Controlling Plague Among Prairie Dogs: A Two Colony Epidemiological Model

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Abstract: In this work we model the spread of sylvatic plague between two prairie dog colonies. The mathematical model is one where a population of fleas transmits the plague to the host population of prairie dogs. Distance between the two colonies is examined as well as using insecticide to increase the death rates on the fleas that spread the disease between prairie dogs. Semi-analytical solutions for equilibria are derived using a perturbation series approach.

Key–Words: Sylvatic Plague, Black Tailed Prairie Dog, Host, Mathematical Model, Epidemiology

1 Introduction

Black Tailed prairie dogs are a rodent primarily found on the plains and western regions of the United States. Though virtually harmless, prairie dog species have fallen victim to urbanization and made enemies with farmers and ranchers. Specifically in South Dakota and other ranching states, the prairie dog burrows occasionally break the legs of cattle and horses and ruin thousands of acres of pasture land. Therefore, little effort has been made in the past to conserve the species and protect the health of the rodent.

In 1985, the Black Footed Ferret *Mustela nigripes* was thought to be extinct after a colony discovered in South Dakota in 1966 disappeared in 1974 (Hillman, 1968) until a small population was discovered in Wyoming (Beers, 2000). Since the discovery, the ferrets were taken into captivity and bred until a reintroduction effort could take place. The ferrets need two things to survive: grassland and prairie dogs. The black footed ferret is an obligate-dependence species on the prairie dog for diet and habitat; therefore, without a large population of prairie dogs, the ferrets have no chance of successful reintroduction (Clark, 1994), (Miller et al., 1988), (Miller et al., 1987), and (Miller & Cully, 2001).

Now that prairie dogs show a purpose in nature, the health of the prairie dog is monitored but is greatly threatened due to the recent outbreak of sylvatic plague(Antolin et al, 2002), (Augustine et al., 2008), (Barnes, 1993), (Collinge et al., 2005), (Cully et al., 1997), (Cully et al., 2006), and (Cully et al., 2000). The plague is similar to that found in humans during the 14th century in England and remote areas today, but is transmitted through saliva rather than buboes. Since prairie dogs do not have much saliva to saliva contact, the main transmitter of the disease in our model is taken to be the flea through blood cross-contamination (Abbott & Rocke, 2012).

In this model, the flea is considered the only vector by which plague is transmitted between prairie dogs; therefore, the governing equations only represent the transfer of plague between prairie dogs and fleas. Support for this is given by (Tripp et al., 2009) where they show the number of fleas present seems to vary directly with plague epizootics. A healthy flea that feeds on a plagued prairie dog then contracts the disease itself. After contracting the disease, the flea will always contain bacterium in the GI tract. When a flea jumps to a healthy prairie dog and feeds, the plague can then be transferred to the healthy prairie dog. In 2009, Georgescu and Van Peursem (Georgescu & Van Peursem, 2009) came up with a mathematical model for the interaction within a single colony. This paper will look further into the interaction between two colonies by adding a migration term so the spread of plague to and from two distinct colonies can be predicted. The model can be used to look at the effectiveness of flea control within colonies to inhibit the spread of plague, as well as the effective and economical control of plague. The model uses four governing differential equations. By modeling total prairie dog population, total flea population, plagued prairie dog population, and plagued flea population, the conditions for plague to increase, decrease, or die off are examined. The main parameter of interest is the death rate of the flea. Our model assumes applying pesticides to prairie dog colony burrows in order to increase this death rate (Seery et al., 2003). When decreasing the vector of the disease, the model shows plague can possibly be eliminated or at least controlled (Hoogland et al., 2004), (Webb et al., 2006), (Lorange et al., 2005), (Hoogland, 1995), (Thiagarajan et al., 2008), and (Eskey, 1940).

2 Mathematical Model

For the mathematical model of our two-colony model we start with the equations of a single colony model of (Georgescu & Van Peursem, 2009) which were loosely based off of the governing equations of a deer-tick model (Gaff & Gross, 2007). The four equations, model the total population of both prairie dogs and fleas as well as the plagued populations of the prairie dogs and fleas. We will follow the same notation and let P be the total number of prairie dogs, F be the total number of fleas, S be the number of infected (sick) prairie dogs, and D be the number of infected (diseased) fleas.

In order to model the interaction between two colonies, we add a migration term into these original governing equations. We let the distance x between two colonies govern the number of prairie dogs which will leave one colony and enter into the other. As x increases, the number of prairie dogs which will transfer between colonies will obviously decrease. So, we take l to be our rate of transfer with units length/time and use l/x as our inverse relationship for the migration term. This assumption seems to be supported by work done by (Cully et al., 2010).

We let P_1 represent the the total prairie dogs of the first population and P_2 be total prairie dogs of the second. Although we allow for different carrying capacities in the two populations, k_{p_1} and k_{p_2}, we assume that both populations want to tend to roughly the same number in that prairie dogs will migrate from the larger population to the smaller population. By taking l/x times the difference between the populations, we get the number of prairie dogs per unit time migrating from one colony to the other. The larger population will lose the prairie dogs while the smaller population gains the same amount. We use d_r for the natural death rate of the prairie dogs. The governing equation for the prairie dogs is then

$$\frac{dP_1}{dt} = r_p \left(1 - \frac{P_1}{k_{p_1}}\right) P_1 + \frac{l}{x}(P_2 - P_1) - d_r P_1 \tag{1}$$

$$\frac{dP_2}{dt} = r_p \left(1 - \frac{P_2}{k_{p_2}}\right) P_2 + \frac{l}{x}(P_1 - P_2) - d_r P_2. \tag{2}$$

If $P_1 > P_2$, we see from the second term in 1 and 2 that P_1 will lose population and P_2 will gain population. In order to model fleas, we simple multiply the number of migrating prairie dogs by m, the average number of fleas per prairie dog. Since we consider dusting (killing fleas) in the two populations at different levels, we use different values for the parameter we will vary later on, the death rates for the fleas, d_{f1} and d_{f2}. The governing flea equations become

$$\frac{dF_1}{dt} = r_f \left(1 - \frac{F_1}{mP_1}\right) F_1 + \frac{lm}{x}(P_2 - P_1) - d_{f_1} F_1 \tag{3}$$

$$\frac{dF_2}{dt} = r_f \left(1 - \frac{F_2}{mP_2}\right) F_2 + \frac{lm}{x}(P_1 - P_2) - d_{f_2} F_2. \tag{4}$$

We see here that , F_1 will have a decrease in population while F_2 gains the same amount for the case $P_1 > P_2$.

When looking at the plagued populations, the situation is more complicated due to the fact that the level of plague may not be the same in both colonies. Therefore, we consider which population is losing prairie dogs and what proportion of those prairie dogs are likely to have plague. The proportion of prairie dogs with plague will either be S_1/P_1 or S_2/P_2 depending on the migrating population. Since we need to consider the possibility of either P_1 or P_2 to be greater, we use the heaviside function $H(x)$ to include both possibilities in the equations. Recall that the heaviside function is zero if $x \leq 0$ and one if $x > 0$. Consider

$$\frac{l}{x}(P_2 - P_1)\left[\frac{S_1}{P_1} H(P_1 - P_2) + \frac{S_2}{P_2} H(P_2 - P_1)\right] \tag{5}$$

and

$$\frac{l}{x}(P_1 - P_2)\left[\frac{S_1}{P_1} H(P_1 - P_2) + \frac{S_2}{P_2} H(P_2 - P_1)\right]. \tag{6}$$

For the case $P_1 > P_2$ equations 5 and 6 imply that $H(P_1 - P_2)$ will be one and $H(P_2 - P_1)$ will be zero. Equations 5 and 6 then become

$$\frac{l}{x}(P_2 - P_1)\left(\frac{S_1}{P_1}\right) \tag{7}$$

and

$$\frac{l}{x}(P_1 - P_2)\left(\frac{S_1}{P_1}\right) \tag{8}$$

showing the correct proportion of prairie dogs with plague leaving S_1 and joining S_2 respectively. Using 5 and 6 in our original governing equations for plagued prairie dogs, we obtain

$$\frac{dS_1}{dt} = t_p\left(\frac{P_1 - S_1}{P_1}\right)D_1 + \frac{l}{x}(P_2 - P_1)\cdot \left[\frac{S_1}{P_1}H(P_1 - P_2) + \frac{S_2}{P_2}H(P_2 - P_1)\right] - c_1 d_r S_1 \tag{9}$$

$$\frac{dS_2}{dt} = t_p\left(\frac{P_2 - S_2}{P_2}\right)D_2 + \frac{l}{x}(P_1 - P_2)\cdot \left[\frac{S_1}{P_1}H(P_1 - P_2) + \frac{S_2}{P_2}H(P_2 - P_1)\right] - c_1 d_r S_2. \tag{10}$$

We note that for the last term we multiply the natural death rate for the prairie dogs d_r by the constant $c_1 > 1$ to indicate the higher deathrate due to the disease.

Similar to the plagued prairie dogs, the plagued flea population uses the heaviside function to determine what proportion of fleas that are transferring have plague. Multiplying our migrating prairie dogs by m and using the appropriate ratios D_1/F_1 and D_2/F_2 we get the following governing equations.

$$\frac{dD_1}{dt} = t_f\left(\frac{S_1}{P_1}\right)(F_1 - D_1) + \frac{ml}{x}(P_2 - P_1)\cdot \left[\frac{D_1}{F_1}H(P_1 - P_2) + \frac{D_2}{F_2}H(P_2 - P_1)\right] - c_2 d_{f_1} D_1 \tag{11}$$

$$\frac{dD_2}{dt} = t_f\left(\frac{S_2}{P_2}\right)(F_2 - D_2) + \frac{ml}{x}(P_1 - P_2)\cdot \left[\frac{D_1}{F_1}H(P_1 - P_2) + \frac{D_2}{F_2}H(P_2 - P_1)\right] - c_2 d_{f_2} D_2 \tag{12}$$

2.1 Governing Equations

The governing equations for the two colony system are then given by equations 1, 2, 3, 4, 9, 10, 11, and 12.

The previous parameters remain the same as the single colony system given by (Georgescu & Van Peursem, 2009). We note these parameters in Table 1 where the values were obtained from different studies and books written about prairie dogs and/or fleas and references are noted within the tables. Many of these were also cited by (Webb et al., 2006). Some additional parameters introduced with this two colony model are the parameters l and x the proportionality constant and the distance parameter respectively. Although, l would typically be unknown, it could be obtained from field studies. We will use $l = 0.1$ and $x = 1000$ (where we consider meters to be our unit of length) simply to obtain information for mathematical analysis.

2.2 Scaling

We scale P_i and D_i by k_{p_i}, F_i and D_i by mk_{p_i} (their respective carrying capacities, and time by the reciprocal prairie dog death rate $1/d_r$. The final scaled equations are given by

Par	Meaning	Value
r_p	Growth Rate of Prairie Dog	0.0866 (Hoogland, 1995)
r_f	Growth Rate of Flea	0.866 [†]
k_p	Carrying Capacity of Prairie Dog	200 (Hoogland, 1995)
m	Maximum Fleas per Prairie Dog	11 (Hoogland et al., 2004)
d_r	Death Rate of Prairie Dog	0.0002 (Hoogland, 1995)
d_f	Death Rate of Flea	0.07 (Burroughs, 1953)
t_p	Transfer Rate from Fleas to Prairie Dogs	0.09 (Eskey, 1940)
t_f	Transfer Rate from Prairie Dogs to Fleas	0.28 (Eskey, 1940)
$c_1 d_r$	Death Rate of Plagued Prairie Dog	0.5 (Cully & Will., 2001)
$c_2 d_f$	Death Rate of Plagued Flea	0.33 (Eskey, 1940)
l	Transfer Rate between colonies	0.1 [$\star$]
x	Distance between colonies	1000 [$\star\star$]

Table 1: Parameter Values and Interpretations with References
† Calculated from the model to be consistent with $m = 11$
$\star$ Unknown that will likely depend on the terrain (Collinge et al., 2005)
$\star\star$ Parameter will vary. Measured in meters.

$$\frac{d\bar{P}_1}{d\bar{t}} = \beta\left(1-\bar{P}_1\right)\bar{P}_1 + \epsilon\left(\mu\bar{P}_2 - \bar{P}_1\right) - \bar{P}_1 \tag{13}$$

$$\frac{d\bar{P}_2}{d\bar{t}} = \beta\left(1-\bar{P}_2\right)\bar{P}_2 + \epsilon\left(\mu^{-1}\bar{P}_1 - \bar{P}_2\right) - \bar{P}_2 \tag{14}$$

$$\frac{d\bar{F}_1}{d\bar{t}} = \kappa\left(1 - \frac{\bar{F}_1}{\bar{P}_1}\right)\bar{F}_1 + \epsilon\left(\mu\bar{P}_2 - \bar{P}_1\right) - \alpha_1\bar{F}_1 \tag{15}$$

$$\frac{d\bar{F}_2}{d\bar{t}} = \kappa\left(1 - \frac{\bar{F}_2}{\bar{P}_2}\right)\bar{F}_2 + \epsilon\left(\mu^{-1}\bar{P}_1 - \bar{P}_2\right) - \alpha_2\bar{F}_2 \tag{16}$$

$$\frac{d\bar{S}_1}{d\bar{t}} = \omega\left(\frac{\bar{P}_1 - \bar{S}_1}{\bar{P}_1}\right)\bar{D}_1 + \epsilon\left(\mu\bar{P}_2 - \bar{P}_1\right)\cdot \left[\frac{S_1}{P_1}H\left(\mu^{-1}P_1 - P_2\right) + \frac{S_2}{P_2}H\left(\mu P_2 - P_1\right)\right] - c_1\bar{S}_1 \tag{17}$$

$$\frac{d\bar{S}_2}{d\bar{t}} = \omega\left(\frac{\bar{P}_2 - \bar{S}_2}{\bar{P}_2}\right)\bar{D}_2 + \epsilon\left(\mu^{-1}\bar{P}_1 - \bar{P}_2\right)\cdot \left[\frac{S_1}{P_1}H\left(\mu^{-1}P_1 - P_2\right) + \frac{S_2}{P_2}H\left(\mu P_2 - P_1\right)\right] - c_1\bar{S}_2 \tag{18}$$

$$\frac{d\bar{D}_1}{d\bar{t}} = \sigma\left(\frac{\bar{S}_1}{\bar{P}_1}\right)\left(\bar{F}_1 - \bar{D}_1\right) + \epsilon\left(\mu\bar{P}_2 - \bar{P}_1\right)\cdot \left[\frac{D_1}{F_1}H\left(\mu^{-1}P_1 - P_2\right) + \frac{D_2}{F_2}H\left(\mu P_2 - P_1\right)\right] - c_2\alpha_1\bar{D}_1 \tag{19}$$

$$\frac{d\bar{D}_2}{d\bar{t}} = \sigma\left(\frac{\bar{S}_2}{\bar{P}_2}\right)\left(\bar{F}_2 - \bar{D}_2\right) + \epsilon\left(\mu^{-1}\bar{P}_1 - \bar{P}_2\right)\cdot \left[\frac{D_1}{F_1}H\left(\mu^{-1}P_1 - P_2\right) + \frac{D_2}{F_2}H\left(\mu P_2 - P_1\right)\right] - c_2\alpha_2\bar{D}_2. \tag{20}$$

where the dimensionless parameters and values are given in Table 2.

The parameters remain the same as the single colony model of (Georgescu & Van Peursem, 2009) with the addition of ϵ and μ. We set $\mu = 0.5$ to represent colony one having twice as large a carrying capacity as colony two and we will examine $\epsilon = 0.5$ closer in a later section.

2.3 Equilibria

By using dusting techniques, it is assumed that we can alter the death rate of the flea by using different amounts of insecticide (Hoogland et al., 2004) and thus be able to obtain the various equilibria states for

Dimensionless Parameters	Set To	Value
α	$\frac{d_f}{d_r}$	350
β	$\frac{r_p}{d_r}$	433
κ	$\frac{r_f}{d_r}$	4330
ω	$\frac{mt_p}{d_r}$	4950
σ	$\frac{t_f}{d_r}$	1400
ϵ	$\frac{l}{xd_r}$	0.5
μ	$\frac{k_{p_2}}{k_{p_1}}$	0.5

Table 2: Dimensionless Parameters with Values

the 4 classes in the two populations. Due to the complexity of the two colony system, we assume ϵ to be small and use a perturbation series approximation in ϵ, to obtain equilibria solutions in a later section. To leading order we get the same equilibria as the one colony system. This is reasonable as the migration parameter will have very little effect on individual colony populations for large separation distances. Because the same equilibria as the single colony model hold to leading order for small ϵ, we have E_1 the trivial equilibria, E_2 only healthy prairie dogs, E_3 only healthy prairie dogs and fleas, and E_4 coexistence of plague and healthy species as the possible equilibria states. We are able to obtain each possible combination of equilibria in the two populations by altering α_1 and α_2 as demonstrated in the next section.

2.4 Graphed Equilibria

The various equilibria possibilities are obtained using the values in Table 2 with population one having twice as large of carrying capacity as population two. We are also using an ϵ value of 0.5. The initial populations were set to $\bar{P}_1(0) = .6, \bar{P}_2(0) = .7, \bar{F}_1(0) = .6, \bar{F}_2(0) = 0.7$. Recall this represents a population being 60% and 70% of the respective carrying capacities. The initial populations of plague were set to $\bar{S}_1(0) = .1, \bar{S}_2(0) = .2, \bar{D}_1(0) = .1$ and $\bar{D}_2(0) = .2$.

We see in Figure 1 that for the case with heavy dusting in both populations at a level that would increase the flea death rate to a little over twelve times the normal rate of the healthy fleas, $\alpha_1 = \alpha_2 = 4250$, we get the equilibria case E_2 where both colonies

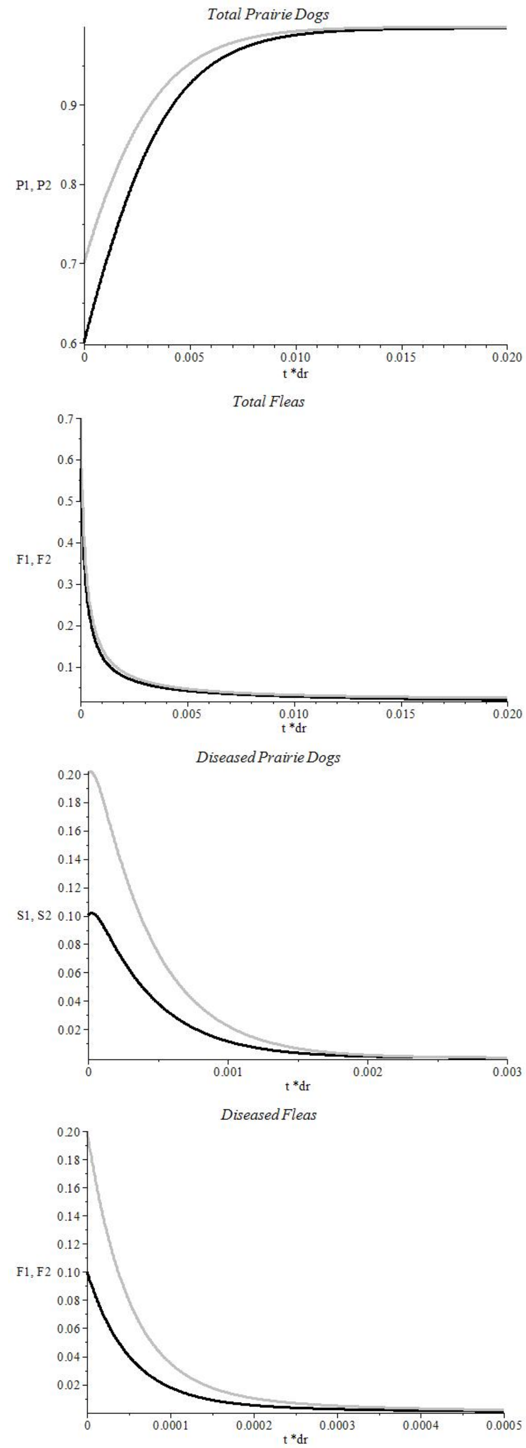

Figure 1: Only Healthy Prairie Dogs Survive for large dusting values of ($\alpha_1 = \alpha_2 = 4250$) with $\beta = 433, \kappa = 4330, \omega = 4950, \sigma = 1400, \mu = 0.5$, and $\epsilon = 0.5$. Population 1 - Black, Population 2- Gray

exhibit the property that only the healthy prairie dogs survive. Both plagued species go extinct as well as the healthy fleas.

We see in Figure 2 that for the case with mild dusting in both populations at a level that would increase the flea death rate to roughly 1.5 times the normal rate of the healthy fleas $\alpha_1 = \alpha_2 = 520$, both colonies exhibit the property that both the diseased populations of prairie dogs and fleas, S and D respectively, go extinct leaving only healthy prairie dogs and fleas.

We see in Figure 3 that we get coexistance in both colonies between plagued and healthy species for $(\alpha_1 = \alpha_2 = 350)$ which corresponds to no dusting, ie the natural death rate for the fleas. This shows that without dusting, or natural flea death rates, the plague will exist in the colonies among both species, prairie dogs and fleas. We see the total populations P and F are at high percentages of their carrying capacities while the plagued populations, S and D, also show a modest percentage of the population. Given that most populations observed display virtually complete die off with the plague, our model supports (Webb et al., 2006) where they argue fleas can't be the only source to maintain an epizootic.

We have shown that for $\epsilon = .5$ we can achieve all the equilibria as the single colony model of (Georgescu & Van Peursem, 2009) which was demonstrated in Figures 1, 2, and 3 where the high flea death rates (high dusting rates) correspond to only healthy prairie dogs surviving, medium flea death rates (medium dusting rates) corresponds to healthy prairie dogs and fleas surviving, and low flea death rates (little or no dusting) corresponds to coexistence between healthy and plagued species of both fleas and prairie dogs. One could also vary the dusting rates with these three values in the two colonies get any combinations of the equilibria states between the two colonies.

3 Analytical Approximation

3.1 Perturbation Approximation

In order to obtain a semi-analytical solution, we use an ϵ-perturbation approximation. Assuming ϵ terms are small in comparison to the others, we approximate our equilibria solutions for the differential equations by a series expansion. We will obtain an order ϵ approximation by assuming $P \approx P_0 + \epsilon P_1$. Using the notation that $P_1 = P_{1_0} + \epsilon P_{1_1}$ and $P_2 = P_{2_0} + \epsilon P_{2_1}$ we note the

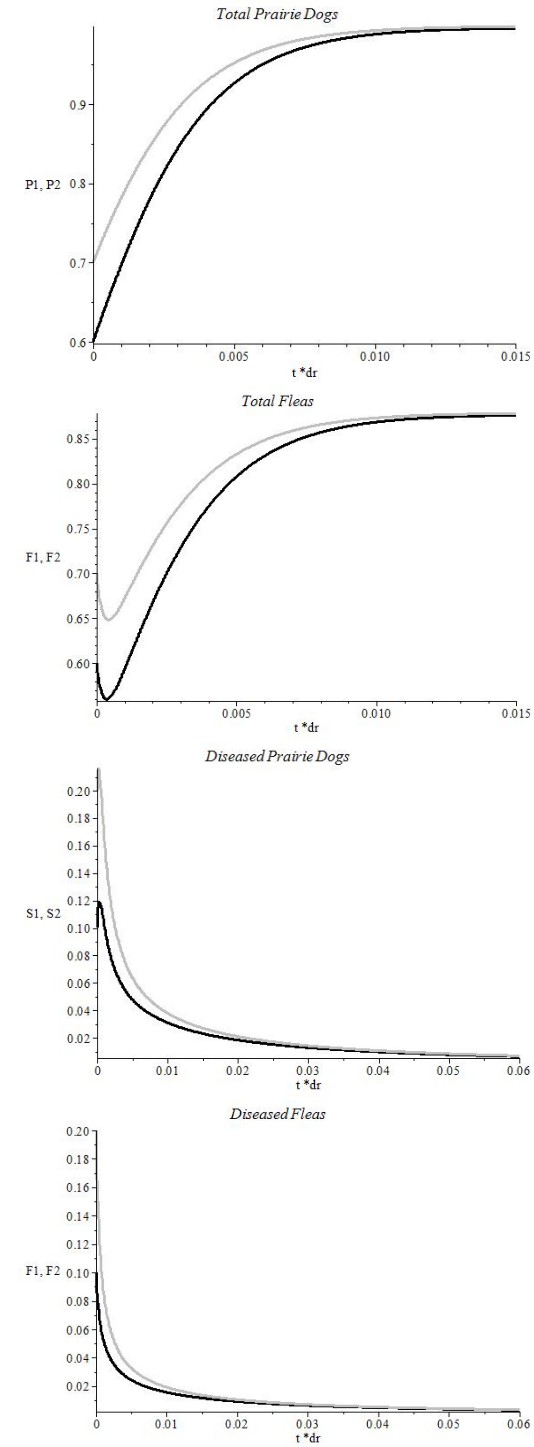

Figure 2: Only Healthy Prairie Dogs and Fleas Survive for medium dusting values of $(\alpha_1 = \alpha_2 = 520)$ with $\beta = 433, \kappa = 4330, \omega = 4950, \sigma = 1400, \mu = 0.5$, and $\epsilon = 0.5$. Population 1 - Black, Population 2- Gray

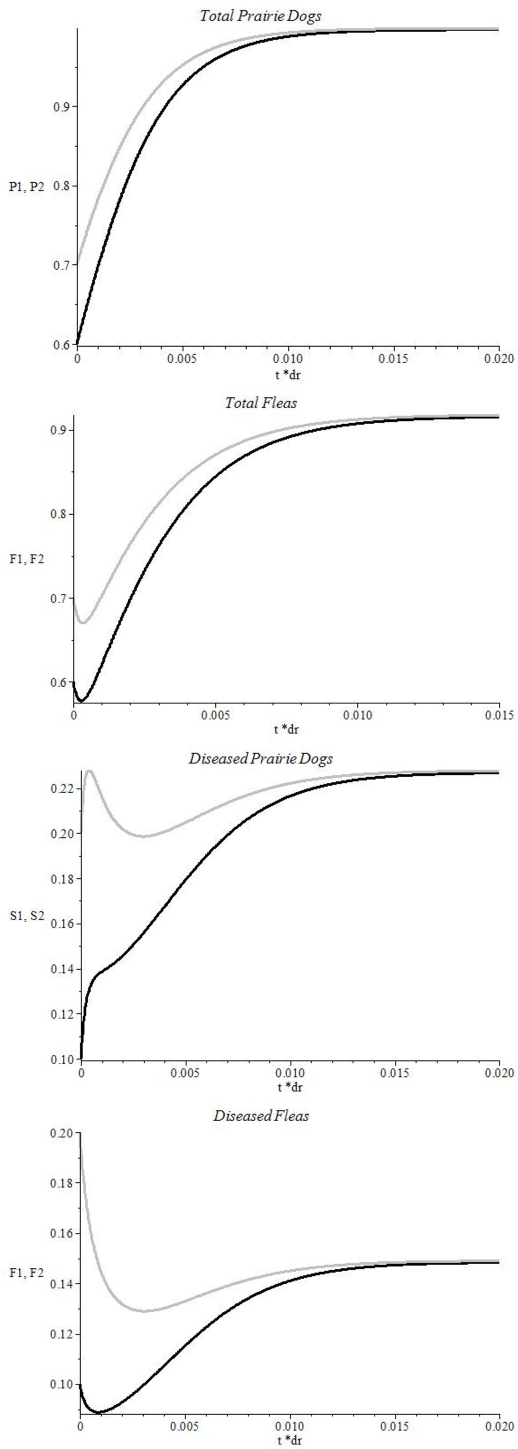

Figure 3: Coexistance of Healthy and Plagued Species for normal flea death rates of $(\alpha_1 = \alpha_2 = 350)$ with $\beta = 433, \kappa = 4330, \omega = 4950, \sigma = 1400, \mu = 0.5$, and $\epsilon = 0.5$. Population 1 - Black, Population 2- Gray

order one solutions turn out to be the equilibria values of the one colony system (Georgescu & Van Peursem, 2009) due to essentially dropping the migration term by setting $\epsilon = 0$. Therefore to leading order the equilibria solutions are given by,

$$P_{1_0} = P_{2_0} = \frac{\beta - 1}{\beta} \tag{21}$$

$$F_{i_0} = \frac{\beta\kappa - \kappa - \alpha_i\beta + \alpha_i}{\beta\kappa}$$

$$i = 1, 2 \tag{22}$$

$$S_{i_0} = \frac{\alpha_i\beta\kappa c_1 c_2 + \alpha_i\beta\omega\sigma - \beta\kappa\omega\sigma - \alpha_i\kappa c_1 c_2 + \kappa\omega\sigma - \omega\sigma\alpha_i}{\beta\sigma(\alpha_i\omega - \kappa c_1 - \kappa\omega)},$$

$$i = 1, 2 \tag{23}$$

$$D_{i_0} = \frac{(1-\beta)(\alpha_i\omega\sigma + \alpha_i\kappa c_1 c_2 - \kappa\omega\sigma)}{\beta\kappa\omega(\alpha_i c_2 + \sigma)},$$

$$i = 1, 2 \tag{24}$$

along with the trivial solutions which are zero. The order ϵ correction terms are given by:

$$P_{1_1} = \frac{\mu P_{2_0} - P_{1_0}}{-\beta + 2\beta P_{1_0} + 1} \tag{25}$$

$$P_{2_1} = \frac{P_{1_0} - \mu P_{2_0}}{\mu(-\beta + 2\beta P_{2_0} + 1)} \tag{26}$$

$$F_{1_1} = \frac{P_{1_0}^3 - \mu P_{2_0} P_{1_0}^2 - \kappa F_{1_0}^2 P_{1_1}}{\kappa P_{1_0}^2 - 2\kappa F_{1_0} P_{1_0} - \alpha_1 P_{1_0}^2} \tag{27}$$

$$F_{2_1} = \frac{\mu P_{2_0}^3 - P_{1_0} P_{2_0}^2 - \mu F_{2_0}^2 P_{2_1}}{\mu\left(\kappa P_{2_0}^2 - 2\kappa F_{2_0} P_{2_0} - \alpha_2 P_{2_0}^2\right)} \tag{28}$$

$$S_{1_1} = \frac{AQ + EC}{EB - AZ} \tag{29}$$

$$S_{2_1} = \frac{LJ + MG}{NL - GK} \tag{30}$$

$$D_{1_1} = \frac{BQ + CZ}{EB - AZ} \tag{31}$$

$$D_{2_1} = \frac{NM + JK}{NL - GK} \tag{32}$$

where,

$$A = \frac{\omega}{P_{1_0}} \left(P_{1_0} - S_{1_0}\right) \tag{33}$$

$$B = \frac{\omega D_{1_0}}{P_{1_0}} + c_1 \tag{34}$$

$$C = \frac{\omega S_{1_0} D_{1_0} P_{1_1}}{P_{1_0}^2} + (\mu P_{2_0} - P_{1_0}) \cdot \left[\frac{S_{2_0}}{P_{2_0}} H(\mu P_{2_0} - P_{1_0}) + \frac{S_{1_0}}{P_{1_0}} H(P_{1_0} - \mu P_{2_0})\right] \tag{35}$$

$$Z = \frac{\sigma}{P_{1_0}} \left(F_{1_0} - D_{1_0}\right) \tag{36}$$

$$E = \frac{\sigma S_{1_0}}{P_{1_0}} + c_2 \alpha_1 \tag{37}$$

$$Q = \frac{\sigma}{P_{1_0}} \left(S_{1_0} F_{1_1} + \frac{S_{1_0} P_{1_1} (D_{1_0} - F_{1_0})}{P_{1_0}}\right) + (\mu P_{2_0} - P_{1_0}) \left[\frac{D_{2_0}}{F_{2_0}} H(\mu P_{2_0} - P_{1_0}) + \frac{D_{1_0}}{F_{1_0}} H(P_{1_0} - \mu P_{2_0})\right] \tag{38}$$

$$G = \frac{\omega}{P_{2_0}} \left(P_{2_0} - S_{2_0}\right) \tag{39}$$

$$N = \frac{\omega D_{2_0}}{P_{2_0}} + c_1 \tag{40}$$

$$J = \frac{\omega S_{2_0} D_{2_0} P_{2_1}}{P_{2_0}^2} + \left(\mu^{-1} P_{1_0} - P_{2_0}\right) \left[\frac{S_{2_0}}{P_{2_0}} H(\mu P_{2_0} - P_{1_0}) + \frac{S_{1_0}}{P_{1_0}} H(P_{1_0} - \mu P_{2_0})\right] \tag{41}$$

$$K = \frac{\sigma}{P_{2_0}} \left(F_{2_0} - D_{2_0}\right) \tag{42}$$

$$L = \frac{\sigma S_{2_0}}{P_{2_0}} + c_2 \alpha_2 \tag{43}$$

$$M = \frac{\sigma}{P_{2_0}} \left(S_{2_0} F_{2_1} + \frac{S_{2_0} P_{2_1} (D_{2_0} - F_{2_0})}{P_{2_0}}\right) + \left(\mu^{-1} P_{1_0} - P_{2_0}\right) \left[\frac{D_{2_0}}{F_{2_0}} H(\mu P_{2_0} - P_{1_0}) + \frac{D_{1_0}}{F_{1_0}} H(P_{1_0} - \mu P_{2_0})\right]. \tag{44}$$

Using the values from Table 2, we are able to calculate the approximate values for the equilibria using our perturbation estimates to order ϵ.

$$P_{1_\epsilon} = P_{1_0} + \epsilon P_{1_1} \tag{45}$$

$$P_{2_\epsilon} = P_{2_0} + \epsilon P_{2_1} \tag{46}$$

$$F_{1_\epsilon} = F_{1_0} + \epsilon F_{1_1} \tag{47}$$

$$F_{2_\epsilon} = F_{2_0} + \epsilon F_{2_1} \tag{48}$$

$$S_{1_\epsilon} = S_{1_0} + \epsilon S_{1_1} \tag{49}$$

$$S_{2_\epsilon} = S_{2_0} + \epsilon S_{2_1} \tag{50}$$

$$D_{1_\epsilon} = D_{1_0} + \epsilon D_{1_1} \tag{51}$$

$$D_{2_\epsilon} = D_{2_0} + \epsilon D_{2_1} \tag{52}$$

We investigate further how sensitive our parameter ϵ is for the accuracy of our analytical approximation. We keep α constant as to not alter the analysis of varying ϵ. Letting $\alpha_1 = \alpha_2 = 350$, which corresponds to the natural death rates of the fleas and no dusting of insecticide, and the remaining parameters are also defined as in Table 2, we compare our perturbation estimates with those obtained numerically using MAPLE to solve the differential equations. Table 3 shows that for $\alpha_1 = \alpha_2 = 350$, the order ϵ approximations are within 2.6% when $\epsilon = 5$ or less. When we increase $\epsilon = 50$ this accuracy goes down with errors up to 21.3%. We also see that in that case, the S and D population classes are the ones with the largest error. This is due to the error being compounded due to the dependence on the P and F population classes. As colonies are spread further and further away, the interaction between the two colonies keeps decreasing. Eventually, the two colonies will be far enough apart where almost no interaction occurs; in this case, the single colony equations are sufficient to model the distinct colonies.

4 Results and Discussion

The issues that have the most application and interest are where two colonies are separated by smaller distances, ie. larger values of ϵ, and one of the colonies will have plague and the other colony does not have plague. This scenario leads to two main issues which we will cover in the next two subsections. The first issue would be that of asking if and how soon will the second colony contract the plague, and the second issue would be that of asking if we can merely dust the plagued colony and not the plague-free colony to prevent the spread of plague. Below, we present two scenarios to address these issues.

$\epsilon = 0.5$				
	P_1	P_2	F_1	F_2
N	0.996	0.998	0.915	0.918
ϵ	0.997	0.999	0.916	0.917
Error	0.1%	0.1%	0.1%	0.1%
	S_1	S_2	D_1	D_2
N	0.227	0.228	0.148	0.149
ϵ	0.227	0.227	0.148	0.149
Error	0.0%	0.4%	0.0%	0.0%
$\epsilon = 5.0$				
	P_1	P_2	F_1	F_2
N	0.991	1.01	0.910	0.928
ϵ	0.992	1.01	0.911	0.918
Error	0.1%	0.0%	0.1%	1.1%
	S_1	S_2	D_1	D_2
N	0.224	0.233	0.147	0.152
ϵ	0.224	0.227	0.147	0.148
Error	0.0%	2.6%	0.0%	2.6%
$\epsilon = 50.0$				
	P_1	P_2	F_1	F_2
N	0.947	1.08	0.866	1.01
ϵ	0.940	1.11	0.858	0.930
Error	0.7%	2.8%	0.9%	7.9%
	S_1	S_2	D_1	D_2
N	0.203	0.269	0.132	0.178
ϵ	0.199	0.227	0.129	0.140
Error	2.0%	15.6%	2.3%	21.3%

Table 3: Perturbation results vs. Numerical Results for $(\alpha_1 = \alpha_2 = 350)$ with $\beta = 433, \kappa = 4330, \omega = 4950, \sigma = 1400, \mu = 0.5$ and $\epsilon = 0.5, 5.0, 50.0$

4.1 How Long Until Plague Arrives

The first issue we address is that of how long would it take for a colony to get plague from another colony with plague. It is worth mentioning that the model encourages spread of plague when the two populations are at different populations and not necessarily different proportions of their carrying capacities. This is reflected in the parameter μ that appears inside the Heaviside Functions. To minimize that confusion, for this section we will set $\mu = 1$ so that differences in ratios of carrying capacities and differences in overall populations will be equivalent. Other parameters will be the same as in Table 2. We see in Figure 4 that plague is incurred in the second population at 1.0% of the carrying capacity when the scaled time reaches $\bar{t} = .0129$ which corresponds to $t = 64.5$ days. Even when $\epsilon = 5*10^{-6}$ the neighboring colony will still acquire plague at the 1% level by 185 days. As expected, we see that the further distances, ie. smaller values of ϵ, act like a time delay for the arrival of plague in the other colony. In actuality, if the delay is long enough, the plague will wipe out the first colony before it has time to spread. This puts a physical limit as to how small ϵ is allowed to be for physical reality.

4.2 Controlling the Spread of Plague

When we fix $\epsilon = 0.5$ and $\alpha_2 = 350$ (no dusting in the plague colony), plague will still spread to the first colony unless one dusts the first colony at the critical value of $\alpha_1 = 520$ that we found earlier. However, this raises the question that if we dust the plague colony at a level to wipe out the plague $\alpha_2 = 520$, can we get by without dusting the plague free colony and still prevent the spread of plague. We see in Figure 5 that the answer is no. The plague merely transfers from one colony to the other. In fact, we need to also dust this colony at the critical value of $\alpha_1 = 520$ in order to prevent the spread of plague.

5 Conclusion

Both the single and two colony model prove to be useful. The single colony model shows it is possible to eliminate plague in a colony by dusting fleas with a pesticide to increase the death rate of the fleas. Scaling the equations and setting the derivatives equal to zero simultaneously, four equilibria are found: E_1 trivial, E_2 only $\bar{P}$, E_3 only $\bar{P}$ and $\bar{F}$, and E_4 coexistance of $\bar{P}$, $\bar{F}$, $\bar{S}$, and $\bar{D}$. Using only the control parameter, α, all three non trivial equilibria are obtained numerically in MAPLE. This shows that plague can

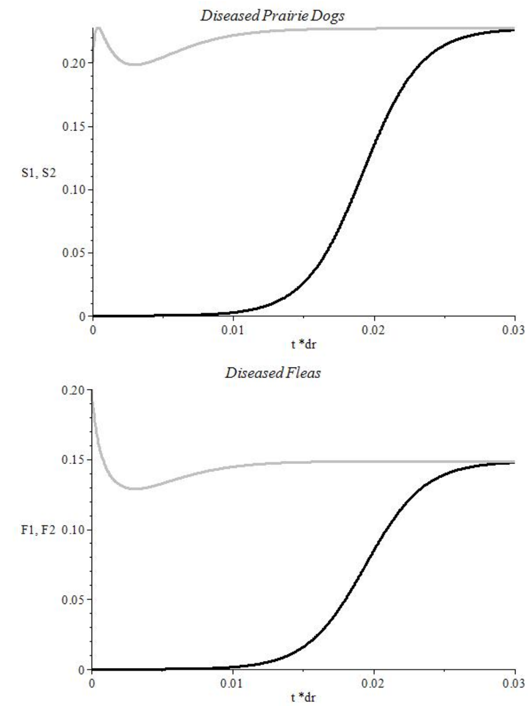

Figure 4: Plague is spread to adjacent colony for initial densities of $P_1(0) = S_1(0) = .6$, $P_2(0) = S_2(0) = .7$, $S_1(0) = D_1(0) = 0$ and $S_2(0) = D_2(0) = .2$ with parameters $(\alpha_1 = \alpha_2 = 350)$ with $\beta = 433, \kappa = 4330, \omega = 4950, \sigma = 1400, \mu = 1.0$, and $\epsilon = 0.5$, Population 1- Black, Population 2- Gray

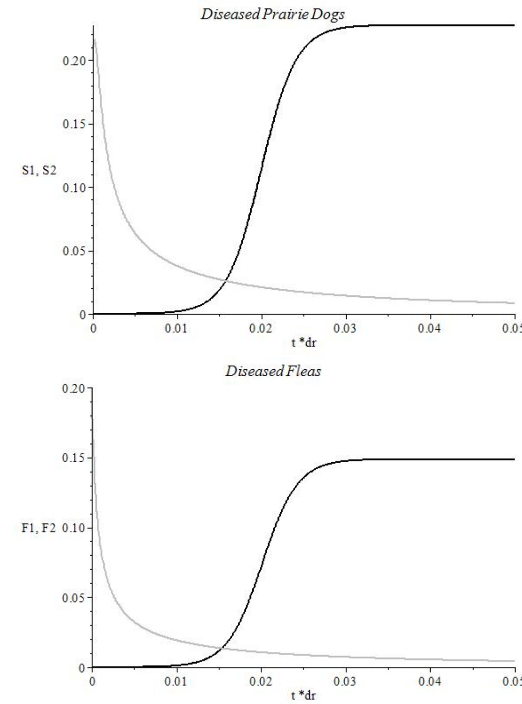

Figure 5: Plague is prevented in a colony by increasing dusting rates to $\alpha_1 = 520$ for parameters $(\alpha_2 = 350)$ with $\beta = 433, \kappa = 4330, \omega = 4950, \sigma = 1400, \mu = 1.0$, and $\epsilon = 0.5$, Population 1- Black, Population 2- Gray

be eliminated by dusting, although it may not be economically possible or practical. It was discovered that one must dust the plague free colony at the critical level $\alpha = 520$ in order to prevent the spread. By assuming a small migration coefficient, ϵ, we are able to numerically show all equilibria found for the single colony model by only altering α_1 and α_2 for each respective colony. We also derived an approximate analytical solution for the populations to order ϵ using a perturbation expansion. In doing so, we find that the perturbation theory is very accurate for $\epsilon \leq 5.0$. Finally, case studies allow us to use the numerical model in MAPLE to find solutions for real-life problems where the distance may or may not be large. We are able to use the model to answer questions about the time frame for which a colony will catch plague from another and if dusting could prevent the spread of plague.

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