75% rate with an immigration rate of 0% resulted in the lowest total number of animals treated (Fig. 3; $\bar{x} = 274$, s.d. = 113.5). For each treatment scenario and rate, we summarised the total percentage decrease and treatment effort, defined as the mean total number of cats treated per 1% population decrease (Table 3). As expected, higher implementation rates resulted in higher population decreases (Table 3) and higher total treatment efforts (Fig. 3). For all scenarios, more females than males were treated (Fig. 3). Euthanasia resulted in greater total population decreases than did TNR and a combination of euthanasia and TNR; however, the total effort required to reduce each population by 1% was highest for euthanasia (Fig. 3, Table 3).

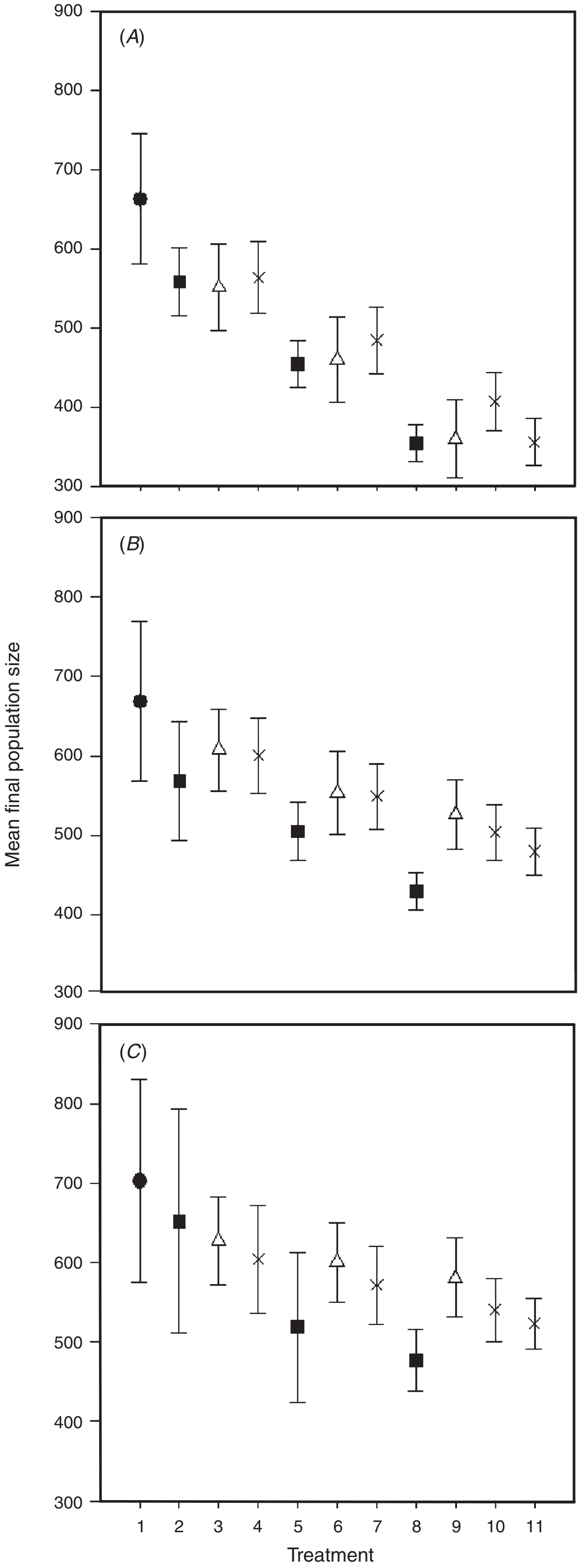

Fig. 2. Mean final population size and standard deviations for free-roaming cats in Caldwell, Texas, USA, using 100 replicate stochastic iterations for 25 years of simulated time of a baseline population with no management (●), 25%, 50%, and 75% treatment rates of euthanasia and trap–neuter–return (TNR) (■ and △ respectively) and 25%, 50%, 75% and 100% treatment rates of a 50 : 50 euthanasia + TNR combination (×). Mean final population size and standard deviation for all treatment rates are shown for maximum immigration rates of (*A*) 0%, (*B*) 25% and (*C*) 50%.

Table 3. Total percentage population change, percentage population change after 1 year and the treatment effort (number of cats treated per 1% population decrease) for model simulations evaluating lethal and non-lethal control strategies to reduce free-roaming cat populations in Caldwell, TX, USA

Each scenario evaluated one of three immigration rates and one of four population-control implementation rates. Final = the final baseline population size subtracted from the final population size for each treatment scenario and divided by the final baseline population size; Year 1 = baseline population size at Year 1 subtracted from the population size at Year 1 for each treatment scenario divided by the baseline population size at Year 1

Immigration maximum (%)	Treatment rate (%)	Population change						Treatment effort		
		Euthanasia		TNR		Combination		Euthanasia	TNR	Combination
		Final	Year 1	Final	Year 1	Final	Year 1			
0	25	–15.7	–15.7	–16.8	0	–14.9	–7.3	165	17	78
	50	–31.3	–30.8	–30.5	–0.3	–26.9	–15.6	134	11	60
	75	–46.4	–47.5	–45.6	–1.3	–38.5	–15.6	105	6	49
	100					–46.2	–30.8			45
0.25	25	–15	–14.5	–9.2	0	–10.3	–7.2	179	36	118
	50	–24.4	–28.7	–17.2	–0.2	–17.9	–14	190	21	102
	75	–35.7	–42.6	–21.3	0	–24.7	–21.9	165	19	90
	100					–28.3	–28.7			95
0.5	25	–7.2	–11.8	–10.7	0.6	–14.1	–5.3	383	33	89
	50	–26.2	–26.8	–14.5	1.1	–18.7	–12.8	185	28	87
	75	–32.1	–39.7	–17.4	–0.3	–23.1	–19.9	201	25	81
	100					–25.6	–26.8			81

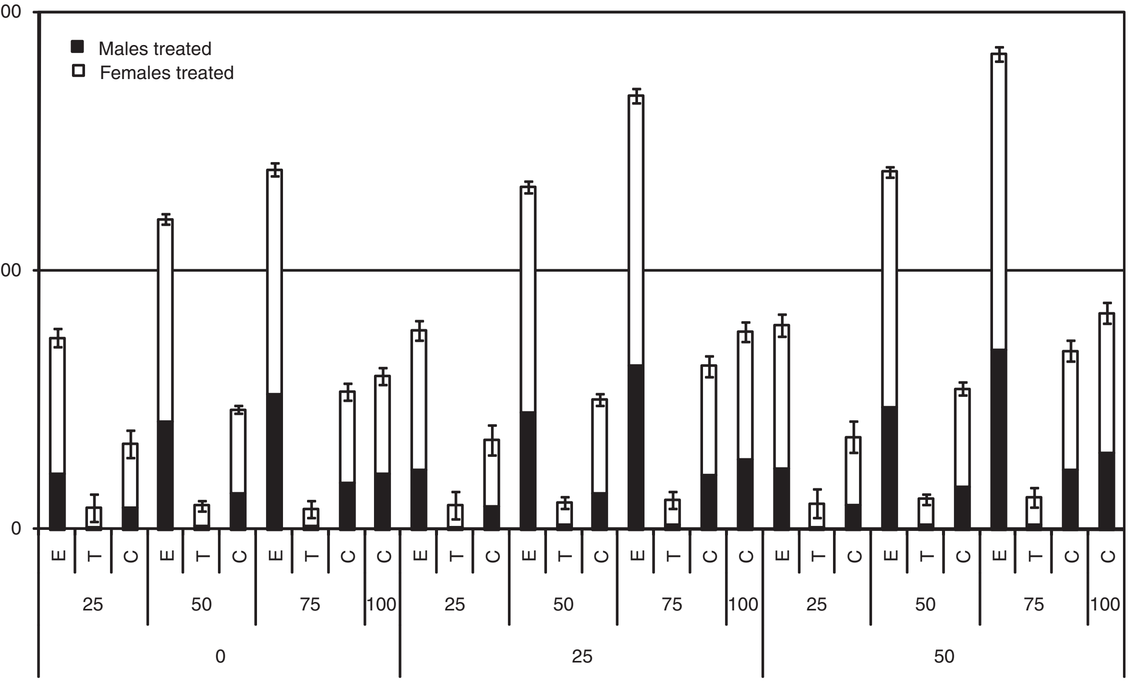

Fig. 3. Mean number of individual free-roaming cats treated by sex (male, female) in Caldwell, Texas, USA, using 100 replicate stochastic iterations for 25 years of simulated time using 25%, 50%, and 75% treatment rates of euthanasia and trap–neuter–return (TNR) and 25%, 50%, 75% and 100% treatment rates of a 50 : 50 euthanasia + TNR combination are shown for maximum immigration rates of 0%, 25% and 50%.

Discussion

For closed population scenarios (i.e. maximum immigration rate of 0%), model results indicated that lethal control of free-roaming cats (i.e. euthanasia) produced population reductions comparable to non-lethal control strategies (i.e. TNR) and a strategy utilising a combination of lethal and non-lethal. For demographically open populations (i.e. maximum immigration rates of 25% and 50%), model results indicated a greater decrease in mean final population size when lethal control strategies were implemented at high rates (75%) than with control strategies utilising a combination of lethal and non-lethal control (TNR) or non-lethal control alone. The model made a simplifying assumption of equal natality rates for the first year of life and subsequent years, an assumption that may overestimate natality because cats are not sexually mature and able to reproduce for that entire year. Increased implementation rates resulted in larger reductions in the mean final population size after 25 years for all treatments and immigration rates. Treatment effort per 1% population decrease increased as implementation rates increased and were highest for lethal control strategies.

Our results differ from model predictions for free-roaming cats provided by Andersen *et al*. (2004) in that euthanasia did not outperform TNR for demographically closed population scenarios; however, the results are consistent with their model predictions for demographically open population scenarios. Our model results also are consistent with initial evaluations of TNR campaigns (Castillo and Clark 2003; Foley *et al*. 2005; Natoli *et al*. 2006). TNR was not effective at reducing free-roaming cat numbers at two parks in Miami-Dade County, Florida (Castillo and Clark 2003). Although the numbers of original colony cats were reduced, the overall population failed to decline because of illegal dumping of cats and stray cats, which were then attracted to supplemental food provided by colony caretakers (Castillo and Clark 2003). Novel use of population models was applied on USA Census Bureau data on pet ownership and TNR trap data, to evaluate cat-population growth rates in San Diego and Alachua Counties, California; results did not indicate a reduction in free-roaming cat-population growth rates or in the number of pregnant females (Foley *et al*. 2005). In Italy, a no-kill policy for free-roaming cats and dogs was implemented in 1991; as a result, TNR has been implemented nationally for more than 10 years (Natoli *et al*. 2006). The first assessment of a nationally mandated TNR campaign in Rome, Italy, found a 16–32% decrease in cat numbers; however, the authors suggested 'control of reproduction of owned pet cats is crucial to achieve control of the feral-cat population', suggesting that immigration from the owned population continues to be a problem (Natoli *et al*. 2006: p. 184). The results of our and other studies suggest reducing immigration rates by curtailing the illegal dumping of cats would improve the efficacy of lethal and non-lethal control strategies. High rates of immigration (36%) were also found for non-native red fox populations targeted for control in California; reducing immigration rates was cited for long-term population control (Harding *et al*. 2001).

TNR advocates have suggested euthanasia creates a 'vacuum effect' by leaving unoccupied space that theoretically may be filled by reproductively viable cats not caught and removed through control efforts or through immigration from outlying areas (Neville and Remfry 1984; Passanisi and Macdonald 1990; Zaunbrecher and Smith 1993; Mahlow and Slater1996; Gibson *et al*. 2002). Natural attrition after implementation of TNR programs also would create open niches resulting in populations eventually returning to previous levels (Stoskopf and Nutter 2004). The results of the present study suggest that individual cats treated with TNR did maintain the population closer to K, thus reducing per capita natality rates; however, any difference between K and N was filled by immigrants under the open-population scenario. In other words, regardless of the treatment type (i.e. lethal or non-lethal control), any population reduction below carrying capacity would result in open niches that would eventually be filled by immigrants. Therefore, both euthanasia and TNR would require immigration to be concomitantly controlled or reduced under both scenarios. Our results are consistent with long-term evaluations of TNR colonies that showed population abundance failed to decrease because of immigration (Castillo and Clark 2003) and with studies that showed high rates of transients and population turnover in feral cats (Langham and Porter 1991; Genovesi *et al*. 1995).

At the Bear River Migratory Bird Refuge, Utah, population management through removal did not change the home-range size or movements of skunks (*Mephitis mephitis*), raccoons (*Procyon lotor*) or foxes (*Vulpes vulpes*), indicating food and shelter resources were not limited in that population (Frey and Conover 2007). If food and shelter resources had been limited, remaining predators would have been expected to increase range size and movements accordingly. Immigration by free-roaming cats from outlying areas is more likely if ubiquitous food and shelter resources raise carrying capacity, thus rendering population reductions following control efforts temporary, unless immigration from nearby areas and the owned cat population is otherwise prevented. Providing food and shelter to cats maintained in TNR colonies is a tenet of TNR advocacy and is considered to be the responsibility of the colony caretaker. The provision of food for colonies managed by TNR could result in increased local carrying capacity and cat survival. In our study population, free-roaming cats were frequently fed *ad libitum* (P. Schmidt, unpubl. data). Increased levels of ownership through feeding were shown to increase survival and fecundity rates and decrease ranges and movements in free-roaming cats (Schmidt *et al*. 2007*a*). As such, cat-immigration rates and population size are more likely to be determined by the reproductive potential of unmanaged source populations or other untreated cats in the area (e.g. reproductively viable owned cats, dumped litters, stray cats from outlying areas) and the carrying capacity of the treatment area as determined by the availability of supplemental food and shelter resources. Our findings are consistent with results from urban raccoon populations that exhibited increased survival, recruitment and site fidelity. Reducing anthropogenic food sources was suggested as the most effective strategy to reduce urban raccoon densities (Prange *et al*. 2003).

We stress that TNR campaigns may not be appropriate in ecologically sensitive areas or in communities with high rates of nuisance complaints for free-roaming cats. Model results showed that population reduction as a result of TNR was not immediate, thus indicating that issues associated with free-roaming cats may continue until populations respond to natural attrition, as has been shown for other species with non-monogamous mating systems (Barlow *et al*. 1997). In addition, there is evidence that sterilisation may increase survival rates for coyotes and free-roaming cats. As such, population reductions modelled via TNR are likely to be liberal as actual population decreases will be slower than modelled. Both euthanasia and TNR programs should include pre- and post-implementation monitoring by standard animal-population monitoring techniques (Williams *et al*. 2002). Those responsible for population management should consider the ecological sensitivity of the local ecosystem, community sentiment towards management options, as well as financial constraints on program implementation. We caution that public preference for free-roaming cat management may not be ecologically appropriate (Ash and Adams 2003; Lauber *et al*. 2007); however, population-control solutions also must include public education to increase awareness of free-roaming cat issues and impacts. Low-cost spay neuter programs for owned cats would compliment free-roaming cat management by reducing the probability that owned cats will serve as source populations, thus negating control attempts.

Acknowledgements

Research was approved by the Clinical Research Review Committee at the College of Veterinary Medicine, Texas AandM University (CRRC 04-30, 04-31). We would like to thank W. Grant for assistance with this model and B. Collier and N. Silvy for helpful review of this manuscript. We are grateful to the City of Caldwell, Caldwell Veterinary Clinic, L. Anderson, and Dr N. L. Carter for assistance with this project and to the residents of Caldwell for permitting us to conduct our research and for enrolling their cats in our study. The National Council on Pet Population Study and Policy provided funding for this research.

References

Andersen, M. C., Martin, B. J., and Roemer, G. W. (2004). Use of matrix population models to estimate the efficacy of euthanasia versus trap-neuter-return for management of free-roaming cats. *Journal of the American Veterinary Medical Association* **225**, 1871–1876. doi: 10.2460/javma.2004.225.1871

Ash, S. J., and Adams, C. E. (2003). Public preferences for free-ranging domestic cat (*Felis catus*) management options. *Wildlife Society Bulletin* **31**, 334–339.

Association of Pet Manufacturers (2004). '2005–2006 APPMA National Pet Owners Survey.' (American Pet Products Manufacturers Association, Inc.: Greenwich, CT.)

Barlow, N. D., Kean, J. M., and Briggs, C. J. (1997). Modelling the relative efficacy of culling and sterilization for controlling populations. *Wildlife Research* **24**, 129–141. doi: 10.1071/WR95027

Castillo, D., and Clark, A. L. (2003). Trap/neuter/release methods ineffective in controlling 'domestic' cat colonies on public lands. *Natural Areas Journal* **23**, 247–253.

Centonze, L. A., and Levy, J. K. (2002). Characteristics of free-roaming cats and their caretakers. *Journal of the American Veterinary Medical Association* **220**, 1627–1633. doi: 10.2460/javma.2002.220.1627

Clarke, A. L., and Pacin, T. (2002). Domestic cat 'colonies' in natural areas: a growing exotic species threat. *Natural Areas Journal* **22**, 154–159.

Conover, M. R. (2002). 'Resolving Human–Wildlife Conflicts: the Science of Wildlife Damage Management.' (Lewis Publishers: Boca Raton, FL.)

Foley, P., Foley, J. E., Levy, J. K., and Paik, T. (2005). Analysis of the impact of trap-neuter-return programs on populations of feral cats. *Journal of the American Veterinary Medical Association* **227**, 1775–1781. doi: 10.2460/javma.2005.227.1775

Forrester, J. W. 1961. 'Industrial Dynamics.' (MIT Press: Cambridge, UK.)

Frey, S. N., and Conover, M. R. (2007). Influence of population reduction on predator home range size and spatial overlap. *Journal of Wildlife Management* **71**, 303–309. doi: 10.2193/2005-417

Genovesi, P., Besa, M., and Toso, S. (1995). Ecology of a feral cat *Felis catus* population in an agricultural area of northern Italy. *Wildlife Biology* **1**, 233–237.

Gibson, K. L., Keizer, K., and Goldberg, C. (2002). A trap, neuter and release program for feral cats on Prince Edward Island. *Canadian Veterinary Journal. La Revue Veterinaire Canadienne* **43**, 695–698.

Gogan, P. J. P., Barret, R. H., Shook, W. W., and Kucera, T. E. (2001). Control of ungulate numbers in a protected area. *Wildlife Society Bulletin* **29**, 1074–1088.

Harding, E. K., Doak, D. F., and Albertson, J. D. (2001). Evaluating the effectiveness of predator control: the non-native red fox as a case study. *Conservation Biology* **15**, 1114–1122. doi: 10.1046/j.1523-1739.2001.0150041114.x

Hughes, K. L., Slater, M. R., and Haller, L. (2002). The effects of implementing a feral cat spay/neuter program in a Florida county animal control service. *Journal of Applied Animal Welfare Science* **5** (4), 285–298. doi: 10.1207/S15327604JAWS0504_03

Jarvis, P. J. (1990). Urban cats as pets and pests. *Environmental Conservation* **17**, 169–171.

Jones, E., and Coman, B. J. (1982). Ecology of the feral cat, *Felis catus* (L.), in South-eastern Australia II.* Reproduction. *Australian Wildlife Research* **9**, 111–119. doi: 10.1071/WR9820111

Krebs, C. J. (2001). 'Ecology: The Experimental Analysis of Distribution and Abundance.' (Benjamin Cummings: San Francisco, CA.)

LaFever, D. H., Schmidt, P. M., Perry, N. D., Faulhaber, C. A., Lopez, R. R., Silvy, N. J., and Forys, E. A. (2008). Use of a population viability analysis to evaluate human induced impacts and mitigation for the endangered Lower Keys marsh rabbit. *Human–Wildlife Conflicts* **2**, 260–269.

Langham, N. P. E., and Porter, R. E. (1991). Feral cats (*Felis catus* L.) on New Zealand farmland. I. Home range. *Wildlife Research* **18**, 741–760. doi: 10.1071/WR9910741

Lauber, T. B., Knuth, B. A., Tantillo, J. A., and Curtis, P. D. (2007). The role of ethical judgements related to wildlife fertility control. *Society & Natural Resources* **20**, 119–133. doi: 10.1080/08941920601052362

Levy, J. K., Gale, D. W., and Gale, L. A. (2003). Evaluation of the effect of a long-term trap-neuter-return and adoption program on a free-roaming cat population. *Journal of the American Veterinary Medical Association* **222**, 42–46. doi: 10.2460/javma.2003.222.42

Mahlow, J. C., and Slater, M. R. (1996). Current issues in the control of stray and feral cats. *Journal of the American Veterinary Medical Association* **209**, 2016–2020.

Marzluff, J. M., Bowman, R., and Donnelly, R. (2001). A historical perspective on urban bird research: trends terms, and approaches. In 'Avian Ecology and Conservation in an Urbanizing World'. (Eds J. M. Marzluff, R. Bowman and R. Donnelly.) pp. 1–18. (Kluwer Academic Publishers: Boston, MA.)

Natoli, E., Maragliano, L., Cariola, G., Faini, A., Bonanni, R., Cafazzo, S., and Fantini, C. (2006). Management of feral domestic cats in the urban environment of Rome (Italy). *Preventive Veterinary Medicine* **77**, 180–185. doi: 10.1016/j.prevetmed.2006.06.005

Neville, P. F., and Remfry, J. (1984). Effect of neutering on two groups of feral cats. *Veterinary Record* **114**, 447–450.

Nutter, F. B., Levine, J. F., and Stoskopf, M. K. (2004). Reproductive capacity of free-roaming domestic cats and kitten survival rate. *Journal of the American Veterinary Medical Association* **225**, 1399–1402. doi: 10.2460/javma.2004.225.1399

Ott, R. L., and Longnecker, M. T. (2001) 'An Introduction to Statistical Methods and Data Analysis.' (Duxbury: Pacific Grove, CA.)

Passanisi, W. C., Macdonald, D. W. (1990). The fate of controlled feral cat colonies. United Federation for Animal Welfare Research Report 4.

Patronek, G. J. (1998). Free-roaming and feral cats–their impact on wildlife and human beings. *Journal of the American Veterinary Medical Association* **212**, 218–226.

Pearl, R. (1927). The growth of populations. *Quarterly Review of Biology* **2**, 532–548. doi: 10.1086/394288

Prange, S., Gehrt, S. D., and Wiggers, E. P. (2003). Demographic factors contributing to high raccoon densities in urban landscapes. *Journal of Wildlife Management* **67**, 324–333. doi: 10.2307/3802774

Schmidt, P. M., Lopez, R. R., and Collier, B. A. (2007*a*). Survival, fecundity and movements of free-roaming cats. *Journal of Wildlife Management* **71** (3), 915–919. doi: 10.2193/2006-066

Schmidt, P. M., Pierce, B. L., and Lopez, R. R. (2007*b*). Estimating free-roaming cat densities in urban areas: comparison of mark-resight and distance sampling. *Wildlife Biology in Practice* **3**(1), 18–27. doi: 10.2461/wbp.2007.3.3

Scott, K. C., Levy, J. K., and Crawford, P. C. (2002). Characteristics of free-roaming cats evaluated in a trap-neuter-return program. *Journal of the American Veterinary Medical Association* **221**, 1136–1138. doi: 10.2460/javma.2002.221.1136

Slater, M. R. (2002). 'Community Approaches to Feral Cats: Problems, Alternatives & Recommendations.' (The Humane Society Press: Washington, DC.)

STELLA® Research (2002). 'Version 7.0.3, Computer Program.' (High Performance Systems, Inc.: Hanover, NH.)

Stoskopf, M. K., and Nutter, F. B. (2004). Analyzing approaches to feral cat management-one size does not fit all. *Journal of the American Veterinary Medical Association* **225**, 1361–1364. doi: 10.2460/javma.2004.225.1361

Verhulst, P. F. (1838). Notice sur la loi que la population suit dans son accroissement. *Correspondence Mathématique et Physique* **10**, 113–121.

White, G. C. (2000). Modeling population dynamics. In 'Ecology and Management of Mammals in North America'. (Eds S. Demarais and R. R. Krausman.) pp. 84–107. (Prentice-Hall: Upper Saddle River, NJ.)

Williams, B. K., Nichols, J. D., and Conroy, M. J. (2002). 'Analysis and Management of Animal Populations.' (Academic Press: San Diego, CA.)

Wisconsin Department of Natural Resources (2005). More than 13 000 attend spring rules hearings. News Release. http://dnr.wi.gov/org/caer/ce/news/rbnews/2005/041205co1.htm

Zaunbrecher, K. I., and Smith, R. E. (1993). Neutering of feral cats as an alternative to eradication programs. *Journal of the American Veterinary Medical Association* **203**, 449–452.

Manuscript received 3 February 2008, accepted 28 November 2008