Effect of TNR Rates on the Population Dynamics of Cats

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1 Introduction

In many communities across the United States, the management of urban feral cat populations is a concern. While there is much debate concerning the ethics of management programs (the main two being Trap, Neuter, Return (TNR) and Trap, Euthanize (TE)), most agree that feral cat populations should be controlled to some extent [5]. Feral cats hunt and kill native wildlife, including birds and small mammals, and are vectors for various diseases [5]. At the same time, many humans enjoy the company of feral cat colonies and help contribute resources like shelter and food. In situations where euthanization is not practiced (often because it is seen as unethical), TNR is often pursued. It ensures that feral cats have the chance to live while hopefully decreasing the population over time via reducing the reproduction rates.

The city of Lubbock, Texas has a significant feral cat population. According to Zachary Kohler of Kat's Alley Cats, a Lubbock nonprofit organization devoted to reducing feral cat overpopulation, notes that if left un-checked, the feral cat population could reach as much as 420,000 [1]. The goal of this project was to model the Lubbock feral cat population and determine the effect of spay/neuter rate on its dynamics.

To this end, Kat's Alley Cats and another Lubbock organization, Lubbock Animal Services, generously provided shelter intake data to the Spring 2025 Math Locally class at Texas Tech University. This data includes sex, spay/neuter status, time in shelter, and age. Using this data, we were able to create data-informed models and analysis of the Lubbock feral cat population.

2 Parameters

In order to determine the parameter values for our models, we referred to the existing literature on feral cats and created our own estimates based on real data. This is the approach of other feral cat models, including the bioeconomic model of Thompson et al. [5]. We consulted the websites of organizations including the Feral Cat Association, The Humane Society of the United States, and Cats in Action.

A significant predictor of feral cat lifespan is whether they are spayed or neutered. For an altered cat, the lifespan of a cat is typically 7-10 years, compared to 2-3 years for an unaltered cat [2]. Exposure to disease, the rigors of childbirth in the wild, and other challenges contribute to a shorter lifespan. To calculate our values for μ, we simply divided 1 by the expected lifespan of the cat (in months).

Kittens have a particularly high death rate - according to the Feral Cat Project, 75% of kittens die before reaching 6 months of age [4]. This high death rate is corroborated by Thompson et al., who omit newborn abandonment for this reason [5]. To convert this to a monthly rate, we consider an initial population of kittens (K_0), the population of kittens after 6 months (K_6), and the monthly kitten survival rate (r):

$$K_6 = (0.25)K_0 = K_0 r^6$$

We solve for r:

$$0.25 = r^6$$
$$0.7937 \approx r$$

And since r is the monthly survival rate, we subtract it from 1 to get our monthly death rate for kittens (μ_K):

$$(1 - r) \approx 0.206 = \mu_K$$

For our reproduction rates α, we instituted a low end of 1.4 litters per year of 3 kittens each, reported by the Feral Cat Project [4]. Dr. Fielding D. O'Niell of Tuckahoe Veterinary Hospital names a slightly higher figure, citing an average of 1.6 litters and 5 kittens per litter per year [3]. To calculate α, we divided the number of kittens an unaltered cat is expected to produce in a year by 12.

Since our main question concerned the effect of spay rate on cat population dynamics, we used many different values for s, ranging from 0.25 to 2. As for the months to maturity, we used 6 months in order to align with the 75% death rate we incorporated. Our abandonment numbers matched reasonable rates we inferred from the local data.

In order to find the proportion of unaltered cats in the population, we used the cats taken in by Lubbock Animal Services as a representative sample. We determined the ratio of unaltered to total cats taken in by month and from there found the monthly average proportion of unaltered cats. This also informed what proportion of the abandonments belonged to each cat population.

Below is a table summarizing our parameter values:

	Description	**Value**	**Source**
α	Reproduction rate	0.667	Feral Cat Project/Tuckahoe
μ_U	Unaltered cat death rate	0.019	Cats in Action
μ_A	Altered cat death rate	0.008	Cats in Action
μ_K	Kitten death rate	0.206	Feral Cat Project/calculation
s	Spay/neuter rate	0.25 - 2	Data (KAC)
m	Months to maturity (kittens)	6	Feral Cat Project
a	Abandonment	5	Estimate: local sources
a_X	Proportion of abandonment from X	Varies	Proportion from Data (LAS)

Table 1: A summary of the main parameters used.

3 Single Population Beverton-Holt Model

We begin by considering the total population of cats in an area, N, which undergoes death during a long continuous period followed by a short discrete period of growth from reproduction. This is the basis of the Beverton-Holt Model used in discrete modeling of populations. We formulate our model as

$$\frac{dN}{dt} = -\mu N^2,$$
$$N^+ = N + \alpha S N,$$

where N^+ is the total population after the discrete reproduction. μ is the natural death rate of cats in the area, α is the reproduction rate of cats, and S is the proportion of reproductive cats in the population. To get the population at the end of the next reproduction cycle we must solve the differential equation then apply the discrete equation. We solve the differential equation at $t = 1$ as

$$N(1) = \frac{N_0}{1 + \mu N_0}.$$

After applying the discrete equation, defining $N_{t+1} := N(1)$ and $N_t := N_0$ we get the solution to our Single Population Beverton-Holt Model,

$$N_{t+1} = \frac{(1 + \alpha S)N_t}{1 + \mu N_t}. \tag{1}$$

Now that we have our model, two key questions must be answered: What are the fixed points and what are their stability? We begin by finding the fixed points by setting $N^* = N_{t+1} = N_t$ and solving for N^*.

$$N^* = \frac{(1 + \alpha S)N^*}{1 + \mu N^*}$$

solved for N^* yields

$$N^* \left(N^* - \frac{\alpha S}{\mu} \right) = 0,$$

thus the fixed points are $N_1^* = 0$ and $N_2^* = \frac{\alpha S}{\mu}$. A fixed point in a discrete model is stable if $|f'(N^*)| < 1$ where $f(N)$ is the right hand side of the discrete model. Similarly a fixed point is unstable if $|f'(N^*)| > 1$. For our model we find that

$$f'(N) = \frac{1 + \alpha S}{(1 + \mu N)^2}.$$

The values of $f'(N)$ at the fixed points are

$$f'(0) = 1 + \alpha S$$

and

$$f' \left(\frac{\alpha S}{\mu} \right) = \frac{1}{1 + \alpha S}.$$

Since $\alpha > 0$ is the reproduction rate and $S > 0$ is the proportion of reproductive cats $1 + \alpha S > 1$. Therefore

$$|f'(0)| = |1 + \alpha S| > 1$$

and

$$\left| f'\left(\frac{\alpha S}{\mu}\right) \right| = \left| \frac{1}{1+\alpha S} \right| < 1.$$

Therefore, we have shown that $N_1^* = 0$ is unstable while $N_2^* = \frac{\alpha S}{\mu}$ is stable, which is similar to the traditional Beverton-Holt model and logistic equation from differential equations.

We present numerical simulations of the single population Beverton-Holt model (1) in Figure 1, which shows how changes in model (1) parameters and initial population size affect the total feral cat population.

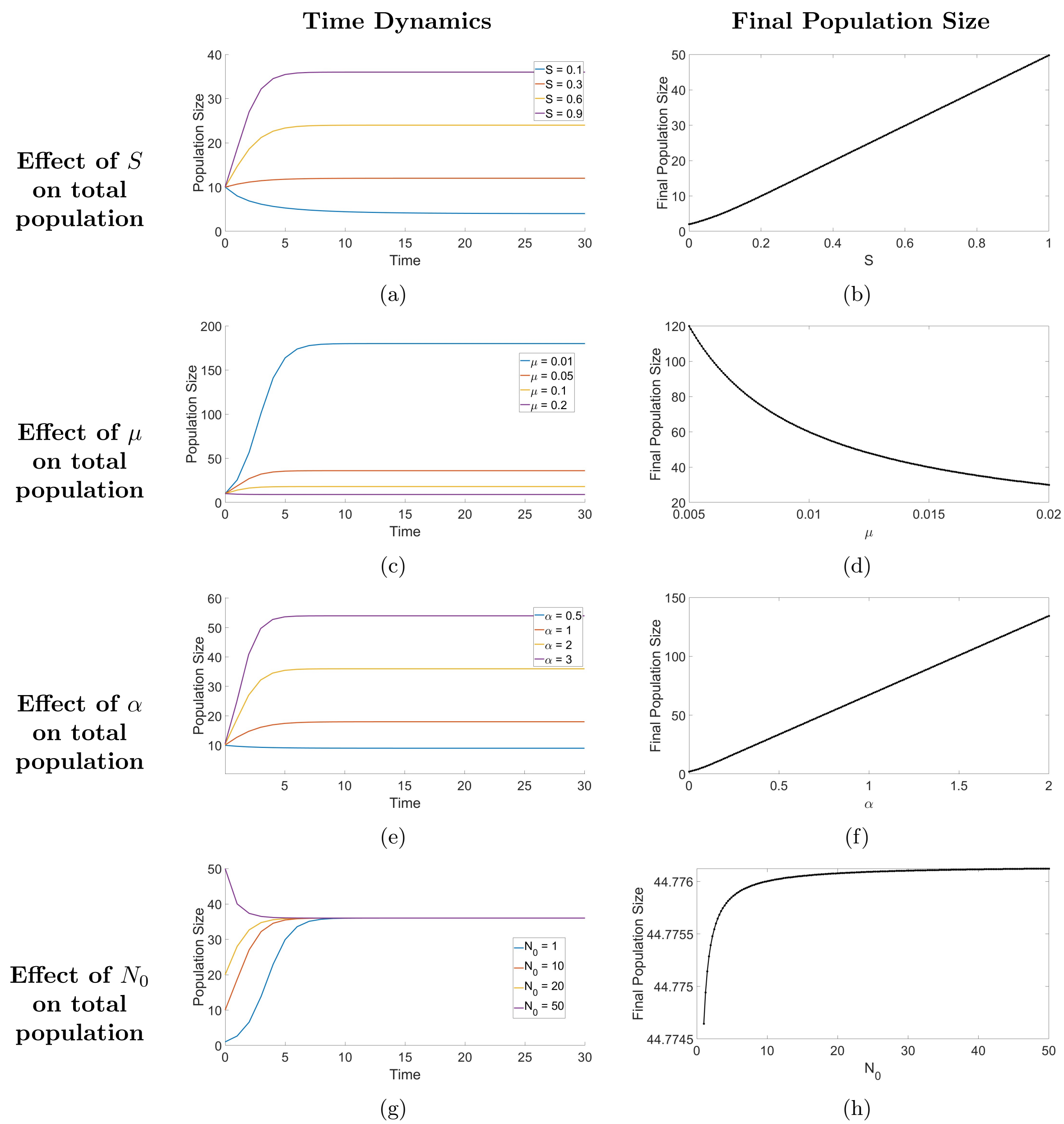


Figure 1: Beverton–Holt single population dynamics under varying parameters. Time series and final population sizes are shown as functions of the reproductive proportion (S), natural death rate (μ), reproduction rate (α), and initial population size (N_0). Simulations were conducted for 30 months.

In Figure 1, the total cat population, displayed in the left column, varies over time in response to changes in key parameters, illustrating how different values of S, μ, α, and N_0 influence the population growth, while the right column shows the corresponding final population sizes, highlighting the long-term impact each parameter has on population equilibrium as the respective parameter increases within the defined range.

As the reproductive proportion S increases, the population grows faster and reaches a higher final size, as seen in Figures 1(a) and (b), since more individuals are reproducing. Figures 1(c) and (d) show that increasing the natural death rate μ causes a clear drop in population sizes. In Figures 1(e) and (f), reproduction rate (α) leads to a faster population growth. Lastly, Figures 1(g) and (h) reveal that while changes in the initial population size N_0 affect early behavior, the population eventually settles at approximately the same level. This suggests long-term outcomes depend more on parameters like S, μ, and α than on the initial population.

4 Two Population Beverton-Holt Model

After making a single population model in the style of a Beverton-Holt model, we consider two populations of cats, Altered and Unaltered. We let A represent the population of altered cats and U represent the population of unaltered. We set $N = A + U$ as A and U are mutually exclusive collectively exhaustive subpopulations. Therefore, the combined differential equation is

$$\frac{dA}{dt} + \frac{dU}{dt} = \frac{dN}{dt} = -\mu N^2 = -\mu(A+U)^2 = -\mu A(A+U) - \mu U(A+U).$$

Recall that S is the proportion of reproductive cats in the total population, therefore, we define $S := \frac{U}{A+U}$. The combined discrete reproduction equation is

$$A^+ + U^+ = N^+ = N + \alpha S N = A + U + \alpha \frac{U}{A+U}(A+U) = A + U + \alpha U.$$

In this model we introduce trap-neuter-return to the dynamics represented by s, the number of neuters and spays each month. Putting together everything we get the system

$$\begin{aligned}
\frac{dA}{dt} &= -\mu A(A+U) \\
\frac{dU}{dt} &= -\mu U(A+U) \\
A^+ &= A + \min(s, U) \\
U^+ &= U + \alpha U - \min(s, U)
\end{aligned}$$

to describe the dynamics between the two populations. Using similar techniques as in Section 3, we find the population after each month to be

$$\begin{aligned}
A_{t+1} &= \frac{A_t}{1 + \mu(A_t + U_t)} + \min(s, U_t) \\
U_{t+1} &= \frac{(1+\alpha)U_t}{1 + \mu(A_t + U_t)} - \min(s, U_t).
\end{aligned} \tag{2}$$

Due to the complexity of the model, finding fixed points for arbitrary α, μ, s for which $A > 0$ and $U > 0$ is difficult. If $U_t < s$, then $A^* = 0, U^* = 0$ is a fixed point of the system. Therefore analyze the local stability of $(A^*, U^*) = (0, 0)$ in a sufficiently small neighborhood. We take the Jacobian of the system of equations with $U_t < s$ to begin the stability analysis of $(0, 0)$.

$$J(A, U) = \begin{bmatrix} \dfrac{1 + \mu U}{(1 + \mu(A + U))^2} & \dfrac{-\mu A}{(1 + \mu(A + U))^2} + 1 \\ \dfrac{-(1 + \alpha)\mu U}{(1 + \mu(A + U))^2} & \dfrac{(1 + \alpha)(1 + \mu A)}{(1 + \mu(A + U))^2} - 1 \end{bmatrix}$$

We then find the eigenvalues and vectors of

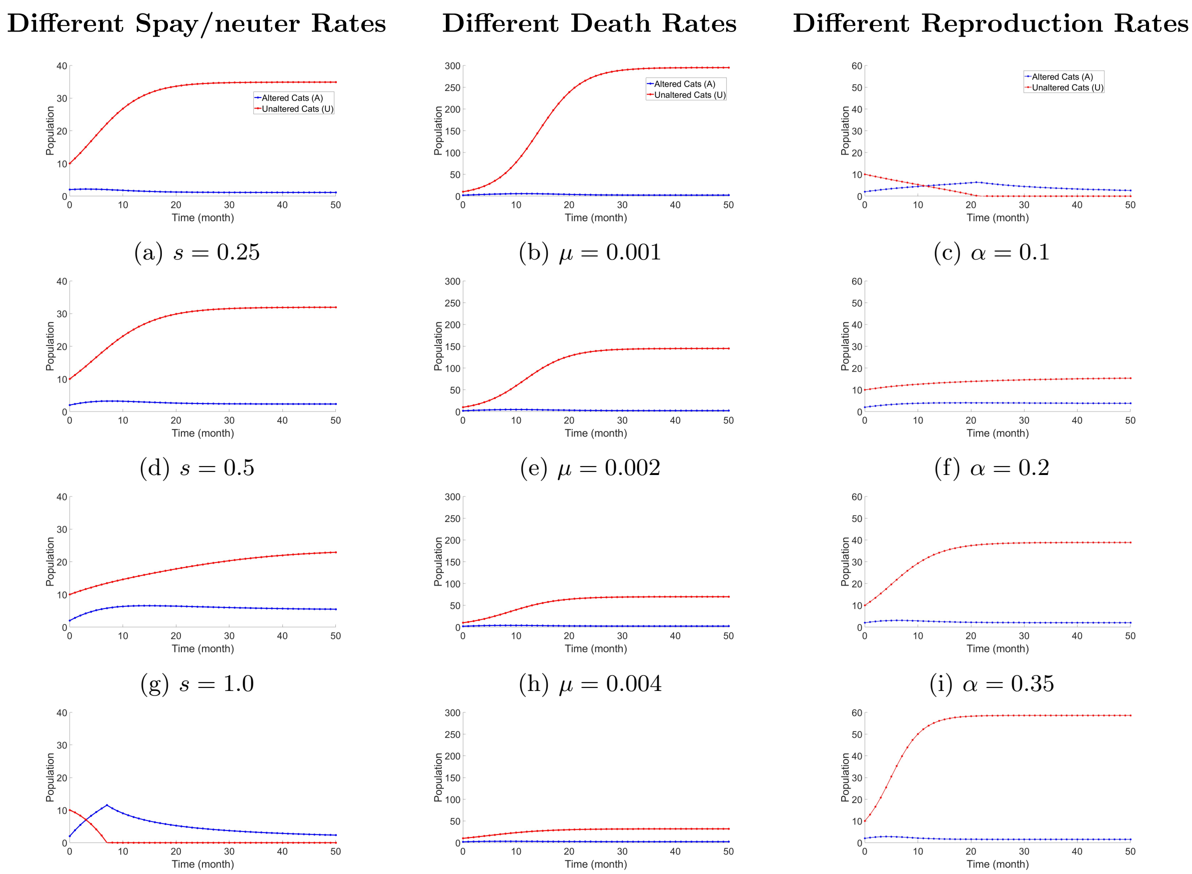
$$J(0, 0) = \begin{bmatrix} 1 & 1 \\ 0 & \alpha \end{bmatrix},$$

which are $\lambda_1 = 1$, $v_1 = \begin{bmatrix} 1 \\ 0 \end{bmatrix}$ and $\lambda_\alpha = \alpha$, $v_\alpha = \begin{bmatrix} \frac{1}{\alpha - 1} \\ 1 \end{bmatrix}$. We assume $0 < \alpha < 1$ since α is the reproduction rate for a single month. Therefore, since this is a discrete model, $(0, 0)$ is locally stable in the direction of v_α. To complete the stability analysis of $(0, 0)$ we will examine the v_1 direction. Since the corresponding eigenvalue is 1 we must use other methods to find the dynamics in the v_1 direction. Consider A_t small and $U_t = 0$, then

$$\begin{aligned} A_{t+1} &= \frac{A_t}{1 + \mu A_t} \\ U_{t+1} &= 0. \end{aligned}$$

Since $1 + \mu A_t > 1$, $A_{t+1} < A_t$ for all t and bounded below by 0 and thus $A_t \to 0$ as $t \to \infty$. Therefore the point $(A, U) = (0, 0)$ is locally stable.

We present numerical simulations of the two population Beverton-Holt model (2) in Figure 2, which shows how variations in the spay/neuter rate s, death rate μ, and reproduction rate α influence the dynamics of altered (A, blue) and unaltered (U, red) cat populations over time.



(a) $s = 0.25$ (b) $\mu = 0.001$ (c) $\alpha = 0.1$

(d) $s = 0.5$ (e) $\mu = 0.002$ (f) $\alpha = 0.2$

(g) $s = 1.0$ (h) $\mu = 0.004$ (i) $\alpha = 0.35$

(j) $s = 2.0$ (k) $\mu = 0.008$ (l) $\alpha = 0.5$

Figure 2: Beverton-Holt two population dynamics under varying parameters. Each column shows the effect of varying one parameter while holding the other two fixed. The altered cat population (A, blue) and unaltered cat population (U, red) evolve over time according to model (2). In Column 1, s is varied while $\mu = 0.008$ and $\alpha = 0.3$ are fixed. In Column 2, μ is varied with $s = 0.5$ and $\alpha = 0.3$ held constant. In Column 3, α is varied with fixed values $s = 0.5$ and $\mu = 0.008$.

As seen in the first column of Fig. 2, increasing the spay/neuter rate reduces the unaltered cat population while increasing the altered cat population, indicating the success of spay/neuter interventions in limiting reproduction. In the second column, increasing the death rate results in a decline of both populations, as higher mortality limits growth (i.e., fewer unaltered cats to reproduce). Finally, the third column demonstrates that higher reproduction rates lead to significant growth in the unaltered population and decline in the altered cat population, since more unaltered cats are being born relative to those being spayed/neutered.

5 Two Population Strictly Discrete Model

We now introduce a new model, a strictly discrete model that is in contrast to the Beverton-Holt style models developed in Sections 3 and 4 with their continuous portions. We will continue to consider the two subpopulations of Altered and Unaltered cats as in Section 4. We combine all the effects discussed in Section 4 into a single discrete system, which we formulate below

$$\begin{aligned} A_{t+1} &= A_t - \mu A_t(A_t + U_t) + \min(s, U_t) \\ U_{t+1} &= U_t + \alpha U_t - \mu U_t(A_t + U_t) - \min(s, U_t) \end{aligned} \tag{3}$$

Once again, due to the complexity of the model, finding fixed points for arbitrary model parameters is difficult while ensuring $A > 0$ and $U > 0$. Therefore, we will investigate the stability of the origin. If $U_t < s$ then $(A^*, U^*) = (0, 0)$ is clearly a fixed point for the system. For the rest of the theoretical analysis, we assume $U_t < s$. The analysis is similar to that of Section 4; therefore, some details will be omitted.

$$J(A, U) = \begin{bmatrix} 1 - 2\mu A - \mu U & -\mu A + 1 \\ -\mu U & 1 + \alpha - \mu A - 2\mu U - 1 \end{bmatrix}$$

We then find the eigenvalues and vectors of

$$J(0, 0) = \begin{bmatrix} 1 & 1 \\ 0 & \alpha \end{bmatrix},$$

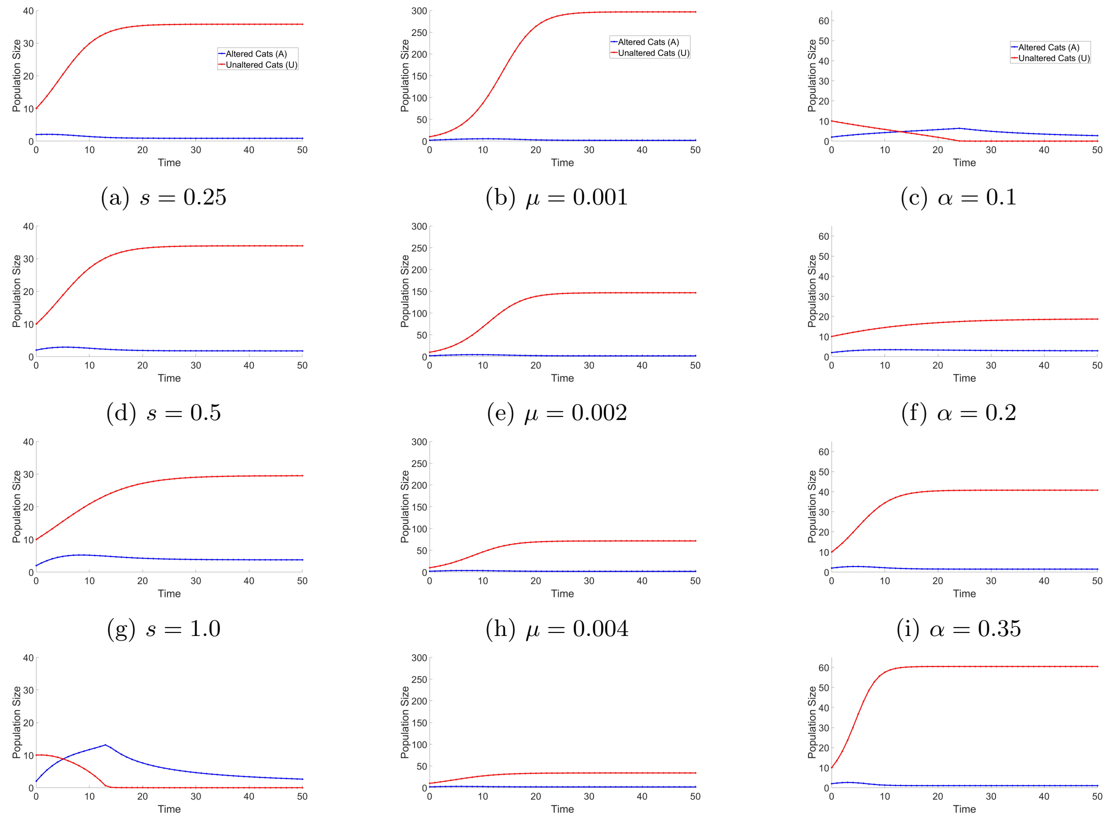
which are $\lambda_1 = 1$, $v_1 = \begin{bmatrix} 1 \\ 0 \end{bmatrix}$ and $\lambda_\alpha = \alpha$, $v_\alpha = \begin{bmatrix} \frac{1}{\alpha - 1} \\ 1 \end{bmatrix}$. Consider A_t small and $U_t = 0$, then

$$\begin{aligned} A_{t+1} &= A_t - \mu A_t^2 = A_t(1 - \mu A_t) \\ U_{t+1} &= 0 \end{aligned}$$

Therefore, if $\mu A_t < 1$ then $A_{t+1} < A_t$. Since $0 < A_{t+1} < A_t$, $A_t \to 0$ as $t \to \infty$. Thus $(A^*, U^*) = (0, 0)$ is locally stable.

We present numerical simulations of the two population strictly discrete model (3) in Fig. 3. The simulation results are similar to those of the Beverton-Holt model (2) discussed earlier, showing similar patterns in population dynamics in response to variations in the spay/neuter rate s, death rate μ, and reproduction rate α. So, we focus on the results of the global sensitivity analysis of model (3) parameters.

Different Spay/neuter Rates **Different Death Rates** **Different Reproduction Rates**



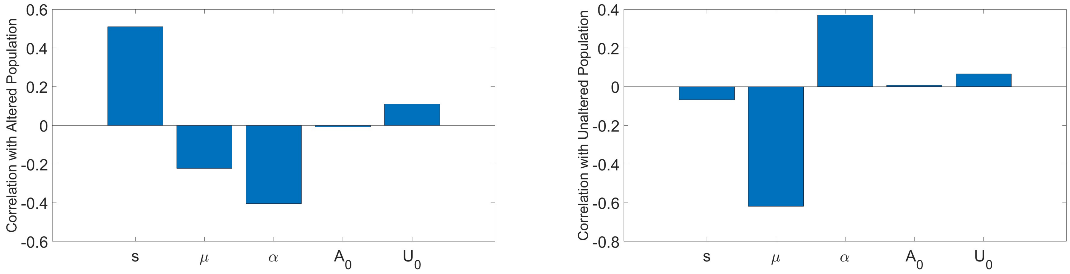
(a) $s = 0.25$ (b) $\mu = 0.001$ (c) $\alpha = 0.1$

(d) $s = 0.5$ (e) $\mu = 0.002$ (f) $\alpha = 0.2$

(g) $s = 1.0$ (h) $\mu = 0.004$ (i) $\alpha = 0.35$

(j) $s = 2.0$ (k) $\mu = 0.008$ (l) $\alpha = 0.5$

Figure 3: Strictly discrete two population dynamics under varying parameters. Each column shows the effect of varying one parameter while holding the other two fixed. The altered cat population (A, blue) and unaltered cat population (U, red) evolve over time according to model (3). In Column 1, s is varied while $\mu = 0.008$ and $\alpha = 0.3$ are fixed. In Column 2, μ is varied with $s = 0.5$ and $\alpha = 0.3$ held constant. In Column 3, α is varied with fixed values $s = 0.5$ and $\mu = 0.008$.



(a) (b)

Figure 4: Global sensitivity analysis of model (3) parameters using Latin Hypercube Sampling (LHS). Bars indicate the correlation of each parameter with the final altered (A) and unaltered (U) cat populations.

Figure 4 shows the results of a global sensitivity analysis of model (3) using Latin Hypercube Sampling (LHS) with 20,000 simulations. Each simulation randomly sampled values for five parameters: spay/neuter rate $s \in [0.25, 2]$, death rate $\mu \in [0.001, 0.02]$, reproduction rate $\alpha \in [0.2, 1]$, and initial populations $A_0, U_0 \in [1, 20]$. The bar plots display the correlation between each parameter and the final altered population (fig.4a) and unaltered population (fig.4b) after 50 months.

The results show that s has a strong positive impact on the altered population and a negative impact on the unaltered population, since spaying / neutering transitions individuals from the unaltered to the altered population. The death rate μ has a strong negative influence on both populations. The reproduction rate α positively affects the unaltered population but negatively affects the altered cat population, maybe due to increased competition for resources as more unaltered cats are reproduced. These findings highlight the most influential parameters shaping long-term population dynamics in the strictly discrete model.

6 Three Population Numerical Model

As we make more detailed models like that in Sections 4 and 5, the theoretical analysis becomes more difficult. Therefore, in this section, we will do a numerical analysis approach with three subpopulations of cats: Altered (A), Unaltered (U), and Kittens (K). Here we define kittens as cats under the age of 6 months old, and we assume that kittens can not be spayed or neutered until they have matured. We formulate our model as

$$\begin{aligned}
A_{t+1} &= A_t - \mu_A A_t(A_t + U_t) + \min(s, U_t) + a \cdot a_A \\
U_{t+1} &= U_t - \mu_U U_t(A_t + U_t) - \min(s, U_t) + \frac{1}{m} K_t + a \cdot a_U \\
K_{t+1} &= K_t - \mu_K K_t + \alpha U_t \frac{U_t}{A_t + U_t} - \frac{1}{m} K_t + a \cdot a_K
\end{aligned} \tag{4}$$

We also have the following rules to prevent any category from becoming negative:
If $A_t - \mu_A A_t(A_t + U_t) < 0$ then

$$A_{t+1} = \min(s, U_t) + a \cdot a_A$$

If $U_t - \mu_U U_t(A_t + U_t) - \min(s, U_t) < 0$ then

$$U_{t+1} = \frac{1}{m} K_t + a \cdot a_U$$

If $K_t - \mu_K K_t - \frac{1}{m} K_t < 0$ then

$$K_{t+1} = \alpha U_t \frac{U_t}{A_t + U_t} + a \cdot a_K$$

We now assume that altered, unaltered, and kittens have different death rates as supported by the data discussed in Section 2. We also assume that altered and unaltered cats must compete with all cats, excluding kittens, while kittens have a natural death rate and do not compete with others. This can represent that kittens are taken care of by their mothers and thus do not compete until they have matured. We also introduce an abandonment term where a certain number of cats are abandoned each month, represented by a, and a_A, a_U, a_K represent the percentage of cats that are abandoned that fall within their respective categories. We also have the reproduction term different from the rest of the models in this report, we include $U_t \frac{U_t}{A_t + U_t}$ as an interaction term that represents that two unaltered cats must meet to reproduce, which becomes more difficult with more altered cats being in the total population. Finally, we have that the cats move from the kitten subpopulation to the unaltered subpopulation at m months, which we set to be $m = 6$ as supported by the data in Section 2.

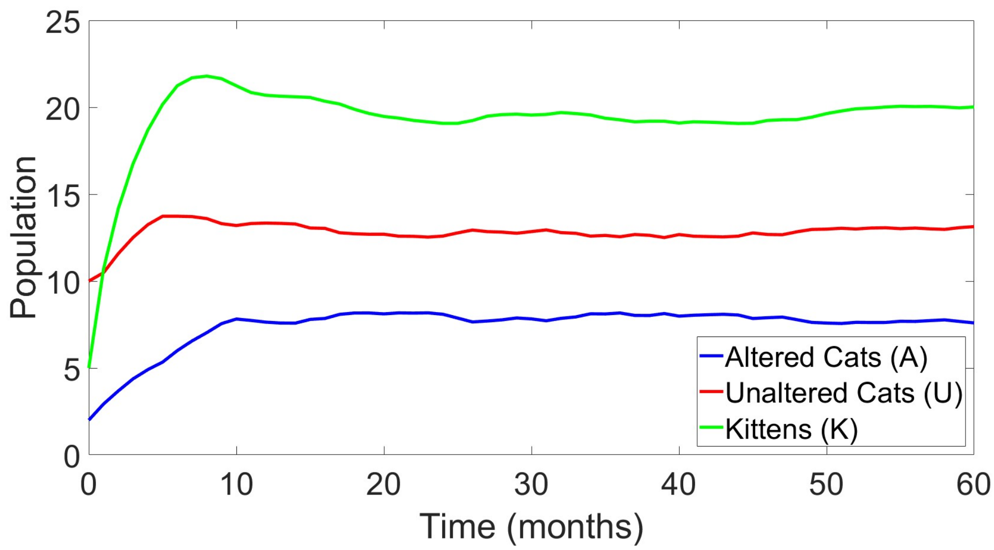


Figure 5: Three population numerical model simulation using actual monthly TNR data from the KAC dataset. The TNR counts were divided by 1000 (our scaling factor) and multiplied by 3 to estimate monthly spay/neuter rates, under the assumption that KAC performs approximately one-third of the total TNR in Lubbock. As a result, all population values are represented in thousands. The simulation shows the dynamics of altered cats (A, blue), unaltered cats (U, red), and kittens (K, green) over 60 months using the model in equation (4).

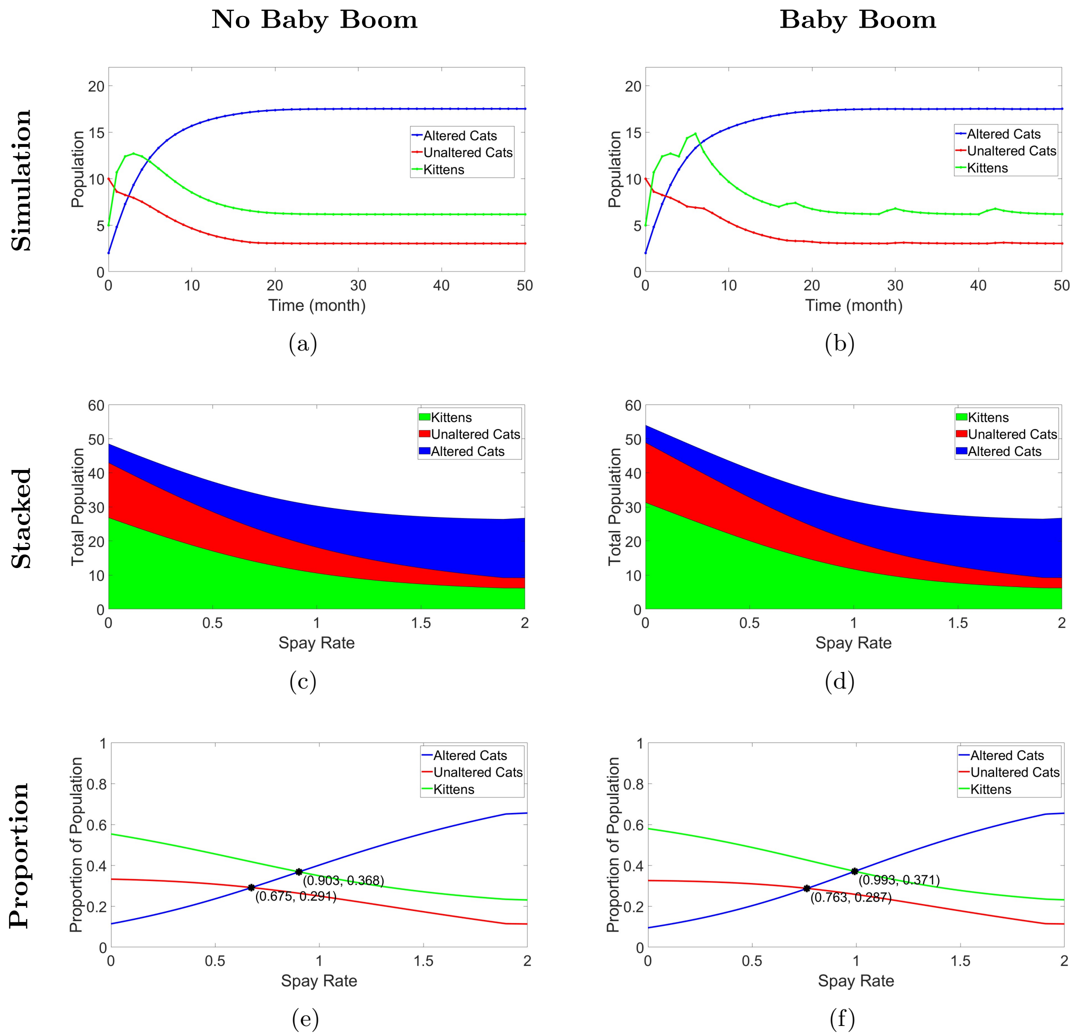


Figure 6: Three population numerical model (4) outcomes under two birth scenarios: No Baby Boom (left column) and Baby Boom (right column). (a) and (b) show time series simulations of altered cats (blue), unaltered cats (red), and kittens (green). (c) and (d) shows the corresponding total population stacked by category as the spay/neuter rate increases. (e) and (f) show the proportions of each population within the total population. The intersection points in these plots indicate the spay/neuter rates at which the altered cat population surpasses both the kitten and unaltered cat populations.

In Fig. 6, we compare the outcome of the three population numerical model (4) under two birth scenarios: Baby Boom and No Baby Boom. These scenarios are defined by the reproduction rate parameter α. In the No Baby Boom case, α is fixed at $\frac{2}{3}$ throughout. However, the Baby Boom case increases α to 1.5 during May and June each year to reflect the effects of the seasonal increase in reproduction on the feral cat's population dynamics.

We observe in figures 6(a) and (b) that the overall population dynamics remains similar between scenarios, except during months with increased reproduction rates, where the Baby Boom scenario produces a brief increase in the kitten population. Figures 6(c) and (d) present the total population size stacked by the different cat populations: altered cats, unaltered cats, and kittens, as the spay/neuter rate increases. In both scenarios, the total population decreases with increased spay rates, and the proportion of altered cats increases. However, the Baby Boom scenario yields a slightly larger total population across the spay/neuter rates due to the increased reproduction rate in some months, which could increase the kitten population. Finally, in Figs. 6(e) and (f), the different population is shown as proportions of the total. These plots reveal a critical threshold: the spay/neuter rate at which altered cats become the largest subpopulation. This crossover occurs earlier in the No Baby Boom scenario, as the increased reproduction rates in the Baby Boom case result in more kittens and unaltered cats, thereby requiring higher intervention levels (i.e., more spaying/neutering) for altered cats to be more than unaltered cats and kittens.

7 Result/Discussion

In our project, we examined the effects of Trap-Neuter-Return (TNR) strategies on feral cat population dynamics using four models: a single population Beverton–Holt model (1), a two-population Beverton–Holt model (2), a strictly discrete two-population model (3), and a three-population numerical model that includes kittens as a separate group (4).

Across all models, we found that increasing the spay/neuter rate consistently led to a decrease in the total cat population. The single population model(1) showed that higher proportions of reproductive cats, which could imply fewer spay/neuter efforts, caused the population to increase. The two-population models (2) and (3) built on this by showing that increasing the spay/neuter efforts not only reduced the number of unaltered cats but also increased the altered cat population over time. This indicates the direct impact of TNR in reshaping population composition.

To further investigate the effect of spay/neuter efforts, we used the three-population numerical model (4), which includes kittens as a distinct population, to identify the spay/neuter rates at which altered cats become the dominant subpopulation. This analysis revealed a critical threshold, and beyond this threshold (approximately 0.90 (i.e., 900 cats spayed/neutered per month) in the No Baby Boom case and 0.99 (i.e., 990 cats spayed/neutered per month) in the Baby Boom case), the number of altered cats surpasses both unaltered cats and kittens.

When we incorporated actual TNR data, the model suggested that current efforts may not be enough to shift the population composition to have more altered cats. Simulations indicated that maintaining a spay/neuter rate close to or above 0.99 (approximately 990 cats spayed/neutered per month) may be necessary for altered cats to become the dominant subpopulation without risking population extinction.

Overall, these results suggest that TNR can be an effective long-term strategy for managing feral cat populations, but its success is based on consistently maintaining a high spay/neuter rate.

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