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How to measure a halo

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Abstract

The terrestrial mammal fauna of Australia has suffered significant declines in population due to predation by the introduced European red foxes (*Vulpes vulpes*) and feral cats (*Felis catus*). Predator-exclusion fences offer protection to these endangered species and allow their populations to flourish. However, these conservation fences do not allow any animals to leave the fenced region, limiting the species from also creating a population outside the fence. An alternative solution to this is to allow animals to leave the fenced region and create a 'halo' effect in the surrounding areas. In this report we will form differential equation models to analyse how many animals we should be releasing from fences and whether a halo of animals will be beneficial for different species and landscapes.

1 Introduction

Australia's terrestrial mammals have experienced significantly high declines in population and extinction rates over the past 230 years [5]. One of the main reasons for this has been the introduced European red foxes (*Vulpes vulpes*) and feral cats (*Felis catus*), which are both widespread across the entire Australian mainland [3]. Of all Australian ground-dwelling mammal species, 30 have been driven to extinction [5] and at least 68 of the surviving species are highly susceptible to foxes and cats, and are at potential risk of extinction [1].

What these susceptible mammals need are conservation fences; tall, wired, high voltage fences with over-hanging mesh wires, that offer refuge from invasive species [1]. Currently, there are 17 functional predator-exclusion fences across Australia protecting 25 distinct endangered mammal species including the bilby (*Macrotis lagotis*), Gilbert's potoroo (*Potorous gilbertii*) and banded hare-wallaby (*Lagostrophus fasciatus*) [3]. Fenced enclosures, along with predator-free islands, are the only solution for extremely susceptible species, as they cannot persist in the wild due to predatorial foxes and cats [5].

However, fences have their limitations. One of the biggest issues is that animal populations flourish inside fences, but there is nothing beyond their walls. A potential solution to this is to build 'imperfect' fences instead of 'perfect' fences, to allow animals to leave the fenced region and create a 'halo' effect in the surrounding area. New Zealand plans to use its predator-free offshore islands and eco-sanctuaries, along with predator management strategies on the mainland to create halo effects for its threatened species [7]. The kiwi (*Apteryx*) has been declining by approximately 2% each year and has vanished from the city of Wellington, but conservationists hope that they will soon thrive in the city as a result of these strategies to create a halo effect, just as the New Zealand falcon (*Falco novaeseelandiae*) and New Zealand pigeon (*Hemiphaga novaeseelandiae*) have [6]. Halos are playing a significant part in the rehabilitation of New Zealand's fauna and this is solid evidence that species which have suffered periods of endangerment can rise back and prosper as they used to.

If we are building imperfect fences, we need to know how imperfect these fences need to be, or in other words, how many animals we should be releasing from the fenced region and hence how big the halo will be. The size of the halo will depend on a number of factors: the level of predation, the growth rate of the endangered species, the diffusivity of the landscape or how fast animals move in the landscape, and the size of the fence. In this paper, we will answer the question of what the rate of escape for animals inside fenced regions should be, for a range of species and landscapes. We will do this by developing models and a spatial optimisation framework which identifies the rate of escape that maximises the total number of endangered animals.

2 Two Patch Model

A common model of a predator-prey system is,

$$\frac{du}{dt} = ru\left(1 - \frac{u}{k}\right) - \alpha P u \tag{1}$$

where u is the total number of prey, r is the per capita growth rate of prey, k is the carrying capacity of prey, P is the number of predators, and α is the predation rate. The first term in Eq. (1) is a logistical model which is a common description of population dynamics, and it represents the population growth of the prey. The second term represents the predator-prey interaction and the predation rate is essentially the number of predator-prey interactions that result in deaths.

To understand how the variables in this model (e.g. growth rate of prey, predation rate) affect the total number of prey, we can solve Eq. (1). We want the solution at equilibrium, so we set

$$\frac{du}{dt} = 0, \tag{2}$$

and then solve for u^*.

$$0 = ru\left(1 - \frac{u}{k}\right) - \alpha P u \tag{3}$$

$$u^* = \frac{k(r - \alpha P)}{r} \tag{4}$$

We shall now refer to the predation rate multiplied by the number of predators, or αP as the 'level of predation'. From the solution in Eq. (4), we can see that if the growth rate is equal to the level of predation, the total number of prey will be 0, i.e. if $r = \alpha P$, then $u = 0$. Similarly, if $r < \alpha P$, then $u < 0$, however the number of prey cannot be negative, so we assume that it is actually 0. If the growth rate is greater than the level of predation, the total number of prey will be greater than zero. Thus, when $r > \alpha P$, the species can persist in the presence of predation.

So, when $r \leq \alpha P$, the prey species require predator-exclusion fences to conserve their population, but when $r > \alpha P$, the prey do not require fences and can co-exist with their predators. Now, this may not always be true when r is only slightly larger than αP, but we will assume that it is true for our models and we will present our solutions based on this.

A simple approach to the problem is to create a model with two separate 'patches'; one patch represents the landscape inside the fence, and the other represents is the landscape outside the fence. There are then two things we must consider: animals leaving the fenced region, and animals dying due to predators outside the fenced region.

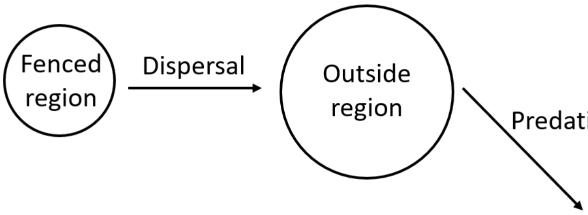

Figure 1: Two patch model

In our two patch model, we need two variants of Eq. (1) to model the abundance of animals inside the fenced region, and the halo of animals outside. Let u_i denote the number of endangered animals in the fenced region, and u_o denote the number outside. Similarly, let k_i and k_o denote the carrying capacity inside and outside the fenced region. To model the dispersal of animals, we subtract the number of animals which leave the fenced region from the equation for the fenced region, and add it to the equation for the outside region. Thus, the two patch model is satisfied by the equations,

$$\frac{du_i}{dt} = ru_i\left(1 - \frac{u_i}{k_i}\right) - u_i F, \tag{5a}$$

$$\frac{du_o}{dt} = ru_o\left(1 - \frac{u_o}{k_o}\right) + {u_i}^* F - \alpha P u_o. \tag{5b}$$

Here F is the flux of animals through the fence, or the percentage of animals leaving the fenced region. The number of animals which leaves the fenced region is given by the number of animals inside, multiplied by the flux of animals through the fence. Note that u_o is dependent on u_i, but not vice versa. The total population of the endangered species is given by,

$$u_t{}^* = u_i{}^* + u_o{}^*. \tag{6}$$

2.1 Analytical Solution

Since we are concerned with the solution at equilibrium, we set

$$\frac{du_i}{dt} = 0, \tag{7a}$$

$$\frac{du_o}{dt} = 0. \tag{7b}$$

Substituting (7a) into Eq. (5a), we then solve for $u_i{}^*$,

$$0 = ru_i\left(1 - \frac{u_i}{k_i}\right) - u_i F, \tag{8}$$

$$u_i{}^* = \left(1 - \frac{F}{r}\right) k_i. \tag{9}$$

Then, substituting Eq. (7b) and (9) into Eq. (5b), and solving for $u_o{}^*$ we get,

$$0 = ru_o\left(1 - \frac{u_o}{k_o}\right) + \left(1 - \frac{F}{r}\right) k_i F - \alpha P u_o. \tag{10}$$

$$u_o{}^* = \frac{r - \alpha P - \sqrt{(r-\alpha P)^2 - \frac{4r}{k_o}\left(1 - \frac{F}{r}\right) k_i F}}{2\frac{r}{k_o}} \tag{11}$$

Thus, substituting Eq.(9) and (11) into Eq. (6), we see the total number of animals is given by,

$$u_t{}^* = \frac{r - \alpha P - \sqrt{(r-\alpha P)^2 - \frac{4r}{k_o}\left(1 - \frac{F}{r}\right) k_i F}}{2\frac{r}{k_o}} + \left(1 - \frac{F}{r}\right) k_i. \tag{12}$$

To find the optimal flux of animals through the fence, we must calculate which value of F gives the maximum total number of animals. So, we find the derivative of $u_t{}^*$ with respect to F, and set it to 0 to solve for the optimal flux.

$$\frac{du_t{}^*}{dF} = 0 = \frac{k_o(2F - r)}{\sqrt{(r-\alpha P)^2 - \frac{4r}{k_o}\left(1 - \frac{F}{r}\right) k_i F}} - k_i, \tag{13}$$

$$F^* = \frac{r}{2} - \left(\frac{(r-\alpha P)^2 + r^2}{8}\right)^{1/2}. \tag{14}$$

To ensure this solution produces a maxima, we differentiate Eq. (13) with respect to F, substitute in $F = F^*$ and check that the value is less than zero. Thus, for any given endangered species' growth rate, r, predation rate, α, and number of predators P, we can calculate the optimal flux of animals through the fence. Substituting this value back into Eq. (12) will then give the total number of animals.

2.2 Results

We also numerically solved Eq. (5) using the Runge-Kutta method. Given the values $r = 0.7$, $\alpha = 0.75$, $P = 1$, $k_i = 0.5$ and $k_o = 4.5$, we changed the value for the flux of animals through the fence and plotted the number of animals:

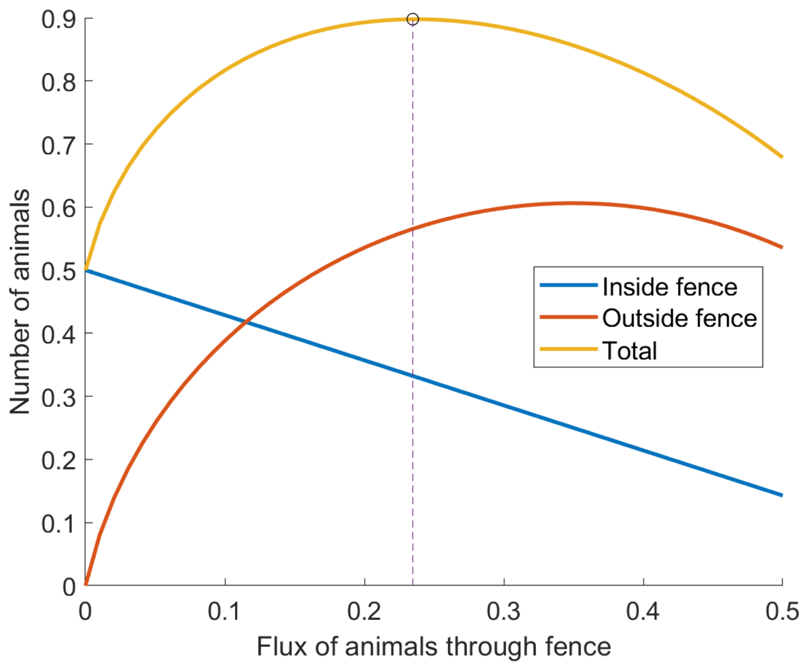

Figure 2: Example solution of Eq. (5) with varying flux

The x-axis is the flux of animals through the fence, and the y-axis is the number of animals. The blue line is the number of animals inside the fence, the red line is the number of animals outside the fence and the yellow is the number of animals in total. As the flux is increased, the number of animals inside the fence decreases. However, the number of animals outside the fence starts out at zero, increases very quickly, then slows down, and then eventually decreases. Naturally, the total number of animals has a similar pattern, except it starts off at 0.5. This decrease is most likely due to the flux being too high, and causing the number of animals inside the fence to become very small, in turn decreasing the number of new animals, hence decreasing the number of animals moving to the outside. It should also be noted since $r < \alpha P$, this species would not be able to survive without fences due to predation.

The optimal flux of animals through the fence is the value that produces the largest total number of animals, which in this scenario is approximately 0.235. This means that 23.5% of animals from the fenced region should be released into the surrounding region, to maximise the total population size.

We then computed the optimal flux of animals through the fence, given by Eq. (14), for different values of predation and growth rates to understand the effects of these variables on the optimal solution.

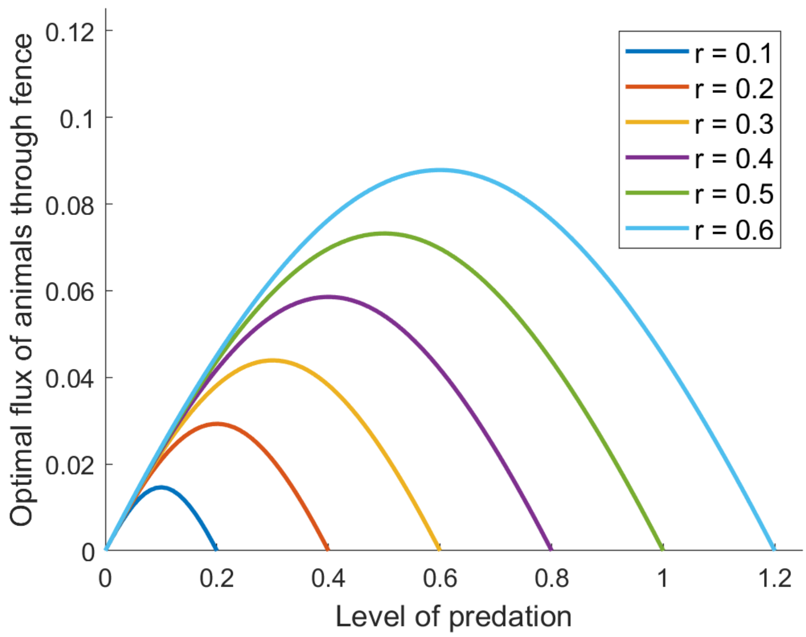

Figure 3: Optimal flux of animals through fence for varying growth and predation rates

The x-axis is the level of predation, the predation rate multiplied by the number of predators or αP, and the y-axis is the optimal flux of animals through the fence. Each curve represents a different per capita growth rate of the endangered species. If the optimal flux is found to be less than zero, this means we need to be moving animals inside the fence, thus we assume the optimal flux is zero would be impractical and/or impossible. For example, when $r = 0.1$, the optimal flux becomes negative when $\alpha P \geq 0.2$, so we assume that it is actually zero.

For the solution to $r = 0.1$, when $\alpha P < 0.1$, the species that doesn't need a fence, but when $\alpha P \geq 0.1$, the species does need a fence. The crossover from not having a fence to having a fence occurs at the stationary point of the curve. Furthermore, whilst the level of predation is less than double the growth rate, the species needs an imperfect fence. However, when it exceeds this value, a perfect fence is needed. Increasing the level of predation for species that need fences, decreases the optimal flux of animals through the fence. This appears to be true for all values of the growth rate in Fig. 3. Additionally, as the growth rate increases, so does the optimal flux.

3 Spatial PDE Model

The two patch model is a simplified model as there exists two different places in space. With a continuous spatial model, the effect of the diffusivity of the landscape on the solution can be analysed, the spatial size of the halo can be measured, and the accuracy of the solution can be improved. The diffusivity of the landscape is how fast animals move in the landscape, and this will affect the size of our halo. Note that this is a one-dimensional model.

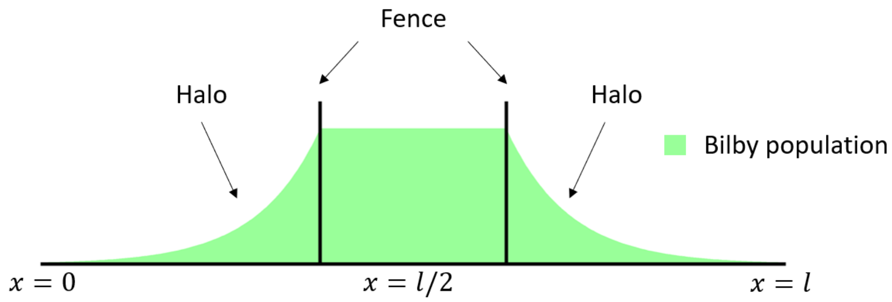

Figure 4: Diagram of halo effect on fence

We assume that the landscape in Fig. 4 is homogeneous, meaning the diffusivity of the landscape is the same everywhere, and hence symmetrical. In other words, the number of animals in the region $0 \leq x \leq l/2$ will be the same as in the region $l/2 \leq x \leq l$. Thus, we will only solve the region, $l/2 \leq x \leq l$.

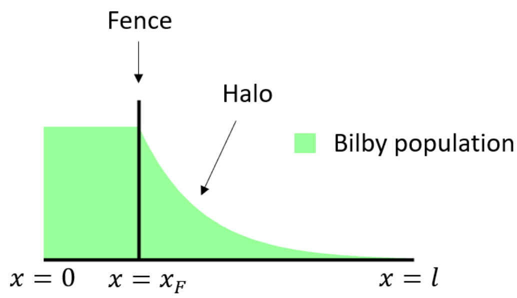

Figure 5: Diagram of landscape to solve

We base our model on Fisher's Equation [4], a commonly used partial differential equation in ecology to model population growth.

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + ru\left(1 - \frac{u}{k}\right) \tag{15}$$

Here, D is the diffusivity of the landscape. The first term in Eq. (15) describes the random movement of animals in the landscape due to diffusion, and the second term describes the growth of the species. However, this equation does not consider the effect of a predatory species. To do this, we add a term to Eq. (15) which describes the predator-prey interaction in our model.

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + ru\left(1 - \frac{u}{k}\right) - \alpha P(x)u \tag{16}$$

Eq. (15) describes a landscape where there is no predator-exclusion fence. So, we must define $P(x)$ as a piece-wise function, such that the third term in Eq. (16) is 0 inside and at the fence.

$$P(x) = \begin{cases} 0 & x \leq x_F \\ P_0 & x > x_F \end{cases} \tag{17}$$

Since we are interested in the solution to Eq. (16) at equilibrium, we set

$$\frac{\partial u}{\partial t} = 0. \tag{18}$$

So, Eq. (16) now becomes an ordinary differential equation,

$$0 = D\frac{d^2 u}{dx^2} + ru\left(1 - \frac{u}{k}\right)1 - \alpha P(x)u \tag{19}$$

To solve Eq. (16), we rewrite it as a system of first order ODEs by setting $u = u_1$ and $u' = u_1' = u_2$.

$$\frac{du_1}{dx} = u_2 \tag{20a}$$

$$\frac{du_2}{dx} = \frac{1}{D}\left[P(x)u_1 - ru_1\left(1 - \frac{u_1}{k}\right)\right] \tag{20b}$$

To solve this system of ODEs for the landscape as in Fig. 5, this system is first solved for the fenced region, i.e. for $0 \leq x \leq x_F$, with the boundary conditions:

$$\left.\frac{du_1}{dx}\right|_{x=0} = 0, \tag{21a}$$

$$\left.\frac{du_1}{dx}\right|_{x=x_F} = -u_1F. \tag{21b}$$

Eq. (21a) states that the rate of change of animals at the start of the fenced region is 0. Eq. (21b) states that the rate of change of animals at the fence is the flux of animals multiplied by the number of animals at the fence. This value is negative because the animals are leaving the fence. The system of ODEs is then solved for the outside region, i.e. for $x_F \leq x \leq l$, with the boundary conditions:

$$\left.\frac{du_1}{dx}\right|_{x=x_F} = -u_1F, \tag{22a}$$

$$\left.\frac{du_1}{dx}\right|_{x=l} = 0. \tag{22b}$$

When solving for the outside region, the solution to the inside region is used as the value of u_1 in Eq. (22a). Since we are matching Dirichlet boundary conditions, Eq.(21b) is the same as Eq.(22a).

3.1 Results

The system of ODEs, Eq. (20), subject to boundary conditions, Eq. (21) and (22), was numerically solved using a finite difference method, since it is difficult to solve analytically. Given the values $r = 0.7$, $\alpha = 0.9$, $P = 1$, $D = 0.5$, $k = 1$ and $F = 0.2$, the solution is:

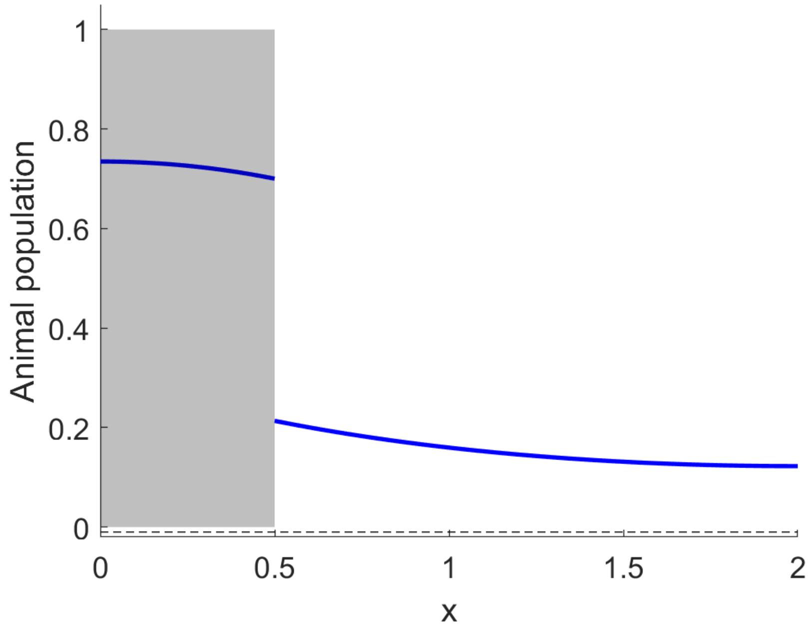

Figure 6: Example solution to Eq. (20)

There is an abundance of animals inside the fence (the grey region) and a halo of animals outside the fence which slowly decreases. This example solution is what we would expect, and looks similar to Fig. 5. However, the number of animals outside the fence is fewer than expected, and this is because the predation is high. There is also a discontinuity at the fence since we are matching Dirichlet conditions, Eq. (23), instead of Neunmann conditions, Eq. (24).

$$\frac{du_i}{dx}\Big|_{x=x_F} = \frac{du_o}{dx}\Big|_{x=x_F} \tag{23}$$

$$u_i(x_F) = u_o(x_F) \tag{24}$$

In other words, the value at the fence is the rate of change of the solution inside rather than the value of the solution inside.

To find the optimal flux of animals through the fence, the system can be solved for different values of F. Given the values $r = 0.7$, $\alpha = 0.75$, $P = 1$, $D = 0.5$ and $k = 1$, the solution is:

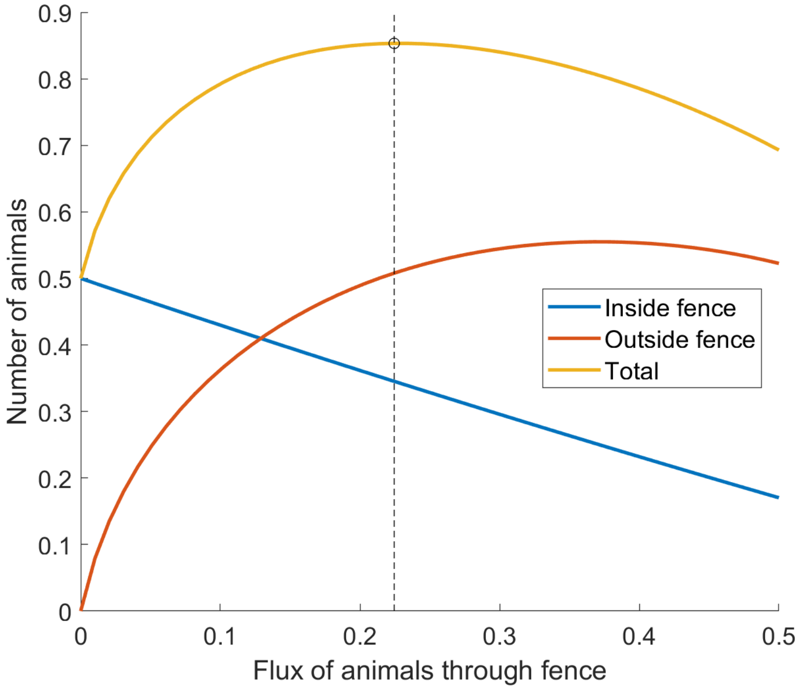

Figure 7: Example solution to Eq. (18) with varying flux

Fig. 7 is very similar to Fig. 2, which is an example solution to the two patch model with varying flux. This is a favourable result because this means our models match. In this example, the optimal flux of animals through the fence is approximately 0.225. This means that 22.5% of animals from the fence should be released into the surrounding area to maximise the total population. Comparing this to the solution for two patch model, we find that the optimal flux for the two patch model is 1% larger, with the given values. This difference can most likely be attributed to the addition of the diffusivity of the landscape in the PDE model.

For varying values of growth rate and level of predation, the optimal flux of animals through the fence can be computed, to find the optimal solution. Given that the carrying capacity of the endangered species is 1 and the diffusivity of the landscape of 0.25, the optimal solution is:

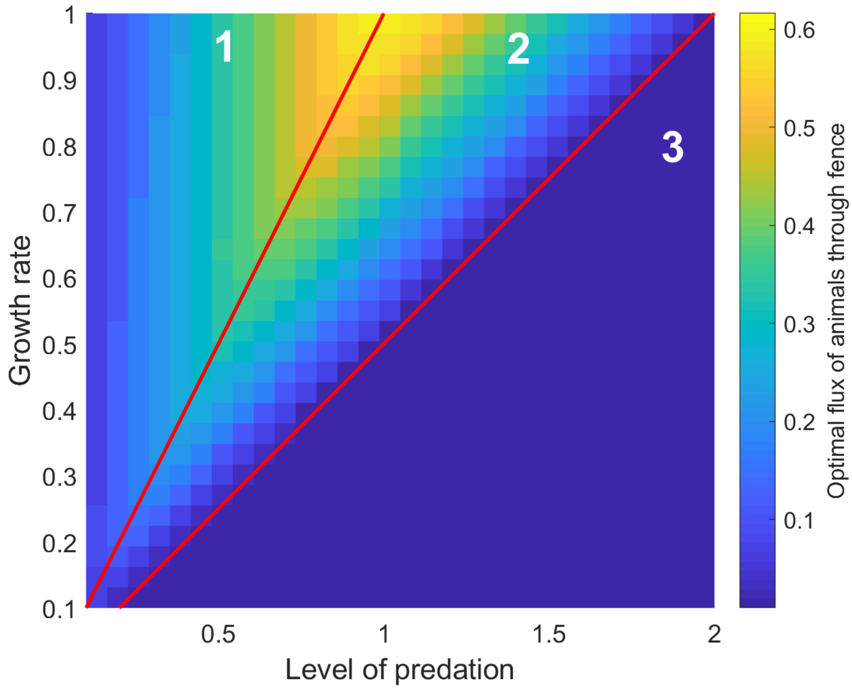

Figure 8: Optimal solution to Eq. (20)

The red lines have been added to Fig. 8, to show the three general types of solutions: no fence (section 1), imperfect fence and halo (section 2), and perfect fence (section 3). A no fence solution is for those species that can survive in the presence of predation, as mentioned earlier. A perfect fence has an optimal flux of 0, meaning that no animals should be allowed to leave the fence. An imperfect fence will have an optimal flux of greater than 0, meaning that some percentage of animals should be allowed to leave the fence to create a halo effect.

Although not immediately evident, Fig. 8 is quite similar to Fig. 3, which shows us the optimal flux of animals through the fence for varying growth rates and predation rates for the two patch model. The change between no fence and imperfect fence occurs when the growth rate is the same as the level of predation, which also appears to be the turning point of a parabolic curve in Fig. 8. Furthermore, the change between an imperfect fence and perfect fence occurs when the level of predation is double the growth rate. Again, this is a promising result, as this means our two patch model and spatial PDE model match.

4 Discussion

To determine whether imperfect fences are a viable option for endangered mammals, we modelled this in two different ways: as a two patch model with two coupled ODEs and as a spatial PDE model. We found that some species need imperfect fences and halos to maximise their population, whilst some species need perfect fences as they cannot survive in the presence of predation at all. We also found that some species don't require fences at all as they can persist in the presence of predation. In general, we saw that if the level of predation is smaller than the per capita growth rate, this is when the species can persist and doesn't require a fence. Once the level of predation reaches the value of the growth rate, this is when the species needs a fence in order to survive. For such species that need fences, the rate of escape of the animals from the fence decreases as the level of predation increases. Until the point when the level of predation becomes double the growth rate, a halo of animals will maximise the total population, but after this point, the fences need to be perfect.

It should be noted that for those species that fall into the category of no fence in our model (section 1 of Fig. 8), it may be the case that this species actually requires a fence to improve the state of the population, especially when the growth rate is approximately the same value as the level of predation. In this case, if conservation managers were to build a fence for such a species, they would still be able to utilise our optimal solution for the rate of escape of animals to maximise the total species population.

In the past, a lot of research has been done on predator-exclusion fences [3] and there's no longer any doubt of whether they work or not; the numerous fences we have built are solid evidence that they do. In recent years, some research has looked into how endangered species can benefit from conservation fences with halo effects, and it has been seen to work in New Zealand [7]. However, to the extent of our knowledge, no work has been done on how imperfect fences should be to maximise different species' populations, and whether all species will benefit from halos.

Arguably, the model we created has many limitations. We treated the diffusivity of the landscape to be homogeneous, but this does not reflect the landscape for the inside of a fence or its surrounding area. We also defined the number of predators to be constant outside the fence, which again does not accurately reflect what it would actually be. The number of predators would depend heavily on the number of prey. Furthermore, many of the values for the variables in our model are unknown, such as the diffusivity of the landscape, and it is difficult to estimate what some of these may be. This could mean that our solution is completely wrong in some cases, and the only way to verify this would be to model this for a real predator-exclusion fence.

In future research, we can improve our model by modelling the diffusivity of the landscape and number of predators more accurately. Further work should also be done on estimating the parameters in our model to more accurately represent the reality for varying species and landscapes. Additionally, by extending our models we could measure the spatial size of halos for different species and landscapes. This would prove highly useful in analysing the benefits of halos. In this project, we have chose the optimal rate of escape such as to maximise the total population of the endangered species, however in future we could chose the optimal rate of escape to instead maximise the spatial size of the halo. Depending on the conservation status of the species, and the goal of the conservation managers, it may be that a larger inhabited land area with a smaller population for a species is more beneficial than a smaller inhabited land area with a larger population, as this may improve the population of the species in the long run.

5 Implications for species conservation

The results from our model, as discussed previously, have significant implications for the conservation of endangered Australian mammals. For example, the long-footed potoroo (*potorous longipes*) has a per capita growth rate of 0.37 [2] and is currently not protected by a predator-exclusion fence or a predator-free island [3]. For the majority of cases for level of predation, this species needs a perfect or near-perfect fence in order to maximise the total population. The rufous hare-wallaby or mala (*lagorchestes hirsutus*) has a growth rate of 0.83 [2] and has a few populations in predator-exclusion fences or predator-free islands [3]. When the predation is relatively low for this species, having a halo around its fence will maximise the total population, but when the predation becomes too high, a perfect fence will maximise the population. On the other hand, a bilby (*macrotis lagotis*) has a growth rate of 3.06 [2] and is currently protected by fences and islands [3]. This species should benefit from a halo in the majority of scenarios as it's growth rate is quite high and will be able to persist in the presence of predation with the help of the halo effect.

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