On costs and decisions in population management

J.V. Ross* P.K. Pollett†

January 20, 2006

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. 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 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 a koala population inhabiting Kangaroo Island, Australia.

Keywords: Environmental management; population management; stochastic models; P. cinereus.

1 Introduction

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

*Department of Mathematics, University of Queensland, QLD 4072, Australia. jvr@maths.uq.edu.au
†Department of Mathematics, University of Queensland, QLD 4072, Australia. pkp@maths.uq.edu.au
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.

Other populations are controlled because they have a direct negative impact on species occupying the same geographical location, an example being the yellow-legged gull (*Larus cachinnans*) in the Mediterranean. Between 1992 and 1996, 25,000 breeding gulls were culled in the colony of the Medes Islands because of their possible role in the transmission of pathogens and as predators of other bird species (see Bosch et al. [1]). Yet another example is that of weeds; many species of weed grow out of control and have numerous adverse effects, in particular on habitat, by degrading its suitability for occupancy. In Australia alone it is estimated that the annual cost of weeds to agriculture exceeds $3.5 billion, and may well be as high as $4.5 billion per year (see Sinden et al. [13]).

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 [16] 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.

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. 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 to 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.
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 \( \lambda \) and \( \mu \) 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

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

where \( \kappa \) 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 decreased birth rate.

Reduction Regime. Under this management policy the population is reduced to a predefined 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

\[
q((x, 0), (x + 1, 0)) = \lambda x , \quad x < U - 1,
\]

\[
q((x, 0), (x - 1, 0)) = \mu x , \quad x < U,
\]

\[
q((U - 1, 0), (U, 1)) = \lambda(U - 1),
\]

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

\[
q((x, 1), (x - 1, 1)) = (\mu + \kappa)x , \quad x < U,
\]

\[
q((U, 1), (U - 1, 1)) = (\mu + \kappa)(U - 1),
\]

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

\[
q((x, 1), (x, 0)) = (\mu + \kappa)x , \quad x < U - 1,
\]

\[
q((U, 1), (U - 1, 0)) = (\mu + \kappa)(U - 1),
\]

\[
q((x + 1, 1), (x, 0)) = \lambda x , \quad x \in \{L + 1, L + 2, \ldots\}.
\]
\[ q(x, 1), (x - 1, 1) = (\mu + \psi)x, \quad x \in \{L + 2, L + 3, \ldots\} \]

and

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

where \( \psi \) 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) and its application to other areas, see Ross and Pollett [10]. Again the model can easily 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 \(\alpha_i\) of reaching \(U\) before 0, starting with a population of size \(i\). For the general birth-death process with birth rates \(\lambda_x\) and death rates \(\mu_x\), 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 \(\rho\) that the population reaches \(U\) before 0 starting from \(i\), we may identify a minimum reduction level \(L_{\text{min}, \rho}\). This is given by \(L_{\text{min}, \rho} := \inf\{i : \alpha_i \geq \rho\}\). For our model,

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

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

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

where \([a]\) denotes the smallest integer greater than \(a\).

Table 1 lists various probabilities \(\rho\) of persistence, and the corresponding minimum reduction levels \(L_{\text{min}, \rho}\), 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.
3.2 Genetic Diversity

Genetic diversity is an important consideration in the context of population management (see Franklin [2], Soule [14] and Lande and Barrowclough [3] 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 [12]). On the other hand, Lande [4] 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 $L_{\text{min}; \rho}$ needed to ensure a chosen minimum effective population size of $N_{e\text{min}}$. Franklin [2] and Lande and Barrowclough [3] 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 [3]. 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 $N_{e\text{min}}$. The effective population size during this phase, starting in state $i$, is given approximately by $N_e \approx \tau_i/\tau_{i_{\text{HM}}}$ (being the harmonic mean of the population size over Phase 0), where $\tau_i$ is the expected time to hit $U$ starting from $i$, conditional on hitting $U$ before 0, and $\tau_{i_{\text{HM}}}$ 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 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

<table>
<thead>
<tr>
<th>$\rho$</th>
<th>$L_{\text{min}; \rho}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.99</td>
<td>8</td>
</tr>
<tr>
<td>0.999</td>
<td>12</td>
</tr>
<tr>
<td>0.9999</td>
<td>16</td>
</tr>
<tr>
<td>0.99999</td>
<td>20</td>
</tr>
</tbody>
</table>

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

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 Ross and Pollett [10] 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

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

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 \( \pi_j = \prod_{i=L+1}^{j} \frac{\lambda(i-1)}{(\mu + \psi)n}, j \geq L + 1 \). 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 \( \tau_i \), namely (3.3). We may now also evaluate \( \tau_i^{\text{HM}} \) using results of Pollett and Stefanov [9] 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

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

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

\[
L_{\text{min};N_e} := \inf \left\{ i : \frac{\tau_i}{\tau_i^{\text{HM}}} \geq N_e^{\text{min}} \right\}.
\]
In practice it will often be difficult to evaluate the required expected times. However, whenever the underlying model is “density-dependent” (the transition rates are a function of the state only through the population density), as it is here, we may approximate the expected times using the analogous deterministic model. For our model we obtain
\[ \tau_i \approx (\lambda - \mu)^{-1} \ln \left( \frac{U}{i} \right) \] (1)

and
\[ \tau_{i_{\text{HM}}} \approx \frac{U - i}{Ui(\lambda - \mu)} \],

and thus
\[ L_{\min;N_e} \approx \inf \left\{ i : \left( \frac{U_i}{U - i} \right) \ln \left( \frac{U}{i} \right) \geq N_{e_{\min}} \right\} . \]

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 \( U = 10,000 \).

<table>
<thead>
<tr>
<th>( N_{e_{\min}} )</th>
<th>( L_{\min;N_e} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>500</td>
<td>110</td>
</tr>
<tr>
<td>1000</td>
<td>270</td>
</tr>
<tr>
<td>1500</td>
<td>467</td>
</tr>
<tr>
<td>2000</td>
<td>700</td>
</tr>
</tbody>
</table>

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. [5]). 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. [15]). 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 (3.3) and approximated by (1), 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

\[
M \approx \left\lceil \frac{U - L}{\ln(U) - \ln(L)} \right\rceil. \tag{2}
\]

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 \( c_U \) presented in the last section, once again in conjunction with results of Pollett and Stefanov [9]. 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

\[
f_j = d\psi^{1+\delta} j,
\]

where \( d \) is the culling cost per individual, per unit of time, and \( \delta \) is a non-negative constant that reflects increasing cost associated with increased culling effort. For a given cost function we choose the culling rate \( \psi \) that minimizes \( c_U \), subject to constraints \( \lambda - \mu < \psi < \psi^{\text{max}} \). Using (3), 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 \( \lambda - \mu < \psi < \psi^{\text{max}} \) by

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

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

\[
\psi = \left( \frac{1 + \delta}{\delta} \right) (\lambda - \mu). \tag{4}
\]
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 Ross and Pollett [10] 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 [6]).

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 \( \xi_L \), 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 Ross and Pollett [10]). For our model, \( \xi_L \) evaluates to

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

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 [9] 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 [9]).

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

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

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 Parameter Estimation

Before proceeding to demonstrate the usefulness of our results, we pause to consider the issue of parameter estimation. Our results are highly dependent on the parameter values particular to the population in question, and so their estimation is vital to the effectiveness of our methods.

There are several different ways to estimate parameters in population models. These include Markov chain Monte Carlo (MCMC) (see for example [7] and [8]), and numerical evaluation of the true likelihood, and approximations to this likelihood, using diffusion processes [11]. Both approaches have the advantage of not requiring complete information about the process. The MCMC methods detailed in [7] and [8] can deal with incomplete data sets and hidden events. The direct likelihood methods detailed in [11] allow observations to be made at successive, but not necessarily equally spaced, time points. They apply to processes that are “density-dependent” (the transition rates are a function of the state only through the population density), and thus are widely applicable in the population modelling context. The parameters should be estimated using abundance data prior to the implementation of any control. Once estimated, the optimal values for the other parameters may be determined, along with other quantities of interest to the practitioner, using the results present above.

## 8 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, $\lambda$ and $\mu$. Based on abundance data (initial population size, and a conservative estimate
of the population size in 2001 (Masters et al. [5]) 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 $L_{\text{min}}$ 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 $\alpha_L$) and corresponds to a healthy effective population size of approximately 4,020. Using equation (2) 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 $\kappa$ 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 (4), 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.

<table>
<thead>
<tr>
<th>Regime</th>
<th>Total Cost/Time</th>
</tr>
</thead>
<tbody>
<tr>
<td>Suppression</td>
<td>$(D + K)/\text{year}$</td>
</tr>
<tr>
<td>Reduction</td>
<td>$(J + 49C)/\text{year}$</td>
</tr>
</tbody>
</table>

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

Acknowledgements. We thank Cindy Hauser, Martin O’Hely, Gideon Weiss and the two referees for comments and suggestions. We also gratefully acknowledge the support of the Australian Research Council Centre of Excellence for Mathematics and Statistics of Complex Systems.

References


