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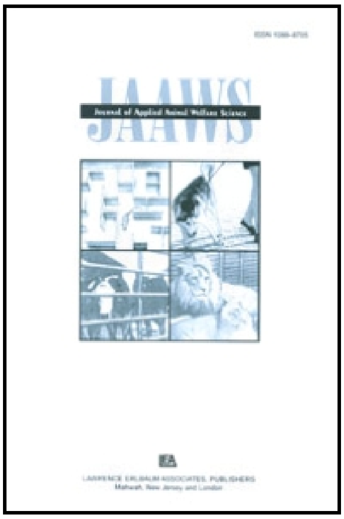

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ARTICLES

Utilization of Matrix Population Models to Assess a 3-Year Single Treatment Nonsurgical Contraception Program Versus Surgical Sterilization in Feral Cat Populations

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This study constructed matrix population models to explore feral cat population growth for a hypothetical population (a) in the absence of intervention; (b) with a traditional surgical sterilization-based trap, neuter, and return program; and (c) with a single treatment 3-year nonsurgical contraception program. Model outcomes indicated that cessation of population growth would require surgical sterilization for greater than 51% of adult and 51% of juvenile (<1 year) intact female cats annually, assuming an approximate 3-year mean life span. After the population stabilizes, this would equate to sterilizing approximately 14% of the total female population per year or having approximately 71% of the total female and 81% of the adult female population sterilized at all times. In the absence of juvenile sterilization, 91% of adult intact females would need to be sterilized annually to halt population growth. In comparison, with a 3-year nonsurgical contraception program, an annual contraception rate of 60% of female juvenile and adult intact cats would be required to halt population growth, assuming that treated cats were retrapped at the same rate after 3 years.

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Free-roaming cats are a problem in many locations. Feral cats are free-roaming cats who are too unsocialized to be placed into a typical companion-animal home (Slater, 2004). Feral cats are part of the companion-animal overpopulation problem because they may be trapped and brought to shelters where euthanasia is the most common outcome. There are also concerns about the welfare of the cats as well as issues related to public health, predation of wildlife, and nuisance complaints. In order to design effective population-control programs, knowledge about the population dynamics of feral cats (the study of the factors that affect the growth, stability, and decline of populations) is crucial.

Sterilization, as part of a comprehensive trap, neuter, and return (TNR) program, is one option for controlling population growth. Data about population growth in feral cat colonies and TNR programs on these populations are limited (Natoli et al., 2006). Mathematical models are one way to evaluate population dynamics when limited data are available. Although population models have been used for a number of years to study wildlife populations, these models are only now beginning to be used for companion-animal populations. Thus far, very few studies have attempted to model the impact of TNR or removal programs on feral cat populations (Andersen, Martin, & Roemer, 2004; Foley, Foley, Levy, & Paik, 2005; Nassar & Fluke, 1991; Short & Turner, 2005). Of the currently available models, none have endeavored to evaluate how a 3-year, nonsurgical contraception program may affect feral cat population growth as compared with a traditional surgical sterilization-based TNR program.

Matrix population models are a specific type of population model that use matrix algebra and estimated stage-specific rates for fecundity and survival to project future population structure. This means that matrix models divide nonhuman animal populations into groups or life stages. In this study, cats were divided into juveniles (<1 year old) and adults; different fecundity and survival rates based on the existing data were used for these two life stages. A second reason to divide feral cat populations into two life stages is the idea that sterilizing a cat before she can give birth should provide the most efficient method of decreasing long-term population growth. Fecundity is a measurement of reproductive success, defined for this study as the number of female kittens/year/female cat. Survival is defined as the proportion of cats in that life stage who survive to the next year. Annual survival is related to life span as follows: Annual survival (S) $= \exp(ln[1 - p]/t)$

Where p is the probability that an individual will die by time (t), matrix models provide an estimate of lambda (λ), the dominant eigenvalue of the population matrix, also known as the intrinsic population growth rate. If λ is >1, the population is increasing. If $\lambda = 1$, the population is stable, with no net change in population size, and if $\lambda < 1$, the population is decreasing.

For this study, matrix population models were constructed to explore feral cat population growth for a generic, hypothetical cat population (a) in the absence of intervention, (b) with a traditional surgical sterilization-based TNR program, and (c) with a 3-year single treatment nonsurgical contraception program with and without retrapping.

METHOD

Using commercially available software Excel (Microsoft Corp., Redmond, WA) and Poptools (CSIRO, Clayton, Australia), matrix population models were constructed to evaluate no-intervention surgical sterilization and 3-year contraception in feral cat populations. Because the goal was to develop basic generic models that could compare interventions and illustrate the inherent variability of feral cat populations, certain assumptions were made:

1. A closed population (no immigration/emigration);
2. A single intermingling breeding population;
3. Half-year survival rates (births take place midway through the time interval; therefore, only reproductively active females who survive to midyear reproduce in that year);
4. No seasonality to breeding;
5. No carrying capacity;
6. Fertile males available;
7. Only sterilized females modeled (the effect of male neutering is not considered);
8. Female sterilization by single-contraceptive injection for 3 years; and
9. Nonsurgical contraception 100% efficacious.

Life cycle parameters (vital rates) included in the model were juvenile fecundity, adult fecundity, juvenile survival, and adult survival. Due to the variability in literature-suggested values for these parameters, a range of values was employed (Table 1a). Diagrammatic representations of the matrices for no intervention, surgical sterilization, and 3-year nonsurgical contraception can be found in the Appendix.

Annual surgical sterilization and nonsurgical contraception rates of 10%, 20%, and 30% of intact juvenile female cats (<1 year of age) and the same percentage of adult intact female cats were modeled. These percentages were selected as being possible to implement across large areas rather than in a single colony. The sterilization rates assumed that each year the appropriate percentage of juvenile and previously unsterilized adult females were trapped and sterilized. Cats treated with a nonsurgical contraceptive were assumed to regain fertility after 3 years. Models were run in the absence of retrapping cats previously treated with the nonsurgical contraceptive agent. In addition, it was assumed

TABLE 1a
Calculations for Fecundity

- Adult fecundity
  - 3.6 kittens/dam (Scott, Levy, & Crawford, 2002)
  - 1.1–2.1 litters/female (Levy, Gale, & Gale, 2003; Scott et al., 2002)
  - sex ratio—50:50
    - Fecundity (adults-low)—(3.6)(1.1)(0.5) = 1.98 female offspring/year
    - Fecundity (adults-high)—(3.6)(2.1)(0.5) = 3.78 female offspring/year
- Juvenile fecundity
  - mean age at first conception—212 days (high), 300 days (low) (Jöchle & Jöchle, 1993; Nutter, Levine, & Stoskopf, 2004)
    - Fecundity (juvenile-low)—((365–300)/365) × 1.98 = 0.352 female offspring/year
    - Fecundity (juvenile-high)—((365–212)/365) × 3.78 = 1.58 female offspring/year

that the same percentages of these cats are retrapped annually as the general adult and juvenile populations. No version was run with a targeted effort to retrap more than the same percentage of fertile cats to be treated that year.

To better understand the possible range of population growth based on the various estimates of fecundity and survival (Table 1b), different combinations of each were chosen.

TABLE 1b
Parameters Utilized in the Models

Parameter	*Value*	*Reference*
Survival of juveniles to age 1 (S_0)		
Low value	0.27	Warner, 1985
Mid value	0.46	Feldman, 1993
High value	0.73	Jöchle & Jöchle, 1993
Annual adult survival (S_1)		
Low value	0.55	Warner, 1985 (geometric mean age 1 year to 7+ years)
Mid value	0.70	Baldock, Alexander, & More, 1979 (geometric mean)
High value	0.78	Warner, 1985 (highest relative survival)
Juvenile fecundity (F_0)		
Low value	0.352	See Table 1a
Mid value	0.745	Geometric mean of high and low value
High value	1.58	See Table 1a
Adult fecundity (F_1)		
Low value	1.98	Andersen, Martin, & Roemer, 2004
Mid value	2.52	Geometric mean of high and low value
High value	3.78	Andersen et al., 2004

Combinations of parameter values assessed included the following:

1. Midrange fertility with high survival;
2. Midrange fertility with midrange survival;
3. Midrange fertility with low survival;
4. Low fertility with midrange survival;
5. High fertility with midrange survival;
6. Low fertility with low survival; and
7. High fertility with high survival.

Each model utilized a hypothetical starting population of 100 adult intact female cats, with the population projected for 10 years, using a 1-year time step. As is customary with population dynamics models, only females are represented in the models.

Sensitivity analysis was performed utilizing matrix elasticities. This provides information on which parameters have the most influence on population growth. Elasticity values were calculated for all combinations of fecundity and survival evaluated. Elasticity analysis allows for the evaluation of how small changes in vital rates (survival and fecundity) affect a population's growth rate. This is done by computing the partial derivative of the intrinsic growth rate (λ) with respect to each individual vital rate while keeping the other vital rates constant. These partial derivatives are also known as sensitivity values (Caswell, 2000). When these values are multiplied by the ratio of the vital rate in question to λ, these values are termed elasticities. Vital rates with higher elasticities tend to contribute more to population growth. Management strategies are anticipated to have a higher impact when they affect vital rate parameters with higher elasticity values. Because reproduction is a composite parameter made up of both fecundity and survival (a female cannot reproduce if she has not survived), the elasticity of λ was calculated in respect to the vital rates (juvenile fecundity, adult fecundity, juvenile survival, and adult survival) rather than the matrix elements. The larger the elasticity, the greater influence that parameter had on overall intrinsic population growth.

RESULTS

Due to the large number of combinations of survival and fecundity parameters evaluated, graphic outputs are displayed only for the population, assuming midrange fertility and high survival rates; this approximates an average 3-year life span (Figures 1 and 2). However, the intrinsic population growth rate (λ) for each modeled population can be found in Table 2. Intrinsic population growth rates are given for all populations in the absence of intervention and with 10%,

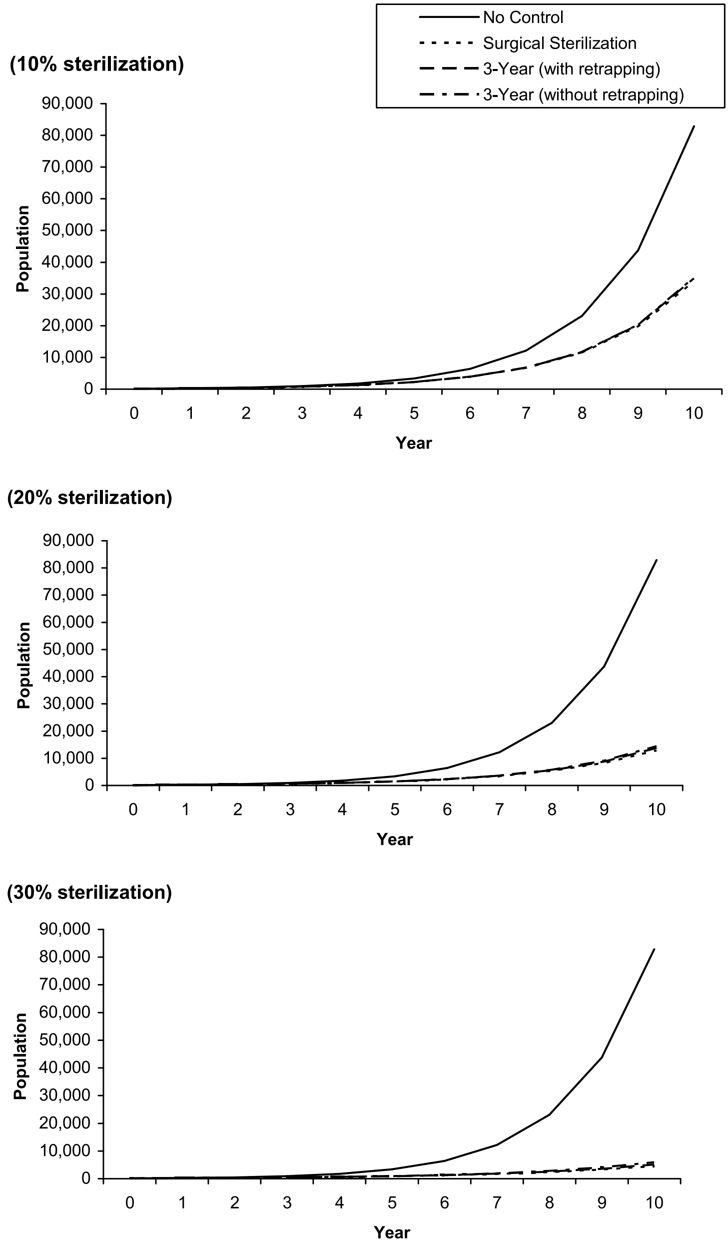

FIGURE 1 Projected population growth for no control surgical sterilization and 3-year single treatment, nonsurgical contraception assuming midrange fecundity and high survival values and 10% sterilization/contraception (top), 20% sterilization/contraception (middle), or 30% sterilization/contraception (bottom).

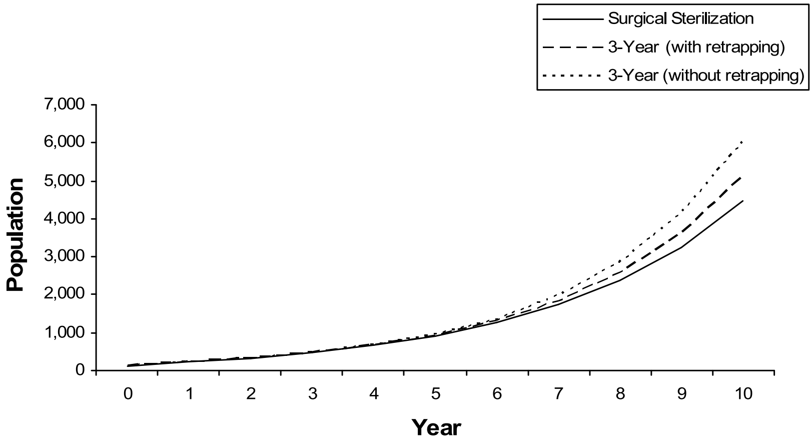

FIGURE 2 Close-up figure of projected population growth for 30% surgical sterilization and 30% 3-year single treatment, nonsurgical contraception assuming midrange fecundity and high survival values.

TABLE 2
Sensitivity Analysis for the Various Models, Including Intrinsic Growth Rate (λ) and Elasticity Analysis. Lambda Values for 3-Year Single Treatment Contraception Include No Retrapping and Retrapping at the Same Prevalence (in Parentheses)

Model	λ	*Elasticities*
Mid fecundity, high survival		
No intervention	1.89	$F_0 = 0.13$, $F_1 = 0.32$,
Surgical		$\mathbf{S_0 = 0.61}$, $S_1 = 0.39$
10%	1.72	
20%	1.54	
30%	1.37	
3-Year contraception		
10%	1.73 (1.73)	
20%	1.58 (1.56)	
30%	1.45 (1.41)	
Mid fecundity, mid survival		
No intervention	1.38	$F_0 = 0.093$, $F_1 = 0.30$,
Surgical		$\mathbf{S_0 = 0.55}$, $S_1 = 0.45$
10%	1.26	
20%	1.13	
30%	1.00	
3-Year contraception		
10%	1.28 (1.27)	
20%	1.19 (1.17)	
30%	1.12 (1.07)	

(*continued*)

TABLE 2
(*Continued*)

Model	λ	*Elasticities*
Mid fecundity, low survival		
No intervention	0.94	$F_0 = 0.26$, $\mathbf{F_1 = 0.65}$,
Surgical		$S_0 = 0.46$, $S_1 = 0.55$
10%	0.86	
20%	0.78	
30%	0.69	
3-Year contraception		
10%	0.87 (0.87)	
20%	0.81 (0.80)	
30%	0.76 (0.72)	
High fecundity, mid survival		
No intervention	1.71	$F_0 = 0.17$, $F_1 = 0.33$,
Surgical		$\mathbf{S_0 = 0.44}$, $S_1 = 0.37$
10%	1.55	
20%	1.39	
30%	1.24	
3-Year contraception		
10%	1.56 (1.56)	
20%	1.43 (1.41)	
30%	1.31 (1.27)	
Low fecundity, mid survival		
No intervention	1.20	$F_0 = 0.054$, $F_1 = 0.25$,
Surgical		$\mathbf{S_0 = 0.63}$, $S_1 = 0.52$
10%	1.09	
20%	0.98	
30%	0.87	
3-Year contraception		
10%	1.12 (1.11)	
20%	1.06 (1.03)	
30%	1.02 (0.96)	
Low fecundity, low survival		
No intervention	0.83	$F_0 = 0.032$, $F_1 = 0.24$,
Surgical		$\mathbf{S_0} = 0.24$, $S_1 = \mathbf{0.48}$
10%	0.81	
20%	0.74	
30%	0.66	
3-Year contraception		
10%	0.77 (0.77)	
20%	0.72 (0.71)	
30%	0.68 (0.65)	
High fecundity, high survival		
No intervention	2.42	$F_0 = 0.27$, $F_1 = \mathbf{0.29}$,
Surgical		$\mathbf{S_0 = 0.29}$, $S_1 = 0.14$
10%	2.19	
20%	1.97	
30%	1.74	
3-Year contraception		
10%	2.20 (2.20)	
20%	1.98 (1.98)	
30%	1.78 (1.76)	

Note. F_0 = juvenile fecundity; F_1 = adult fecundity; S_0 = juvenile survival; S_1 = adult survival. Parameters in bold are expected to have the greatest influence on the intrinsic rate of population increase.

20%, and 30% of the intact female juvenile and adult cat population surgically sterilized annually as well as with 10%, 20%, and 30% of the intact female juvenile and adult cat population treated with a nonsurgical contraceptive agent annually.

Cessation of population growth ($\lambda = 1$) would require that greater than 51% of adult and 51% of juvenile female intact cats be surgically sterilized annually, assuming midrange fertility and an approximate mean lifespan of 3 years. After the population has stabilized, this would equate to sterilizing approximately 14% of the total female population per year or having approximately 71% of the total female and 81% of the adult female population sterilized at all times. In the absence of juvenile sterilization, 91% of adult intact cats would need to be sterilized annually in order to prevent population growth.

In contrast, with a 3-year nonsurgical contraception program, an annual female juvenile and adult contraception rate of 60% of intact cats would be required to halt population growth, assuming that cats previously treated were retrapped at the same rate after 3 years. In the absence of retrapping cats who become refertile after 3 years, cessation of population growth would be unlikely ($\lambda = 1.09$) with nonsurgical contraception alone, assuming midrange fertilities and a 3-year mean survival.

DISCUSSION

Evaluation of the matrix models suggests that achieving zero ($\lambda = 1$) or negative ($\lambda < 1$) growth in a very large feral cat population may be unrealistic in certain populations, given the massive undertaking necessary to sterilize the often-required number of animals. It may, however, still be possible to drastically decrease population growth over time with lower sterilization rates. There are very few studies that have looked at the long-term (greater than 5 years) impact of an extensive TNR program. A study conducted in urban areas of Rome, Italy, did appear to show a decrease in overall feral cat populations after 10 years of a government-supported TNR program (Natoli et al., 2006). However, it is not possible to determine colony-specific sterilization rates from this study.

In a subset of colonies, from this study, it does appear that a sterilization rate of approximately 66% was achieved after 2 to 6 years of TNR, with a 22% decrease in the total population of all of the colonies combined. Actual per-colony sterilization rate and population growth or decrease are, however, not available. Traditionally, the literature has stated the necessity of achieving a 70%+ sterilization rate to stop population growth (Andersen et al., 2004; Foley et al., 2005; Nassar & Mosier, 1982). The current models also indicate that a very high sterilization rate (approximately 71% of the female population, including both juveniles and adults, needs to be sterilized at all times) must be achieved to halt population growth; assuming the most likely midrange fecundity and mean 3-year life span, this might not be the most practical immediate goal. These models also assume that juvenile sterilization is an important aspect of a TNR program. Without juvenile sterilization, it was estimated that approximately 91% of intact adult female cats would have to be sterilized annually to halt population growth. Therefore, it is crucial to focus a component of the intervention on cats less than 1 year of age to have the greatest impact on growth rate.

Models were based on sterilizing a proportion of adult and juvenile intact animals annually versus a preset number of animals. For larger populations, a larger number of animals would need to be sterilized per year, which may not be logistically feasible in some areas. Table 3 illustrates the actual number of female cats sterilized for each intervention assuming a 30% sterilization rate. As sterilization rates become higher, the total number of cats who need to be sterilized actually starts to decrease as the overall population size decreases. Therefore, a higher sterilization rate might require more effort in the initial years of the program; in the long run, however, fewer animals would actually need to be sterilized.

Because a generic feral cat population was being modeled, a number of assumptions were made. Modeled growth rates were based on published intrinsic growth rates of cats (Table 1b). For the span of the 10 years of our models, we assumed no other influences on growth except for the interventions. However, we expect that cat populations, like other mammal populations, have factors that slow growth over time. One factor that slows growth is the carrying capacity, the innate ability of a location to support a certain number of animals based on food and shelter. We can make a valid case for a carrying capacity for cats where food and shelter are restricted, but we have no data on what a given carrying capacity for cats is for a specific type of location. Therefore, we did not include the influence of carrying capacity on growth in these models.

The second major factor that limits growth of populations is some type of catastrophic event. This could be climate-related like hurricanes, floods, and drought or health-related such as a disease epidemic. It is plausible that some cat populations are dramatically decreased when the population density reaches a certain level because it makes it more likely for an infectious disease like feline panleukopenia or upper respiratory diseases to sweep through the population and kill the young, the old, and the ill or injured. We selected a relatively short time frame for the models (10 years) with the recognition that exponential growth would not likely occur across a more extended period.

Matrix models traditionally model only the female of the species. This is based on the assumption that there are enough males to provide breeding services to all the females and that the males are not geographically or behaviorally constrained from finding the intact females. This would seem a reasonable assumption for feral cats.

TABLE 3
Projected Population Numbers and Number of Juvenile and Adult Female Cats Sterilized or Contracepted, Assuming Midrange Fecundity and High Survival Values, for 30% Surgical Sterilization and 30% 3-Year Single Treatment Nonsurgical Contraception

	Surgical Sterilization (30%): λ = 1.37						
Year	*Juvenile Pop. in That Year*	*Adult (NS) Pop. in That Year*	*Adult (S) Pop. in That Year*	*Total Annual Pop.*	*Juveniles Sterilized in That Year*	*Adults Sterilized in That Year*	*Total Sterilized in That Year*
0	0	100	0	100			
1	158	55	23	236	0	23	23
2	147	111	66	323	35	13	47
3	231	135	109	475	32	26	58
4	302	192	167	661	51	32	82
5	418	259	242	919	66	45	111
6	569	355	341	1,265	92	61	152
7	779	485	473	1,737	125	83	208
8	1,063	662	653	2,379	170	113	284
9	1,453	905	897	3,255	233	155	388
10	1,985	1,236	1,230	4,451	318	212	530
						Total	1,884

	3-Year Single Treatment Nonsurgical Contraception Assuming No Retrapping (30%): λ = 1.45						
Year	*Juvenile Pop. in That Year*	*Adult (NS) Pop. in That Year*	*Adult (S) Pop. in That Year*	*Total Annual Pop.*	*Juveniles Contracepted in That Year*	*Adults Contracepted in That Year*	*Total Contracepted in That Year*
0	0	100	0	100			
1	158	55	23	236	0	23	23
2	147	111	66	323	35	13	47
3	231	135	109	475	32	26	58
4	302	192	167	661	51	32	82
5	442	275	225	943	66	45	111
6	645	395	318	1,358	97	61	157
7	937	576	451	1,964	141	86	227
8	1,365	835	650	2,849	205	124	329
9	1,979	1,215	939	4,134	299	180	479
10	2,870	1,765	1,360	5,996	433	261	695
						Total:	2,209

	3-Year Single Treatment Nonsurgical Contraception Assuming Retrapping (30%): λ = 1.41						
Year	*Juvenile Pop. in That Year*	*Adult (NS) Pop. in That Year*	*Adult (S) Pop. in That Year*	*Total Annual Pop.*	*Juveniles Contracepted in That Year*	*Adults Contracepted in That Year*	*Total Contracepted in That Year*
0	0	100	0	100			
1	158	55	23	236	0	23	23
2	147	111	66	323	35	13	47
3	231	135	109	475	32	26	58
4	302	192	167	661	51	35	86
5	428	271	230	929	66	51	117
6	600	380	323	1,303	94	67	161
7	844	535	451	1,830	131	93	224
8	1,187	753	632	2,572	185	128	313
9	1,669	1,060	887	3,615	260	180	439
10	2,346	1,491	1,246	5,083	365	252	617
						Total:	2,086

Note. Pop. = population; NS = nonsterilized or noncontracepted; S = sterilized.

The models utilized in this study did not assume immigration/emigration due to lack of available data and the large variability between feral cat populations. Instead, a closed population was assumed. We recognize that, in reality, few cat populations are closed (there is usually some immigration or emigration between owned and feral cats, even if the feral cats are geographically isolated). Because the primary objective of this study was to compare a traditional surgical-based TNR program with a proposed 3-year, nonsurgical contraception program, these assumptions should not affect this comparison.

We assumed a single breeding population for the model. This means that all the cats in the population could intermingle and were considered one group. However, there are many ways to define the population of interest for a specific intervention or program. The population could be (a) the colony of cats fed behind a restaurant, (b) the cats living in a park, (c) the cats in a four-block square area, (d) the cats in a small town or community, or (e) the cats in a city or county. Defining a population that can be readily identified and where the intervention can be applied to 10% or 30% of juvenile and adult cats will be crucial if the results of these models are to begin to be extrapolated to the real world. There tends to be a seasonal component to feral cat breeding; however, because of the possibility of seasonal differences between feral cat-colony locations this was also not taken into account (Hurni, 1981; Scott, Levy, & Crawford, 2002).

The modeled 3-year contraception program was successful in reducing population growth for all scenarios tested. No difference was seen between surgical sterilization and nonsurgical contraception in the first years of the program, assuming the same proportion of cats was sterilized or contracepted and that nonsurgical contraception was 100% efficacious. Only after 3 years would there start to gradually be differences between the two interventions. Long-term impact of a 3-year contraception program depends on average life span (survival) of the population and percentage of cats who would be retreated after the nonsurgical contraceptive is no longer active. Table 3 illustrates the subtle difference between no retrapping and retrapping 30% of cats previously treated with the contraceptive agent. The differences begin to appear in the number of adults treated in Year 4.

Ten-year population size was always smaller with surgical sterilization, assuming that not all cats treated with the contraceptive agent would be retrapped or die within 3 years; however, differences in population growth between the use of surgical sterilization and 3-year nonsurgical contraception were relatively small compared with the no-intervention scenarios. For example, after 10 years of a sustained surgical control program (with a starting population of 100 intact adult females) that sterilized 30% of the intact juvenile and adult female population annually, a total of approximately 1,884 cats would be surgically sterilized with a final population of 4,451. In comparison, after 10 years of a sustained 3-year nonsurgical contraception program, if no retrapping occurred, 2,209 animals would be treated with a final population of 5,996 (Figure 1). Although still representing substantial population growth, this low contraception rate produces a large impact when compared with a 10-year population of 82,882 in the absence of control.

It is clear from the variation in fecundity and survival in the published literature that cat-population dynamics are highly variable from location to location. The variability in vital rates may be influenced by food, shelter, climate, population density, genetics, predation, and myriad other factors. Data on specific populations are needed before a more exact level of sterilization or contraception can be determined. This is particularly important for the 3-year nonsurgical contraceptive, where longer survival times would have a strong, positive effect on population growth and limit the utility of this approach without substantial retrapping efforts.

Models can be tailored to assess specific feral cat colonies or populations if data on fecundity, survival, immigration, and emigration are available. Because even colony-specific data are often variable, stochastic methods can be utilized to account for some of this inherent variability. The next logical step would then be to use population-growth projections to perform a cost-benefit analysis for a 3-year contraception program compared with a traditional surgery-based program employing the various contraception and sterilization rates. The potential for a program incorporating both traditional surgical sterilization and 3-year nonsurgical contraception also exists and will need to be explored, especially for populations with higher survival rates.

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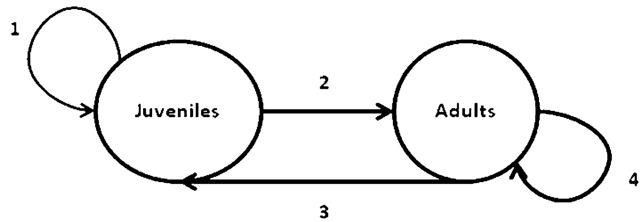
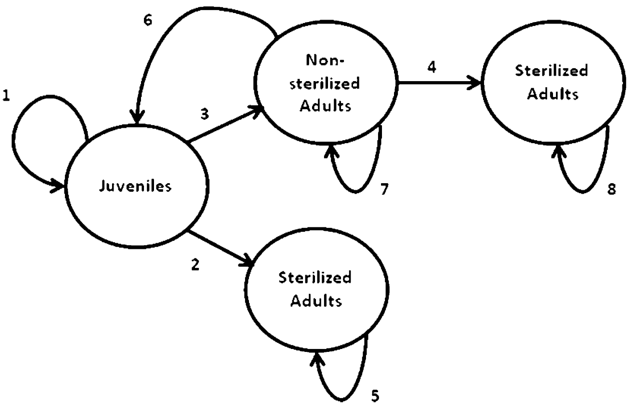
APPENDIX

Diagrammatic Representation of the Matrix Model for No Intervention



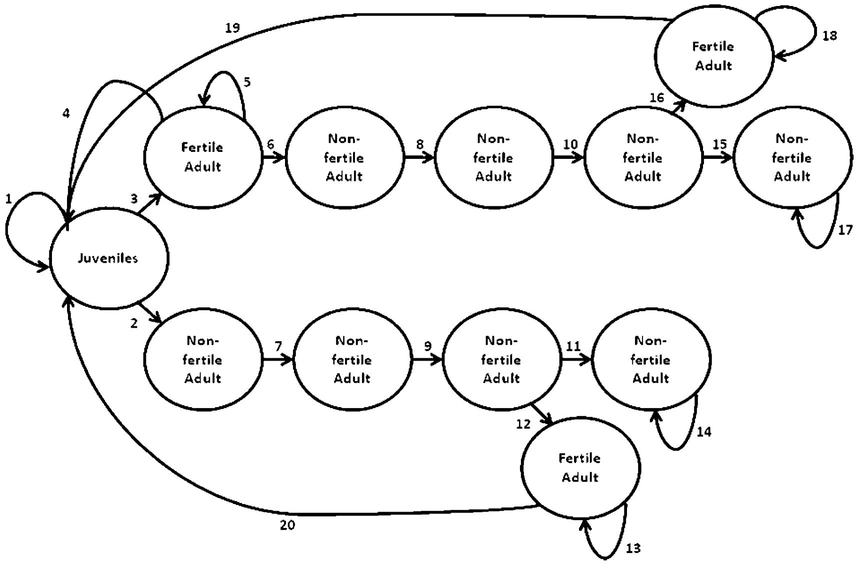
1. Juvenile fecundity × Juvenile survival
2. Juvenile survival
3. Adult fecundity × SQRT(Juvenile survival) × SQRT(Adult survival)
4. Adult survival

Diagrammatic Representation of the Matrix Model for Surgical Intervention



1. Juvenile fecundity × Juvenile survival × (1 − Juvenile sterilization rate)
2. Juvenile survival × Juvenile sterilization rate
3. Adult survival − (Juvenile sterilization rate × Juvenile survival)
4. Adult survival × Adult sterilization rate
5. Adult survival
6. (Juvenile fecundity × SQRT(Juvenile survival) × SQRT(Adult survival) × (1 − Adult survival × Adult sterilization rate)
7. Adult survival − Adult sterilization rate × Adult survival
8. Adult survival

Diagrammatic Representation of the Matrix Model for 3-Year Nonsurgical Contraception



1. Juvenile fecundity × Juvenile survival × (1 − Juvenile contraception rate)
2. Juvenile survival × Juvenile contraception rate
3. Adult survival − (Juvenile survival × Juvenile contraception rate)
4. (Juvenile fecundity × SQRT(Juvenile survival) × SQRT(Adult survival) × (1 − Adult survival × Adult contraception rate)
5. Adult survival − (Adult survival × Adult contraception rate)
6. Adult survival × Adult contraception rate
7. Adult survival
8. Adult survival
9. Adult survival
10. Adult survival
11. Adult survival × Retrap rate
12. Adult survival − (Adult survival × Retrap rate)
13. Adult survival
14. Adult survival
15. Adult survival × Retrap rate
16. Adult survival − (Adult survival × Retrap rate)
17. Adult survival
18. Adult survival
19. Adult fecundity × SQRT(Adult survival) × SQRT((Adult survival) × (1 − Retrap rate))
20. Adult fecundity × SQRT(Adult survival) × SQRT((Adult survival) × (1 − Retrap rate))