Costs and decisions in population management: koalas on Kangaroo Island

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EXTENDED ABSTRACT

Many populations have a negative impact on their habitat, or upon other species in the environment, if their numbers become too large. For this reason they are often managed using some form of control. The objective is to keep numbers at a sustainable level, while ensuring survival of the population.

One such population is the koalas (*Phascolarctos cinereus*) of Kangaroo Island, South Australia. Between 1923 and 1925, 18 koalas were introduced to the island as a conservation measure to protect them (they were classified as a threatened species). Today, the Kangaroo Island koalas are considered to be a pest. Their overabundance has had a significant negative impact on the health of the Rough-barked Manna-gum (*Eucalyptus viminalis cygnetensis*), along with other high-quality koala habitat. As a response to poor and insufficient habitat, numbers are predicted to decline sharply, and, because of the increased risk of extinction of the koalas and of other species, control and management programs have been proposed.

Here we present models that allow population management programs to be assessed. Two common control regimes will be considered: reduction and suppression. Under the suppression regime the population is maintained close to a particular threshold through near continuous control, while under the reduction regime, control (for example culling or sterilisation) begins once the population reaches a certain threshold and continues until it falls below a lower pre-defined level.

We discuss how to best choose the control parameters, and we provide tools that allow population managers to select reduction levels and control rates. Additional tools will be provided to assess the effect of different control regimes, in terms of population persistence and cost. In particular we consider the effects of each regime on the probability of extinction and the expected time to extinction, and compare the control methods in terms of the expected total cost of each regime over the life of the population.

The usefulness of our results will be illustrated with reference to the control of the koala population. We select a suitable reduction level based on a specified probability of persistence, the genetic diversity of the population and the expected time between control phases. All are important in the management of native fauna. Firstly, while we are aiming to control the population, we wish to ensure the survival of the species without introducing risk additional to that faced prior to control. Next, genetic diversity, which is often overlooked when managing populations, is of utmost importance. The aim is to avoid inbreeding depression and to allow for evolutionary change. We must select a minimum reduction level that ensures a high probability of persistence, while maintaining an adequate level of genetic diversity. We find that a reduction level larger than that derived through these considerations will often be allowable in practice. To aid in selecting the reduction level, we also provide an explicit formula for the expected time between culling phases. Population managers can then select a reduction level so that the time between implementing successive controls is larger than some stipulated minimum (necessitated, for example, by resource constraints). The optimal rate of culling is then obtained by minimizing the cost of each culling phase, before finally selecting the optimal regime for control in terms of the expected cost of control over the life of the koala population.

Our results can be easily extended to various control types (for example, sterilisation and translocation), and birth and death rates other than the ones considered here (for example, we may employ logistic birth rates). Consequently, we anticipate that our approach will be useful in a variety of population management contexts.

1 INTRODUCTION

Many populations have a negative impact on their environment once their numbers become too large. This impact may be so great that extinction is predicted. This is true of the koala population on Kangaroo Island, South Australia, which is having a significant negative impact on the health of the Rough-barked Manna-gum and other high-quality koala habitat. The high koala density has resulted in degradation of habitat, which is predicted to lead to a sharp population decline and thus an increased risk of extinction of the koalas and of other species (see Masters *et al.* (2004)). Populations with this characteristic—negative impact on the environment or other species—are often controlled. Additionally, for many populations of this type (such as the koalas on Kangaroo Island), while we are aiming to control them, we also wish to ensure the survival of the species without introducing risk additional to that faced prior to control. The management objective is to keep numbers at a sustainable level, while ensuring survival of the population. We consider the control option of *culling* to present our work, but many forms of control may be accounted for in the model. In reality, for the koalas on Kangaroo Island, culling would most likely be a one-off event followed by a strict sterilisation program. Our approach can be easily modified to accommodate such situations. We study two common control regimes: *reduction* and *suppression*. Under the suppression regime the population is maintained close to a chosen threshold through near continuous control, while under the reduction regime culling begins once the population reaches a critical threshold and continues until it falls below a lower pre-defined level. Yamauchi (2000) uses a diffusion approximation to investigate the economic cost and reduced persistence under both regimes. Our models have the advantage of a discrete state space, thus providing a more accurate description of real populations. Additionally, we consider some of the problems faced by management teams. In particular, we provide methods for selecting suitable thresholds and culling rates. We model the controlled population using a continuous-time Markov chain. The basic model, without control, is the linear birth-death process. However, our methods extend easily to any birth-death process.

Under the reduction regime we are able to select a minimum reduction level based on three quantities: a specified probability of persistence, the level of genetic diversity and the expected time between culling phases. The selection of the culling rate is also investigated in terms of minimizing the cost of culling. We assess the total cost of each policy over the lifetime of the population by employing a method developed by Pollett and Stefanov (2002), where formulae are derived for the distribution and the expectation of the total cost of any Markovian model over its lifetime. Finally, we examine the problem of choosing an optimal management policy in terms of these costs and population persistence.

2 THE MODELS

2.1 Birth-death Processes

Denoting the population size at time t by $x(t)$, a birth-death process is a continuous-time Markov chain $(x(t),\, t \geq 0)$ taking values in $S := \{0, 1, \ldots\}$ governed by non-zero transition rates

$$q(x, x+1) = \lambda_x \quad \text{and} \quad q(x, x-1) = \mu_x,$$

being the birth and the death rate, respectively, when the population size is x.

A special case of the birth-death process, which we use here, is the *linear* birth-death process. This has $\lambda_x = \lambda x$ and $\mu_x = \mu x$, where λ and μ are the per capita birth and death rates, respectively. We might have used the more common logistic birth rate $\lambda_x = \lambda x(1 - x/N)$, with a population ceiling N, but, as we anticipate that culling will occur at population sizes much smaller than the ceiling, a linear rate will suffice.

2.2 Control Models

Suppression Regime. This management policy dictates the removal of individuals from a population when at or above a particular threshold M, to keep the population size maintained around that level. Therefore when the population size reaches or exceeds the chosen threshold M, the death rate is increased to a value larger than the birth rate. Thus, our *linear birth-death process with suppression* has the same state space S, but non-zero transition rates $q(x, x+1) = \lambda x$, for all x, and

$$q(x, x-1) = \begin{cases} \mu x, & x \leq M \\ (\mu + \kappa)x & x > M, \end{cases}$$

where κ is the rate of culling, required to be larger than $\lambda - \mu$. We assume here *per-capita* culling, reflected in the form of the death rate $(\mu + \kappa)x$. In many cases constant culling (rate $\mu x + \kappa$) may be more appropriate. The choice depends on the particular management program used. The model can easily be modified to account for other management programs, such as sterilisation; instead of an increased death rate, we would have a deceased birth rate.

Reduction Regime. Under this management policy the population is reduced to a pre-defined level L once the population size reaches the critical level U. Therefore when the population is in state U $(> L)$ the death rate is increased to account for culling and restored once the population size is reduced to L. Our model here is a continuous-time Markov chain with state space $S := \{0, 1, \ldots\} \times \{0, 1\}$ and non-zero transition rates

$$q((x, 0), (x+1, 0)) = \lambda x, \qquad x < U - 1,$$

$$q((x,0),(x-1,0)) = \mu x, \qquad x < U,$$

$$q((U-1,0),(U,1)) = \lambda(U-1),$$

$$q((x,1),(x+1,1)) = \lambda x, \quad x \in \{L+1, L+2, \ldots\},$$

$$q((x,1),(x-1,1)) = (\mu+\psi)x, x \in \{L+2, L+3, \ldots\}$$

and

$$q((L+1,1),(L,0)) = (\mu+\psi)(L+1),$$

where ψ is the rate of culling, once again required to be larger than $\lambda - \mu$. A typical state (x, f) has x being the population size and f being an indicator variable, which is 0 in the non-culling phase and 1 in the culling phase. For a description of a general version of this kind of process (a *birth-death process with two phases*), see Pollett and Ross (2005). Again the model can be adjusted to account for sterilisation programs.

3 CHOICE OF REDUCTION LEVEL

We present a method for selecting the reduction level L, the population size following a culling phase. We base this selection on a specified probability of population persistence, the level of genetic diversity and the expected time between culling phases.

3.1 Population Persistence

The persistence measure we use is the probability α_i of reaching U before 0, starting with a population of size i. For the general birth-death process with birth rates λ_x and death rates μ_x, this probability is given by $\alpha_i = s_i/s_U$, where $s_0 = 0$, $s_1 = 1$ and, for $2 \leq i \leq U$,

$$s_i = 1 + \sum_{j=1}^{i-1} \prod_{k=1}^{j} \frac{\mu_k}{\lambda_k}.$$

Thus, for a chosen minimum probability ρ that the population reaches U before 0 starting from i, we may identify a minimum reduction level $L_{\min;\rho}$. This is given by $L_{\min;\rho} := \inf\{i : \alpha_i \geq \rho\}$. For our model,

$$\alpha_i = \frac{1 - (\mu/\lambda)^i}{1 - (\mu/\lambda)^U}$$

(being the familiar Gambler's Ruin probability), and so clearly

$$L_{\min;\rho} = \left\lceil \frac{\ln\{1 - \rho[1 - (\mu/\lambda)^U]\}}{\ln(\mu/\lambda)} \right\rceil,$$

where $\lceil a \rceil$ denotes the smallest integer greater than a.

Table 1 lists various probabilities ρ of persistence, and the corresponding minimum reduction levels $L_{\min;\rho}$, for a population with $\lambda = 0.18$, $\mu = 0.1$ and $U = 10,000$. The reduction levels for the particular parameter values are small, and thus larger reduction levels could be implemented in practice.

ρ	$L_{\min;\rho}$
0.99	8
0.999	12
0.9999	16
0.99999	20

Table 1: Various probabilities ρ of population persistence and the corresponding minimum reduction levels $L_{\min;\rho}$.

3.2 Genetic Diversity

Genetic diversity is an important consideration in the context of population management (see Franklin (1980), Soule (1980) and Lande and Barrowclough (1987) for a discussion). Maintaining a sufficient level of genetic diversity avoids inbreeding depression, while allowing for evolutionary change. This amounts to ensuring an adequate *effective population size*: the number of individuals in an ideal population that would have the same genetic properties (in terms of random genetic drift) as an actual population with its own complex traits (for example, demographics and varying sex ratios). It is widely recommended that the effective size N_e of a population be at least 500, and this has been incorporated into management plans for other populations (see for example Seal and Foose (1983)). On the other hand, Lande (1984) warns that even populations with N_e of the order of 10^3 may incur a substantial risk of extinction from fixation of new mutations.

We therefore calculate the minimum reduction level $L_{\min;N_e}$ needed to ensure a chosen minimum effective population size of N_e^{min}. Franklin (1980) and Lande and Barrowclough (1987) discuss the calculation of effective population size for a number of different scenarios. For simplicity, and due to a lack of information on the koalas of Kangaroo Island, we assume equal population sizes of males and females. Ideally one should know (or estimate) the sex ratio, as it has a significant impact on the effective population size. We use a continuous-time version of the overlapping generations model discussed in Lande and Barrowclough (1987). We need only consider the growth phase, that is the period following a cull until the population reaches the critical threshold (Phase 0). We require that the effective population size during this phase be greater than N_e^{min}. The effective population size during this phase, starting in state i, is given approximately by $N_e \approx \tau_i/\tau_i^{\mathrm{HM}}$ (being the harmonic mean of the population size over Phase 0), where τ_i is the expected time to hit U starting from i, conditional on hitting U before 0, and τ_i^{HM} is the path integral (area under the curve) of the inverse of the population size over the period.

3.3 Expected Phase Times

We digress to consider the expected phase times of the reduction regime model, needed to evaluate the effective population size. Under the reduction regime, both the culling and non-culling and phases will incur costs, in the latter case because of monitoring. It will therefore be useful to know the expected time to reach the critical threshold U. It will also be useful to know the expected time to return to L from U, because increased monitoring will be required when the population size approaches these critical thresholds. Additionally, we may be able to decrease monitoring in the intermediate periods to reduce costs. The expected time spent in the culling phase also provides us with an estimate of the time needed to cull the population: useful for selecting culling rates in the reduction model. We use results of Pollett and Ross (2005) to derive explicit expressions for these expected times.

Non-Culling Phase (Phase 0). For a general birth-death process with two phases, the expected time spent in the non-culling phase, conditional on reaching state U, is given by

$$\tau_L = \sum_{i=L}^{U-1} \frac{1}{\lambda_i \pi_i \alpha_i \alpha_{i+1}} \sum_{j=1}^{i} \alpha_j^2 \pi_j,$$

where $\pi_1 = 1$ and $\pi_j = \prod_{i=2}^{j} \frac{\lambda_{i-1}}{\mu_i}$, $j \geq 2$. For our model this evaluates to

$$\tau_L = \frac{1}{\lambda} \sum_{i=L}^{U-1} \frac{1}{[1-(\mu/\lambda)^i][1-(\mu/\lambda)^{i+1}]} \times \sum_{j=1}^{i} \frac{1}{j} \left[\left(\frac{\mu}{\lambda}\right)^j - 1\right]^2 \left(\frac{\lambda}{\mu}\right)^{j-i}. \quad (1)$$

Culling Phase (Phase 1). The expected duration of the culling phase is simply the expected time to hit L starting from U for a birth-death process with rates corresponding to those for the culling phase. This is given by

$$\gamma_U = \sum_{k=L+1}^{U} \frac{1}{(\mu+\psi)k\pi_k} \sum_{j=k}^{\infty} \pi_j,$$

where $\pi_L = 1$ and $\pi_j = \prod_{i=L+1}^{j} \frac{\lambda(i-1)}{(\mu+\psi)i}$, $j \geq L+1$, For our model this evaluates to

$$\gamma_U = \frac{1}{\mu+\psi_2} \sum_{j=0}^{\infty} \sum_{k=L+1}^{U} \frac{1}{j+k} \left(\frac{\lambda}{\mu+\psi_2}\right)^j.$$

3.4 Effective Population Size

We now return to problem of calculating the effective population size N_e. We already have an expression for τ_i, namely (1). We may now also evaluate τ_i^{HM} using results of Pollett and Stefanov (2002) concerning the evaluation of path integrals. We get

$$\tau_i^{\text{HM}} = \sum_{k=i}^{U-1} \frac{1}{\lambda_k \pi_k \alpha_k \alpha_{k+1}} \sum_{j=1}^{k} f_j \alpha_j^2 \pi_j,$$

where $\pi_1 = 1$ and $\pi_j = \prod_{k=2}^{j} \frac{\lambda_{k-1}}{\mu_k}$, $j \geq 2$, and $f_j = 1/j$. This evaluates to

$$\tau_i^{\text{HM}} = \frac{1}{\lambda} \sum_{k=i}^{U-1} \frac{1}{[1-(\mu/\lambda)^k][1-(\mu/\lambda)^{k+1}]} \times \sum_{j=1}^{k} \frac{1}{j^2} \left[\left(\frac{\mu}{\lambda}\right)^j - 1\right]^2 \left(\frac{\lambda}{\mu}\right)^{j-k}.$$

For a chosen minimum effective population size N_e^{min} we may identify the minimum reduction level $L_{\min;N_e}$. This is given by

$$L_{\min;N_e} := \inf\left\{i : \frac{\tau_i}{\tau_i^{\text{HM}}} \geq N_e^{min}\right\}.$$

In practice it will often be difficult to evaluate the required expected times. However, whenever the underlying model is *density-dependent* (see Pollett (2001)), as it is here, we may approximate the expected times using the analogous deterministic model. For our model we obtain

$$\tau_i \approx (\lambda-\mu)^{-1} \ln(U/i) \quad (2)$$

and

$$\tau_i^{\text{HM}} \approx \frac{U-i}{Ui(\lambda-\mu)},$$

and thus

$$L_{\min;N_e} \approx \inf\left\{i : \left(\frac{Ui}{U-i}\right) \ln\left(\frac{U}{i}\right) \geq N_e^{min}\right\}.$$

The effect of varying the minimum effective population sizes N_e^{min} on the minimum reduction level $L_{\min;N_e}$ is illustrated in Table 2 for a population with $U = 10,000$.

N_e^{min}	$L_{\min;N_e}$
500	110
1000	270
1500	467
2000	700

Table 2: Minimum effective population sizes and the resulting minimum reduction level for a population with $U = 10,000$.

The minimum reduction level $L_{\min}$ can then be taken to be the maximum of $L_{\min;\rho}$ and $L_{\min;N_e}$. Whilst this provides us with a workable minimum, population dynamics may change at lower densities and thus in most cases we will choose a level larger than this minimum. Also, many populations are relocated to regions where the species is declining in the hope of increasing its persistence. Such translocation is also frequently implemented in an attempt to control populations, as was the case between 1997 and 2000 for the koalas of Kangaroo Island (see Masters *et al.* (2004)). For populations that are growing rapidly and require control in one area, but are declining in other areas, such translocation would be similar in effect to captive breeding for prolonging the persistence of declining species. For these situations techniques exist for the optimal management (see for example Tenhumberg *et al.* (2004)). One advantage of this, for the type of population considered here, is the high probability of persistence, since the population is not captive but, rather, occupies optimal habitat. Such translocation will also warrant a larger reduction level. The expected duration of the first phase, given by (1) and approximated by (2), may also be useful for selecting a suitable reduction level; we may choose a level such that the expected time between culling phases is larger than some acceptable minimum.

4 CHOICE OF SUPPRESSION THRESHOLD

Having selected a suitable reduction level L we may now select a suitable suppression threshold M. A sensible choice for M is the average population size under the reduction regime. We evaluate this using the expected times and path integrals for our density-dependent deterministic model, as outlined above, and arrive at

$$M \approx \left\lceil \frac{U-L}{\ln(U)-\ln(L)} \right\rceil . \tag{3}$$

5 CHOICE OF CULLING RATES

In this section we discuss how to choose appropriate culling rates for our models. For the reduction model we base this choice on minimizing the cost of culling.

Suppression Regime. The only constraint on the culling rate for the linear birth-death suppression model is the obvious requirement that $\mu + \kappa > \lambda$. The choice will be based mainly on the cost of culling, since under this regime the control is almost continuous in time.

Reduction Regime. After selecting the reduction level we can calculate the cost for a particular culling rate from the formula for γ_U presented in the last section, once again in conjunction with results of Pollett and Stefanov (2002). The expected cost of a culling phase is given by

$$c_U = \sum_{k=L+1}^{U} \frac{1}{(\mu+\psi)k\pi_k} \sum_{j=k}^{\infty} f_j \pi_j ,$$

where $\pi_j = \prod_{i=L+1}^{j} \frac{\lambda(i-1)}{(\mu+\psi)i}$ and f_j is the cost per unit time of culling a population of size j. To minimize c_U we must first specify f_j. We will use the cost function

$$f_j = d\psi^{1+\delta} j, \tag{4}$$

where d is the culling cost per individual, per unit of time, and δ is a non-negative constant that reflects increasing cost associated with increased culling effort. For a given cost function we choose the culling rate ψ that minimizes c_U, subject to constraints $\lambda - \mu < \psi < \psi^{max}$. Using (4), the cost of the culling phase is

$$c_U = \frac{d\psi^{1+\delta}(U-L)}{\mu+\psi-\lambda}.$$

This is minimized over the range $\lambda - \mu < \psi < \psi^{max}$ by

$$\min\left\{ \left(\frac{1+\delta}{\delta}\right)(\lambda-\mu), \psi^{max} \right\}.$$

So, when $\delta = 0$, we should cull at the fastest rate possible, while if $\delta > 0$, the optimal rate of culling is given by

$$\psi = \left(\frac{1+\delta}{\delta}\right)(\lambda-\mu). \tag{5}$$

6 EXTINCTION AND COSTS

6.1 Extinction Probabilities

Extinction occurs with probability 1 for the per-capita culling models. While at first this may seem undesirable, because it is contrary to the management objective, eventual extinction is inevitable under these models if we are to satisfy the desirable objective of preventing unbounded growth. Additional support will commonly be found when consideration is given to the time scale over which the competing causes of extinction are expected to occur. For the koalas of Kangaroo Island, for example, extinction without control is imminent, particularly in comparison with extinction due to control (as discussed below). For situations when constant culling is used we may invoke formulae in Pollett and Ross (2005) to evaluate the probability of extinction. The probability will be close to 1, as a consequence of selecting a suitable culling rate.

6.2 Extinction Times

We now present formulae for the expected time to extinction for each of our models. While we are attempting to control populations, in most situations we also wish to choose a method that ensures, to as large an extent as possible, population persistence. Therefore these times are of interest for choosing between different control regimes; we can investigate and compare the effect of the different culling methods on population persistence.

Suppression Regime. Our suppression regime model is simply a (linear) birth-death process, for which an explicit expression for the time to extinction exists (see Norris (1997)).

Reduction Regime. The expected extinction time for the reduction regime model, starting in state U with culling, is given by

$$\phi_U = \gamma_U + (\tau_L + \gamma_U)\left(\frac{\alpha_L}{1-\alpha_L}\right) + \xi_L,$$

where ξ_L, the expected time to hit 0 starting from L conditional on hitting 0 before U, is given by

$$\xi_L = \sum_{j=1}^{L} \frac{1}{\mu_j \pi_j (1-\alpha_j)(1-\alpha_{j-1})} \sum_{k=j}^{U} (1-\alpha_k)^2 \pi_k$$

(see Pollett and Ross (2005)). For our model, ξ_L evaluates to

$$\xi_L = \frac{1}{\mu}\sum_{j=1}^{L}\frac{1}{[(\mu/\lambda)^j-(\mu/\lambda)^U][(\mu/\lambda)^{j-1}-(\mu/\lambda)^U]} \times \sum_{k=j}^{U}\frac{1}{k}\left[\left(\frac{\mu}{\lambda}\right)^k-\left(\frac{\mu}{\lambda}\right)^U\right]^2\left(\frac{\lambda}{\mu}\right)^{k-j}.$$

6.3 Total Costs

The final consideration in choosing a management policy (or control regime) is the economic costs of the policies. In this section we adapt the methods of Pollett and Stefanov (2002) to evaluate the expected total cost of each management policy over the lifetime of the population. The resulting formulae are similar to our extinction time formulae, because the expected total cost is simply the expected time to extinction for a process with modified transition rates (see the remark in the last paragraph of Pollett and Stefanov (2002)).

For the suppression regime we use the cost function $f_i = D + K$, where D is the cost per unit time of monitoring and K is the cost per unit time of controlling the population. For the reduction regime, we use

$$f_{(i,0)} = J, \qquad f_{(i,1)} = Ci + J,$$

where C is the cost per capita, per unit time, of controlling the population, and J is the per unit time cost of monitoring.

For both models we have continuous monitoring of the population. The purpose of this monitoring is to determine when control should be implemented, to ensure the correct rate of control and to ensure cessation of control at the appropriate time. It is also useful to ensure that the population does not start to decline, due to some external influence. In such a case, a management program to boost population size may be implemented, in contrast to the control management programs considered here. The cost of culling under the suppression regime is assumed to be constant through time, as individuals are being killed frequently to maintain the population size around M, while under the reduction regime control only occurs during the culling phase, and the per capita cost is used to reflect the per capita rate of culling.

7 THE KOALAS OF KANGAROO ISLAND

We illustrate the usefulness of our results by considering the control of the Kangaroo Island koalas. The first step is to estimate the per capita birth and death rates, λ and μ. Based on abundance data (initial population size, and a conservative estimate of the population size in 2001 (Masters *et al.* (2004)) and a conservatively chosen average lifetime of 10 years ($\mu = 0.1$), we arrive at a growth rate of $\lambda = 0.18$. We must also select the carrying capacity. About 9 years ago a taskforce recommended the culling of $2,000$ koalas, based on an estimated population size of $5,000$. The population size was re-estimated to be around $27,000$ in 2001, and it was recommended in 2004 that the population be reduced by a minimum of $20,000$ to ensure its survival (at which time it was estimated to consist of $30,000$ koalas). We therefore use an estimated maximum carrying capacity of $U = 10,000$.

Using these estimates, we will use the methods described above to select suitable control parameters. First we select a reduction threshold by way of our reduction regime model. From Tables 1 and 2 we see that the reduction level $L_{\min}$ should be at least 700 (using a conservative choice of $2,000$ for the minimum effective population size). As discussed previously, we might select a reduction level larger than this to guard against changes in population dynamics at lower densities and to allow for the possible implementation of translocation strategies. We choose $L = 2,000$, which corresponds to implementing control approximately every 20 years only (ensuring an extremely large probability of persistence α_L) and corresponds to a healthy effective population size of approximately $4,020$. Using equation (3) we thus arrive at the suppression threshold $4,971$, which we round to $5,000$; that is, we set $M = 5,000$.

We now consider the choice of culling rates. For the suppression regime we only require that κ be chosen such that $\mu + \kappa > \lambda$, and so we choose $\kappa = 0.2$. For the reduction regime we must select a $\delta \geq 0$ to reflect increasing cost associated with increasing culling effort. Using $\delta = 0.05$, in conjunction with equation (5), we arrive at the culling rate $\psi = 1.68$, for which the cost of culling is minimized.

Figure 1 depicts a simulation of both models for the parameter values given above. We can see that for the suppression regime, the population size fluctuates around $M = 5,000$, while for the reduction model, there is roughly linear decline in the population from $U = 10,000$ to $L = 2,000$, followed by growth back to U taking approximately 20 years. It can be seen that under the reduction regime, the culling phase is expected to much shorter than the non-culling phase. The final set of tools provided allows population managers to decide which regime is optimal in terms of population persistence and cost. Using results of the last section we may evaluate the expected time to extinction of the koala population under both management regimes, and also evaluate the expected total cost of control over the life of the population. Since both expected extinction times are extremely large for the koala population, they would not be used as a criteria for selection of optimal management policy. Also, a fair comparison of the costs of control under each regime should be averaged over the expected life of the population under that regime, that is, the comparison should be made on the cost per year of implementation. These costs are given in the table below.

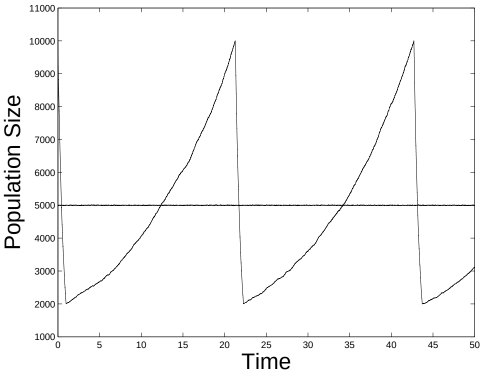

Figure 1. Simulation of the suppression and reduction regime models corresponding to the koalas of Kangaroo Island.

Regime	*Total Cost/Time*
Suppression	$\$(D + K)$/year
Reduction	$\$(J + 49C)$/year

The optimal control regime, in terms of cost per unit time, will thus depend on the values of D, K, J and C. The annual cost can then be used to decide which regime should be implemented.

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